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Floral visitor diversity of ruderal plants in San Gerardo de Dota, Costa Rica: a highland agricultural-natural landscape

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ABSTRACT

Introduction: Wild plants rely mainly on insects for pollination, and many of these plants are essential to maintaining a diverse and abundant community of crop insect-pollinators. In Costa Rican highland ecosystems, the diversity and abundance of insect floral visitors have been poorly studied, despite their importance and proximity to crops in this area.

Objective: to determine the richness and composition of floral visitor insect species of native and ruderal herbaceous plants close to cultivated areas in San Gerardo de Dota, Costa Rica.

Methods: We systematically collected flower-visiting insects along transects in two different sites and identified them to the lowest taxonomic level. We estimated alpha diversity for each season and 11 plant groups created specifically for this study. We defined these plant groups based on flower morphology, life history traits, and their taxonomic relatedness. We also compared the insect community composition across seasons and plant groups.

Results: We collected a total of 1306 insects, mainly flies (Diptera), from 62 families on 46 plant species during 12 sampling visits. Insect diversity (alpha diversity) increased during the rainy season, possibly because resources (e.g., food and reproductive sites) for flies increase during this season. Insect species composition varied among plant groups. The most abundant insect communities overlapped extensively among plant groups, but other communities compose mainly by some tachinids, chloropids and wasps did not overlap between other plant groups.

Conclusion: Seasonal differences in flower-visiting insects could be attributed to a greater availability of resources during the rainy season. Differences in the composition of visitor insects across plant groups were likely influenced by temporal variation in blooming of the different plant groups, blooming intensity, and flower traits. To preserve the rich diversity of floral visitors and the pollination services they provide, a diverse array of ruderal plants must be maintained.

Keywords: Diptera; Hymenoptera; insect communities; pollinators; flower-visiting insects.

RESUMEN

Diversidad de visitadores florales de plantas ruderales en San Gerardo de Dota, Costa Rica: un paisaje agrícola y natural de zonas altas

Introducción: Las plantas silvestres dependen principalmente de insectos para su polinización, y a su vez, muchas de estas plantas son esenciales para mantener una comunidad de insectos polinizadores estable, que beneficia a las especies cultivadas. En los ecosistemas de zonas altas de Costa Rica, la diversidad y abundancia de insectos visitadores florales ha sido poco estudiada, a pesar de su importancia y de la proximidad de cultivos en el área.
Objetivo: Determinar la riqueza y composición de especies de insectos visitadores florales de plantas herbáceas nativas y ruderales en un paisaje agrícola en la zona de San Gerardo de Dota, Costa Rica.
Métodos: Recolectamos insectos visitadores florales sistemáticamente por dos años, a lo largo de transectos en dos sitios, y los identificamos al nivel taxonómico más bajo posible. Estimamos la diversidad alfa para las estaciones seca y lluviosa y entre grupos de plantas. Estos grupos de plantas fueron definidos con base en sus características florales, otros rasgos de vida, y su relación taxonómica. Además, comparamos la composición de insectos visitadores florales entre estos grupos.
Resultados: Colectamos un total de 1306 insectos, principalmente moscas, de un total de 65 familias en 46 especies de plantas durante 12 visitas de muestreo. La diversidad alfa de insectos, particularmente de moscas (Diptera) fue mayor durante la época lluviosa, debido, posiblemente, a la mayor disponibilidad de recursos (e.g., alimento y sitios para reproducción) para este grupo de insectos. La composición de especies varió entre plantas agrupadas por su morfología floral. Algunas de las comunidades de insectos se traslaparon extensivamente en algunos grupos de plantas, mientras que para otras comunidades el traslape fue mucho menor.
Conclusión: Las diferencias estacionales en los insectos visitadores florales se pueden atribuir a la mayor disponibilidad de recursos durante la época lluviosa. Las diferencias en la composición de insectos visitadores florales entre los distintos grupos de plantas fueron probablemente influenciadas por variaciones temporales en las floraciones, la intensidad de estas floraciones y las características de las flores en cada grupo de plantas. Para conservar la diversidad de insectos visitadores florales y los servicios de polinización que estos proveen, es necesario mantener una diversidad alta de plantas ruderales.

Palabras clave: Dípteros; Himenópteros; comunidades de insectos; polinizadores; insectos visitantes de flores.

INTRODUCTION

Plant-pollinator interactions in natural ecosystems play an essential role in the reproduction of flowering angiosperm plants (Fontaine et al., 2006), and around 94 % of the tropical plant species rely on insects for pollination (Ollerton et al., 2011). Additionally, over 60 % of global food production depends, to varying degrees, on insect pollination (Hoehn et al., 2008; Klein et al., 2007). Native pollinating insects improve the quality and quantity of pollination-dependent crop yields (Carvalheiro et al. 2011; Garibaldi et al., 2013; Hoehn et al., 2008; Klein et al., 2007; MacInnis & Forest, 2019; Pérez-Méndez et al., 2020). However, despite the role played by insect pollinators, knowledge of the diversity and composition of flower-visiting insects in tropical ecosystems remains limited (Aizen et al., 2008). Understanding insect interactions in natural ecosystems surrounding cultivated areas is critical for ensuring the long-term viability of these ecosystem services.

In highland ecosystems, the diversity and abundance of some insect pollinating groups such as Hymenoptera, Lepidoptera and Coleoptera are lower compared to flies, which play a greater role as pollinators in these ecosystems (Brenes, 2017; Cristóbal-Pérez et al., 2024; Inouye et al., 2015; Lefebvre et al., 2018; Maglianesi et al., 2020). When comparing ecosystems of different altitudes in the montane forest and paramo of Costa Rica, results show that both pollinator interaction networks and species richness are lower in the Páramo (Cristóbal-Pérez et al., 2023; Cristóbal-Pérez et al., 2024). At high elevations, insects tend to be more generalist, which allows them to forage in wild plants like herbs and shrubs that are in bloom at the moment (Cristóbal-Pérez et al., 2024). Flower-visiting insects also have a greater sensitivity to seasonal environmental fluctuations at higher elevations. For example, the decrease in precipitation and temperature experienced during the dry season negatively impacts the richness and abundance of pollinating insects in these montane habitats because availability of resources for insects decreases with the progress of the dry season, and low temperatures limit the flying capability of insects (Cristóbal-Pérez et al., 2023; Kaiser-Bunbury et al., 2010; Memmott et al., 2007; Minachilis et al., 2021).

Therefore, it is important to evaluate and understand the role of insect communities in the wild vegetation surrounding crops that rely on entomophilous pollination and are located close to protected natural areas. It has been shown that protected areas around crops provide important ecosystem services by maintaining pollinator populations (Klein et al., 2003). Because there has been an increase in the cultivation of crops (e.g., avocados, apples) in some Costa Rican highland communities, studying floral visitation in the surrounding vegetation allows us to assess the ecosystem services that protected areas provide to crops and the community as a whole.

The objective of this study was to characterize the communities of insect floral visitors of herbaceous and shrubby vegetation in the natural areas surrounding crops in a highland agricultural landscape. Specifically, we focused on determining the richness and abundance of floral visiting insects of herbaceous and shrubby vegetation in the San Gerardo de Dota area throughout the year to evaluate the potential role of these plants in maintaining the community of pollinating insects, which could contribute to the pollination of crops in this area. Knowing the communities of floral visitors and pollinating insects is crucial to the preservation of these ecosystems and promoting the continuous development of sustainable human activities.

MATERIALS AND METHODS

Study Site: The study site was located in the mountainous region of San Gerardo, Dota, San José province, Costa Rica (9°40’ N; 83°58’ W), between 2 180 and 2 400 m a.s.l. The vegetation on the site is typical of the lower montane forest, consisting of heterogeneous evergreen forests, with a 20-25 m canopy with abundant moss and small epiphytes (Hartshorn, 1991). Some plants, common at higher elevations also grow at this altitude, like *Quercus* spp. which can reach 50 m in height (Hartshorn, 1991). This region possesses a unique combination of natural protected areas, low-intensity commercial agriculture (mostly avocado, blackberry, plum, and apple crops), and low-impact nature tourism. The mean annual temperature at this site is 16.9° C, with minimum temperatures of 12.5° C in January and February, and maximum temperature of 19.5-20.5 °C. Minimum and maximum temperatures are reached during the dry season (amply daily variation), but temperatures are also high at the beginning of the rainy season (May-July). The mean annual precipitation is of 2 600 mm (Climate-data.org, 2021). Precipitation has a strong seasonality with a dry season from December through April, and the rainy season begins in May and extends throughout November (Climate-data.org, 2021).

Sampling Sites: Four transects, two in each of the two sampling sites, were established to assess the diversity of floral visiting insects of wild plant species (Fig. 1). Transects (150 m x 2 m) were selected based on two criteria: 1. Sites included a perceivable high richness and abundance of native and naturalized herbaceous and shrubby plants with flowers; 2. sites were near or within cultivated areas. The first site selected was “Tajo”, a secondary growth area on the edge of the main road along a quarry (9°34’17” N; 83°48’49” W). The second

Fig. 1. Map of the two selected sampling sites in San Gerardo de Dota, Costa Rica. Transects used within the sites to collect and record flower-visiting insects are indicated by blue and orange lines, for the Tajo and Suria sites, respectively.

transect, named "Suria", was located along a secondary road (9°32'51" N 83°48'45" W). Sites were highly diverse and shared only a few species between them. Both sites were located between 200 m and 500 m from a farm. In each transect we collected insects from vines, herbaceous plants, and small and medium-sized shrubs (< 2 m high); rare species or those with low insect visitation were not considered for analyses. All plants were identified to the species level (Table 1).

Data collection: We collected insects that were in contact (any part of their body) with flowers from 7:00 to 13:00 hours; sampling was interrupted if rain began early. At each site, two transects of 150 x 2 m were used to search for flowering plants (Fig. 1), and samplings encompassed between 0.5 and 5 hours per transect, depending on weather conditions and species flowering phenology. We walked at a slow, steady pace and stopped and collected insects for about 5 min in individual flowering plants but collected for up to 15 min in large flower patches. Entomological nets or transparent plastic bags were used to collect flower-visiting insects. Sampling sessions were conducted between July 2021 and August 2022.

Identification: Each collected insect was identified to the lowest possible taxon using the keys of the Central American Manual of Diptera (Brown et al., 2009; Brown et al., 2010), the Manual of North American Bees (Michener et al., 1994), and comparison with specimens of the Entomology Collection of the Museum of Zoology at the University of Costa Rica and the National Museum of Costa Rica. The insect specimens from this study are deposited in the Entomology Collection of the Museum of

Table 1

List of herbaceous and shrubby plant species on which insects were collected in two natural areas adjacent to crops in San Gerardo de Dota, Costa Rica. Plant groups are comprised of species that combine similar flower morphology and habit. Monthly flowering is indicated by the gray cells, and the percentage of insects captured per plant species in each group is included.

Group	Genus/Species	%	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Set	Oct	Nov	Dec
Asteraceae-1	*Hypochaeris radicata*	46.88	■	■	■	■	■	■	■	■		■	■	■
	Crepis capillaris	42.86	■	■	■	■	■	■	■	■	■	■	■	
	Sonchus oleraceus	10.27			■	■		■	■	■	■	■	■	
Asteraceae-2	*Dahlia imperialis*	9.09	■								■	■	■	■
	Vigueira cordata	3.98	■	■	■								■	■
	Bidens reptans	44.89	■	■			■	■	■				■	■
	Bidens pilosa	40.91	■			■	■	■	■	■	■	■	■	■
	Leucanthemum vulgare	1.14										■	■	■
Asteraceae-3	*Ageratina bustamenta*	38.00	■	■	■									■
	Ageratum conyzoides	24.00	■	■					■	■	■	■	■	■
	Pseudognaphalium attenuatum	4.67		■	■	■								
	Conyza sumatrensis	8.00						■	■	■	■			
	Jaegeria hirta	4.00	■	■						■	■	■	■	■
	Clibadium leiocarpum	21.33						■		■	■	■	■	
Open-flowers	*Monochaetum floribundum*	2.15							■	■	■			
	Rubus adenotrichus	4.30				■		■	■					
	Rubus costaricanus	4.30	■	■										■
	Impatiens sodenii	5.38	■	■				■	■	■		■		■
	Wigandia urens	55.91	■	■	■							■	■	■
	Senna guatemalensis	7.53	■	■	■	■								
	Passiflora ligularis	20.43		■			■	■	■			■	■	■
Cucurbitaceae-vines	*Sechium pittieri*	99.15	■	■	■		■	■	■	■	■	■	■	
	Cyclanthera langaei	0.85								■	■	■		
Small-flower-vines	*Muehlenbeckia tamnifolia*	98.20	■					■	■	■	■	■	■	■
	Cissus obliqua	1.80					■	■	■	■				
Tubular-flowers	*Fuchsia paniculata*	2.47								■	■	■	■	
	Thunbergia alata	2.47		■	■	■		■	■		■	■		■
	Brugmansia arborea	25.93	■	■	■	■	■	■	■	■	■	■	■	■
	Hemichaena fruticosa	3.09	■	■	■			■	■	■	■	■	■	■
	Phaseolus dumosus	6.79					■	■		■	■	■	■	
	Ipomoea purpurea	59.26	■	■	■	■	■	■	■	■	■	■	■	■
Herbs-1	*Veronica serpyllifolia*	8.33				■	■	■	■	■	■			
	Geranium seemannii	66.67	■				■				■	■	■	■
	Lepidium virginicum	18.75					■	■	■	■	■			
	Arenaria lanuginosa	2.08					■	■	■					
	Hypericum thesiifolium	4.17						■	■	■	■	■		
Herbs-2	*Verbena littoralis*	64.47	■		■	■	■	■	■	■	■	■	■	■
	Spermacoce remota	35.53						■	■	■	■			
Herbs-3	*Persicaria capitata*	80.00	■	■	■	■	■	■	■	■	■	■	■	■
	Rumex obtusifolius	4.21				■	■		■	■	■	■		
	Trifolium repens	11.58	■	■	■	■	■	■	■	■	■	■	■	■
	Solanum americanum	4.21					■	■	■	■	■			
Lopezia miniata	*Lopezia miniata*	100.00	■	■	■	■			■	■	■	■	■	■

Zoology at the University of Costa Rica. Plant identification was carried out through the collection of herbarium specimens and the collaboration of the plant taxonomist Dr. Alfredo Cascante. These identifications yielded lists of insect and plant genera and species.

Statistical analysis data curation and handling: We classified the sampled plants into eleven plant groups based on floral morphology (shape and size), plant size, and the taxonomic relationship of the plant species in that order of priority. The names of the plant groups are shown in Table 1, and each plant group's morphological and general traits are grouped in Table 2. Floral morphology and flower size are related to the types/groups of pollinators that visit the flowers, so this classification allows species with few visits to be included in the analyses (Dellinger, 2020). The number of insects collected for each plant group was plotted using ggplot2 (Wickham et al., 2016).

For alpha diversity analyses, we created an abundance matrix, with groups of plants and seasons as rows and insect species as columns. Data consisting of insects recorded on only 1 or 2 plants, 1 or 2 insects captured of the same species or morphospecies, or captured in sampling sessions lasting less than 2 hours, were considered insufficient and were excluded from the analyses. Data handling was performed using the dplyr (Wickham et al., 2023) and tidyverse (Wickham et al., 2019) packages in the R statistical language (R Core Team, 2024).

Because there were many cells with zeros, analyzing beta diversity required two additional modifications to the data matrix. The first modification consisted of combining the abundance by morphospecies within each insect family; the taxa that were identified as species were maintained as such. The second modification consisted of combining the data from every two sampling sessions. These modifications allowed the evaluation of beta diversity across plant groups and seasons.

Analysis of alpha diversity patterns: We used Hill numbers (D^0, D^1, and D^2) to compare alpha diversity of flower-visiting insects between sites (i.e., Suria and Tajo) and seasons (dry and rainy). All three statistics compare different aspects of diversity among plant groups and seasons: D^0 estimates species richness, D^1 (Hill-Shannon) estimates diversity with equal

Table 2
General characteristics and flower morphology of the species included in each plant group.

Plant group	Flower morphological and plant description
Asteraceae-1	Dandelion type flowers with homogamous lingulate capitula.
Asteraceae-2	Daisy type flowers with heterogamous radiate capitula.
Asteraceae-3	Discal type flowers with both heterogamous discoid and homogamous discoid capitula.
Open flowers	Open to bowl-shaped flowers of varied shapes, colors, and sizes.
Cucurbitaceae-vines	Actinomorphic unisexual flowers, with big anthers that are fussed in the middle, greenish white color.
Small-fower-vines	Panicles or cymes of minute cup-shaped white flowers with visible anthers.
Tubular-flowers	Tube, bell or funnel-shaped big to medium flowers of various pink, yellow and purple colors. Vines or trees. Purple, white or yellow.
Herbs-1	Herbs with tiny to small 4 to 5 petal rotate flowers purple, white and yellow.
Herbs-2	Herbs with clusters of tiny salverform-shaped flowers, purple and white.
Herbs-3	Herbs with tiny bell-shaped flowers packed in panicles, and one species of Solanum with a small star-shaped flower with joined big stamens at the center. Pink, white or yellow.

weight for rare and common species, and D^2 (Hill-Simpson) estimates diversity with greater weight for common species (Chao et al., 2014b). We estimated diversity with respect to the number of individuals and sample coverage (sample completeness) (Roswell et al., 2021), as well as rarefaction curves.

Considering that the results from all three estimators show the same trend (Fig. 1 Supplementary Material), we only present the results of the Hill-Shannon estimator, which weights equally both rare and abundant species (Alberdi & Gilbert, 2019). This estimator is recommended when the sampling may not accurately reflect the real number, in this case, of insect floral visitors (Alberdi & Gilbert, 2019). We performed these analyses with the iNEXT package, using the *iNext* and *ggiNEXT* functions (Chao et al., 2014a; Chao et al., 2014b; Hsieh et al., 2022). The total richness of visiting insects of each plant group was estimated with the ChaoRichness function of the iNEXT package (Chao, 1984).

Analysis of species composition (beta diversity): To compare species composition of insect communities (beta diversity) between plant groups and seasons, we used a non-metric multidimensional scaling (NMSD) analysis based on a Bray-Curtis dissimilarity matrix with 1 000 permutations (Oksanen et al., 2022). We then conducted a distance-based PERMANOVA (Permutational Multivariate Analysis of Variance) with the *adonis* function of the vegan package (Oksanen et al., 2022). We included season and plant group as predictor variables in the model.

We evaluated the assumption of the homogeneity of variance of the data with the *betadisper* function (Oksanen et al., 2022); variances were homogeneous between seasons ($F = 0.29$, $p = 0.98$), and among groups of plants ($F = 0.29$, $p = 0.99$). Lastly, we compared the dissimilarity, species turnover, and nesting of insect species communities between seasons and plant groups, using the *beta.pair.abund* function of the betapart package (Baselga, 2023). We also used the bipartite package's *visweb* function to plot the network matrix to show the interactions between the taxa and plant groups (Dormann et al., 2008).

RESULTS

We collected 1 306 insects from 62 families on 43 shrubs, lianas and small herbaceous plant species over the course of 29 sampling sessions (97 hours). We established 11 plant groups to categorize plants, with insects assigned to each plant group (Table 1). For most plant groups, there were flowers available year-round (e.g., Asteraceae-1, tubular-flowers), but not all species within a group produced flowers throughout the entire study period (e.g., *Ipomea purpurea*, *Persicaria capitata*). Differences in number of flowering plant species likely responded to species specific phenologies and mortality caused by seasonal changes in precipitation.

Most insects collected were of the orders Diptera (27 families, 611 individuals), Hymenoptera (14 families, 530 individuals) and Coleoptera (8 families, 90 individuals). The number of flower visitors varied depending on the season and plant group, but flies, bees, and wasps visited flowers in most plant groups (Fig. 2, Table 1 Supplementary Material, Table 2 Supplementary Material, Table 3 Supplementary Material). Only three visits of hummingbirds (possibly *Selasphorus flammula* and *Panterpe insignis*) were observed.

Alpha diversity: The diversity (alpha) of insects, as estimated by Hill-Shannon, varied among sites and seasons. In both sites, the highest diversity of insects was recorded during the rainy season, but diversity was larger at the Tajo site for both seasons, particularly in the rainy season (Fig. 3). Differences in alpha diversity between sites are likely influenced by the larger number of species and individuals collected in the Tajo transect (Fig. 3), which is adjacent to a large tract of protected montane forest. The richness curves and Chao estimates between the plant groups show no apparent differences

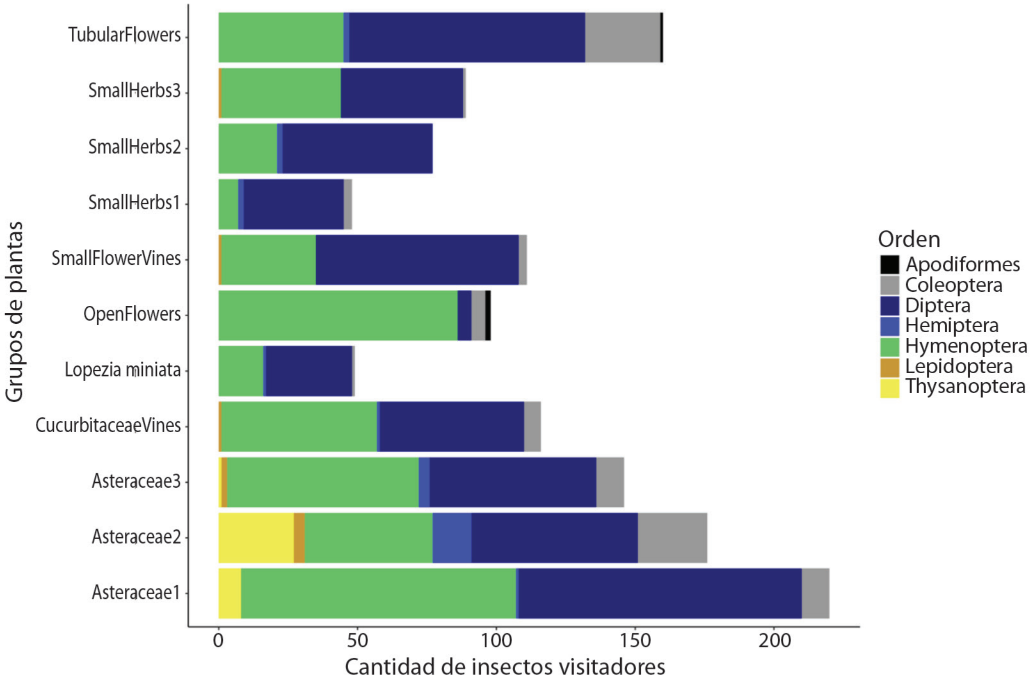

Fig. 2. Composition and abundance of insect orders collected in each group of plants at the study sites.

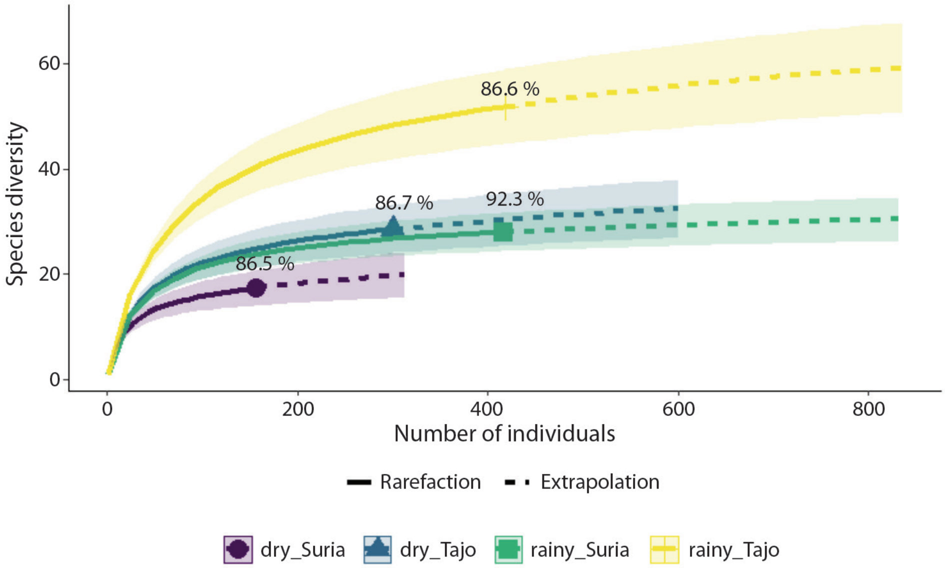

Fig. 3. Diversity of insects collected in two sites (Suria and Tajo) in both the dry and rainy seasons is shown in lines of different colors and the 95% upper and lower confident limits are represented with the shaded area that surrounds the curve. The percentage coverage of the Hill-Shannon estimator is indicated for each site-season combination.

between the richness of the plant groups, due to their wide confidence intervals (Table 4 Supplementary Material, Fig. 2 Supplementary Material).

Community analysis (beta diversity): The composition of insects differed between seasons (F = 2.44, P = 0.003, R^2 = 0.03) and between plant groups (F = 2.86, P = 0.001, R^2 = 0.37), but most of the variance explained was attributed to differences between plant groups. Insect communities of some plant groups overlapped extensively. This occurred, for example, with the two plant groups that comprise Asteraceae. In contrast, insect communities associated with other plant groups (e.g., tubular flowers, small herbs-2) showed little overlap with communities of other plant groups (Fig. 4, Fig. 3 Supplementary Material, Fig. 4 Supplementary Material, Fig. 5 Supplementary Material).

Species dissimilarity differed significantly between seasons (t = -2.87, P = 0.005; Fig. 5A). This difference was likely a consequence of a more heterogeneous distribution of insect species among plant groups during the dry season. Species turnover did not show a significant difference between the dry and rainy seasons (t = -0.27, P = 0.79, Fig. 5B), suggesting that there was not a notable change in the composition of species between seasons. However, species nestedness changed drastically between dry and rainy seasons (t = -4.65, P < 0.001, Fig. 5C), suggesting that during the dry season flower-visiting insects in different plant groups are

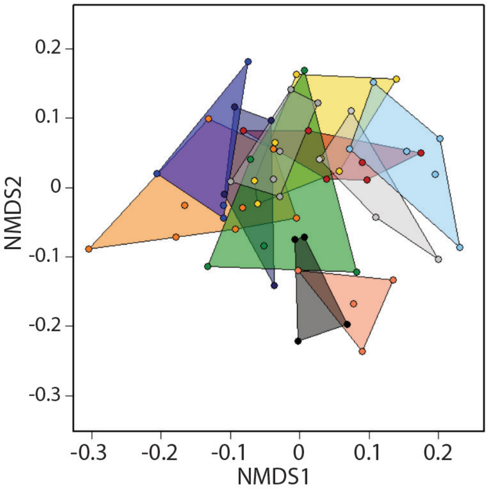

Fig. 4. Non-metric multidimensional scaling analysis (NMDS) of the composition of flower-visitor insects based on the Bray-Curtis index, using the abundance of insects collected in each plant group. Plant groups follow Table 1 and are shown in different colors: Orange: Asteraceae-1, Yellow: Asteraceae-2, red: Asteraceae-3, Navy blue: Cucurbit-vines, Blue: *Lopezia miniata*, Green: Open-flowers, Orange-red: Small-flower-vines, Dark gray: Small-herbs-3, Light gray: Herbs-1, Black: Herbs-2, Light blue: Tubular-flowers. The verified model's voltage was 0.2135.

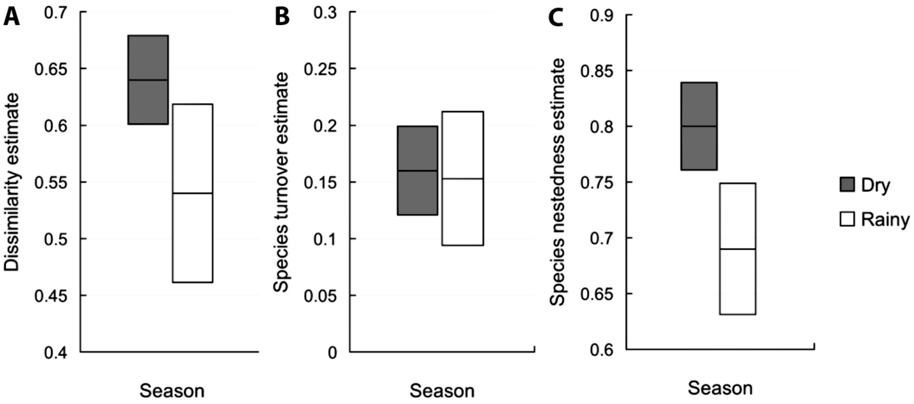

Fig. 5. Comparison of insect communities between dry and rainy seasons **A.** Total dissimilarity. **B.** Species turnover. **C.** Species nestedness**.** The line is the average value of the betapar estimates, the boxes represent the beta-diversity standard deviation of the statistical estimates calculated from the upper and lower intervals. The total dissimilarity and nesting were significantly different between the dry and rainy seasons.

subsets of the communities of insects attracted to flowers in the rainy season.

DISCUSSION

We found a predominance of flies (Diptera) in flower-visiting insect communities, which is consistent with previous research on insect flower visitors in Costa Rica's highlands and similar regions (Arroyo et al., 1984; Cristóbal-Pérez et al., 2024; Elberling & Olesen, 1993). At high elevations, flies far exceed the abundance of other floral visitors such as bees, butterflies, and beetles (Cristóbal-Pérez et al., 2024). Abundant flies like hoverflies, are associated with multiple plant groups and potentially play an important role in plant pollination in natural environments at high elevations (Jauker & Wolters, 2008; Montero et al., 2025). Other abundant groups of flies, such as Muscidae and Tachinidae, can also play an important role as pollinators (Orford et al., 2015) and were diverse in some plant communities, particularly during the rainy season (Cristóbal-Pérez et al., 2024; Kearns, 1992).

Bees, native and managed, were the second most diverse group of flower visitors. For instance, the native *Lasioglossum* sp., *Meliwillea bivea*, *Partamona grandipennis*, and *Bombus ephippiatus*, as well as honeybees, were very abundant visitors of most plant groups. Social insects, such as the aforementioned bees (except *Lasioglossum*), form large colonies with high caloric demands, and as a result they tend to be more generalists, relying on a diverse array of plant species to meet their caloric needs (Roubik, 1989; Potts et al., 2003). During the dry season, there is a reduction in richness and diversity in the insect communities composed of a subset of communities associated with different plant groups during the rainy season. However, insects tend to use a wide range of flowers as a possible consequence of a reduction in resource availability during the dry season, as predicted by the theory of optimal foraging (Cristóbal-Pérez et al., 2024; Fontaine et al., 2008; Robinson & Wilson, 1998). Similar patterns of visitation have been observed in other habitats with limited resources (Dupont et al., 2003; Smith-Ramírez et al., 2005; Souza et al., 2017).

The dissimilarity in the composition of insect visitors among habitats increased in the dry season, likely as a consequence of the notable reduction in richness, mainly of some Diptera, and a reduction of flowering plants during this season, which results in more heterogeneous communities of flower visitors (Orford et al., 2015). On the contrary, the onset of the rainy season favors both the reproduction of insects and the richness of blooming plant species, increasing the richness of floral visiting insects in these environments (Cristóbal-Pérez et al., 2024; Inouye et al., 2015). The differences between the communities of insects associated with different groups of plants indicate the coexistence of both specific and generalist floral visitors, which visit various types of plants depending on the season or flowering periods (Fig. 4, Cristóbal-Pérez et al., 2024). Changes in richness are more noticeable in Diptera, which do not typically fluctuate on a seasonal basis but rather respond to non-seasonal fluctuations in environmental factors such as temperature, moisture, wind and light intensity (Inouye et al., 2015; Kudo et al., 2023). Except for some hoverflies that are also present in the dry season.

Some groups of plants, such as herbaceous plants types 1 and 2, attracted groups of flower-visiting insects that differed substantially from other insect communities that visit other plant groups like tubular-flower plants, small-flower vines and, to a lesser extent, Asteraceae-3 (Fig. 4). For example, some species in the Asteraceae type 3 plant group, such as *Ageratina bustamenta*, had their flowering peak in the dry season,which only a few other plants come into flower in those months. Blooming at this particular time attracts a distinct community of flower-visiting insects, such as the bee *Exomalopsis* sp. (Janovský & Štenc, 2023; Junker et al., 2013; Olesen et al., 2008). Other species, such as *Muehlenbeckia tamnifolia*, present in the plant group Small-flower-vines, were also visited by a large and diverse insect community of both flies and wasps, that were not present in other plant groups as it has been registered for other species of the genus (Primack, 1978). Tubular-flower plants such as *Ipomoea* sp. and *Brugmansia* sp. were visited primarily by bees, but also by a group of small insects that use these flowers for their reproduction and feeding, such as some Drosophilidae flies and Nitidulidae beetles (e. g., *Conotelus* sp.) (Ishikawa et al., 2022; Da Paz et al., 2013; Santos et al., 2020; Schmitz & Valente, 2019). Differences between insect groups are likely associated with temporal correlation between the phenology of some plant groups and some insect groups, abundance of flowers or by the preference of some insects for specific flowering plants (Da Paz et al., 2013; Janovský & Štenc, 2023).

Open-flowered plants together with cucurbit-vines, herbs-3 and, to a lesser extent, Asteraceae groups 1 and 2 shared a large proportion of their floral visiting insect communities. Open-flowered plants, like cup-shaped flowers and Asteraceae flowers that have accessible pollen and nectar, are more likely to have a wider array of visitors (Herrera, 2019; Ollerton et al., 2007). However, these open-flowered groups were visited by fewer species, in contrast to Asteraceae-3 which was visited by a large community of insects (Fig. 2 Supplementary Material). This suggests that accessibility to floral rewards is not the only factor influencing visitation, but the type and quality of resources, as well as color and odor, abundance and phenology may also play an important role in selecting the insect groups that visit different groups of plants (Fenster et al., 2004; Herrera, 2019; Junker et al., 2013; Pardo et al., 2020, Reverté et al., 2016).

Naturalized herbaceous plants (all Asteraceae-1 and some in herbaceous plants) were visited by insects that also visited a wide array of plants (Fig. 4). In this study, the rarest or least frequent native floral visitor insects mainly visited native species, such as cucurbits or small-flowered vines (Fig. 5 Supplementary Material). This is an interesting result that suggests that maintaining a diverse group of native herbaceous plant species is important for the conservation of flower-visiting insect communities and the role they play in providing pollination services to local plants and cultivars (Montero et al., 2025). Introduced or naturalized plant species can provide additional and novel resources for abundant groups of insects (Memmott & Waser, 2002).

In conclusion, the interaction between plants with different flower morphology and phenology and visiting insect communities are essential to maintain the high species richness of insects and plants in this ecosystem. The richness of flower-visiting insects varied among plant groups on a seasonal basis. During the rainy season the richness and diversity of flower-visiting insects increased, as did the diversity and abundance of flowering plants. Some plant groups share the most abundant visitor insect communities; however, other plant groups are only visited by specific insect groups, and floral rewards and morphology likely influence these differences. Therefore, to maintain the diverse community of floral visitors and the pollination services they provide, it is necessary to maintain a large diversity of native plants, since they provide food and shelter for adults and possibly for their eggs and larvae.

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See supplementary material
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