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Unveiling Wasps as Potential Pollinators: Floral Traits and Wasp Sociality Intensify Network Centrality in a Highly Diverse Tropical Ecosystem

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ABSTRACT

Wasps, members of over 90 hymenopteran families, exhibit diverse behaviours, including pollination, predation and parasitism. While wasps are known pollinators in specialised systems, such as the intricate mutualism of fig trees and the deceptive pollination of certain orchids, they have historically been considered ineffective pollinators, with their role often overlooked. Despite frequent visits to flowers, especially in neotropical savannas like the Cerrado, the wasp and floral traits associated with wasp visitation and their influence on plant–pollinator networks are still poorly understood. This study consolidates data on flower–wasp interactions in the Cerrado, Brazilian biodiversity hotspot to explore how floral and wasp traits shape interaction networks. We constructed a mutualistic interaction network comprising 185 wasp species and 144 plant species, performing 728 interactions, and calculated centrality indices. We assessed whether wasp traits (e.g., sociality, life form) and floral traits (e.g., symmetry, anthesis time, inflorescence type) predict network centrality. Social Vespidae wasps, particularly *Brachygastra* and *Polybia* species, were frequent floral visitors. Most plants had small, actinomorphic, nectar-rewarding flowers, with crepuscular anthesis and inflorescence architecture increasing plant centrality. Sociality increased wasp centrality, indicating that behavioural traits enhance their role in network cohesion. This study underscores that wasps may play a significant yet underappreciated role in pollination, particularly in generalist flowers. By identifying the floral traits most associated with wasp visitation, this study advances our understanding of wasps as potential pollinators in diverse plant communities. These findings suggest the need for further research on wasp pollination behaviour, especially to evaluate their effectiveness as pollinators. Understanding the contributions of wasps could provide critical insights for the pollination of endemic and endangered species, supporting conservation efforts in the Cerrado's biodiverse and threatened ecosystems.

1 | Introduction

Wasps are a diverse group of Hymenoptera within the suborder Apocrita, excluding Antophila (bees) and Formicidae (ants), comprising over 90 families (Peters et al. 2017). While larvae of most wasp species are carnivorous (O'Neill 2019; Sumner 2022), the Mansarinae wasps exclusively provision their larvae with pollen (Gess and Gess 2010). But regardless of their wide variety of morphological traits, such as variation in size, and behavioural traits such as sociality, which can present as solitary or social, and lifeform, which comprises species that are predators, herbivores, parasites or parasitoids; adults primarily consume carbohydrate-rich resources such as nectar (Richter 2000; O'Neill 2019; Sumner 2022). This dietary need associated with their ability to transfer pollen and ensure the reproduction of certain angiosperms (Shuttleworth and Johnson 2009; Mello et al. 2011; Borchardt et al. 2024), configures wasps as a functional group of pollinators (sensu Fenster et al. 2004).

Despite their frequent floral visits, wasps are primarily recognised as pollinators in specialised systems, which are rare in nature (Armbruster 2017). For example, Agoninae wasps pollinate fig trees (Ficus, Moraceae), where females access the fig's syconium to oviposit. The eggs hatch inside and develop in a specific environment to develop a gall (Weiblen 2002). When fully developed, the wasps exit the syconium structure carrying pollen to other syconia, enabling fig cross-fertilisation (Herre et al. 2008). In another specialised system, Thynnidae wasps and the genus Campsomeris (Scoliidae) are attracted to the flowers of some species in the genera *Caladenia*, *Chiloglottis*, and the species *Geoblasta pennicillata* (Orchidaceae) through visual cues and volatile compounds, leading males to perform pseudocopulas with the flowers, thereby enabling pollination by deceit (Bower 1996; Ciotek et al. 2006; Coombs et al. 2009).

The main literature in pollination was built over the pollination syndromes, which correlate floral traits with specific pollinator groups (e.g., Faegri and Van Der Pijl 1979), but this approach remains debated (Ollerton et al. 2009; Rosas-Guerrero et al. 2014). Wasp pollination is broadly categorised as a type of entomophilous or melittophilous pollination, with no floral characteristics exclusively associated with wasps (Faegri and Van Der Pijl 1979; Endress 1994; Fenster et al. 2004). Recent studies suggest that wasps are frequent visitors of flowers with freely exposed rewards, such as actinomorphic species typical of generalist pollination systems (Mello et al. 2011; Carstensen et al. 2014, 2016; Borchardt et al. 2024). Primarily, foraging for nectar to sustain themselves or their colonies, wasps are mostly diurnal, though there are some reports of floral visitation in some crepuscular plant species (Souza et al. 2016; Soares and Morellato 2018; Souza et al. 2022). They often visit less conspicuous flowers—like those with greenish or white corollas—and are common on larger flowers and dense inflorescences, which offer abundant, accessible resources and facilitate rapid foraging by both pollinating and antagonistic species (Fenster et al. 2004; Mello et al. 2011; Souza et al. 2016; Gélvez-Zúñiga et al. 2018, 2024; Pereira 2024).

While wasp pollination efficiency has been recently reexamined (Borchardt et al. 2024), studies have identified them as effective pollinators in some cases, including in crops (Campbell et al. 2019; Shaik et al. 2017). Moreover, there are records of consistent floral visitation by wasps (Bernhardt and Goldblatt 2006; Goldblatt and Manning 2006; Ollerton et al. 2003), as well as pollen adhesion to their bodies, suggesting that, in fact, wasps may be as effective as bees (Borchardt et al. 2024), which are considered the primary pollinators worldwide (Ollerton et al. 2011). Nevertheless, the negative public perception of wasps (Sumner et al. 2018; Oi et al. 2024), combined with historical exclusion from pollination studies, limits conservation efforts for these insects (Oi et al. 2024). Expanding our understanding of their ecological roles is essential in the face of increasing biodiversity loss (Cowie et al. 2022).

Approaches involving the nature of flower–wasp interactions from a mutualistic network perspective are limited, and detailed records of these insects' behaviour while accessing floral resources are even scarcer (but see Carstensen et al. 2014, 2016; Gélvez-Zúñiga et al. 2018). Regarding the interactions between plants and flower-visiting wasps, the network's topological and centrality properties are relatively well studied (e.g., Santos et al. 2010; Mello et al. 2011; Santos et al. 2022; Borchardt et al. 2024). For instance, networks involving flowers and social wasps exhibit greater complexity but lower specialisation and nestedness in riparian forest vegetation compared with rocky outcrops (Clemente et al. 2012). Moreover, social wasps show high degrees of connectivity and are generalists in terms of the plants they visit (Santos et al. 2010). Additionally, comparisons between plant interactions involving wasps and bees reveal that the network structures of both groups are equivalent in terms of modularity, asymmetry, and nestedness (Borchardt et al. 2024). However, each group interacts more frequently within distinct modules of the plant community (Borchardt et al. 2024). These examples suggest that wasps play a crucial role in the pollination ecology of many plant species by ensuring reproductive success, supporting species persistence and maintaining plant–pollinator stability within communities. Therefore, deepening our understanding of the role played by wasps in the pollination processes of specific plant species across different ecological scenarios is highly relevant for better comprehension of community structure, functioning (Pilosof et al. 2017) and pollination services.

Biodiverse ecosystems can serve as exceptional models to understand species interactions and the importance of plant species pollinated by a wide array of pollinator functional groups (Martín González et al. 2010). The Cerrado, a Brazilian neotropical savanna, represents a highly diverse ecosystem with remarkable endemism but is experiencing significant habitat loss and, as a result, it is classified as a global biodiversity hotspot (Myers et al. 2000; Fernandes et al. 2020). Although wasps are frequently reported as floral visitors of Cerrado plant species in studies on the reproductive biology of generalist flowers (e.g., Gama et al. 2011; Maruyama et al. 2018; Oliveira and Gibbs 2000; Monteiro et al. 2021), and flower–visitor interaction networks (e.g., Carstensen et al. 2014, 2016; da Silva et al. 2022; Souza et al. 2018; Gélvez-Zúñiga et al. 2024), their function as pollinators has historically been overlooked. In fact, some studies examining the frequency of plant–pollinator interactions in the Cerrado and other Brazilian grasslands demonstrate that wasps visit 3%–20% of flower species (Freitas and Sazima 2006; Monteiro et al. 2021). These records suggest that the true

potential of wasps as pollinators in the Cerrado, as well as the floral traits associated with wasp visitation, remain unexplored and undoubtedly underestimated.

As wasps are frequent floral visitors in the Cerrado and previous studies have documented flower–wasp interactions in this neotropical savanna, our study aimed to consolidate the available information on flower–visitor interactions, with an emphasis on wasp species interacting with floral resources, and elucidate their potential role as pollinators in these plant communities. Using an interaction network approach, we visually explored the plant and wasp species with recorded interactions and assessed whether wasp and plant centrality and species importance are determined by wasp and floral traits, respectively. We tested whether these wasp and plant traits influenced centrality indices in the interaction network, such as normalised degree (ND), betweenness, closeness centrality and species strength (SS). Specifically, we expected that wasp centrality would be primarily influenced by traits, such as wasp sociality, life form and body size (Richter 2000; Santos et al. 2010; Sumner 2022). From the other perspective, we expected that plant centrality is mainly determined by traits related to floral attraction in generalist flowers (Fenster et al. 2004; Mello et al. 2011; Souza et al. 2016; Borchardt et al. 2024; Gélvez-Zúñiga et al. 2024), such as large, nectar-rewarded, diurnal flowers with actinomorphic (radial) corollas arranged in inflorescences. Finally, we highlight promising systems for testing the efficiency of wasps as pollinators in neotropical savannas, a diverse and threatened biodiversity hotspot.

2 | Materials and Methods

2.1 | Literature Review

To access available information on flower–wasp interactions in the cerrado, we performed a literature review using the ISI Web of Science platform (https://clarivate.com/webofsciencegroup/solutions/web-of-science/), selecting the "all databases" option. The search terms used included: "pollinat*", "floral biology", "reproductive biology", also in Portuguese (polin*, "biologia floral", biologia reprodutiva") combined with terms relevant to the region of interest: "cerrado", "campo rupestre", "rupestrian", "montane grassland*", "altitudinal", "espinha*o", "rupic*".

The search results were filtered to include studies on flower–wasp interactions conducted in Brazil, within the cerrado domain or other Brazilian grassland vegetation. We included interactions based on: (i) systematic direct field observations of pollen transfer among flowers by wasps, thereby promoting fruit set, and (ii) systematic direct field observations of wasps contacting the flower's reproductive structures (stamen and/or stigma), thus indicating potential for pollination (adapted from Monteiro et al. 2021). Both categories may include data on visitation frequency, visitation length, floral biology and floral visitor collection. The literature review encompassed all studies available up to May 2024. Additionally, records of floral visitation by wasps to *campo rupestre* plant species were included (Gélvez-Zúñiga et al. 2025).

2.2 | Wasp and Floral Traits

We checked wasp species' names looking for synonyms and the most recently accepted name according to the Brazilian Fauna Taxonomic Catalogue (BFTC, http://fauna.jbrj.gov.br/). For plant species, we used Plantminer (Carvalho et al. 2010) and Flora do Brasil 2020 (BFG 2020). To assess whether the wasp and floral traits influenced plant centrality in the flower–wasp interaction network, we extracted information from the literature and checked the BFTC. The traits considered for the wasp species were: (i) sociality, understood as solitary or social; (ii) life form, classifying species into herbivore, parasite, or predator; and (iii) wasp size (mm), designated as small (< 10), medium (10–20), large (20–30) or very large (> 30). In the parasite category, we included both parasites and parasitoids. To categorise species size, we performed a cross-search in the same literature review databases using the genera or species name (e.g., *Brachygastra* or *Brachygastra lecheguana*).

Plant species with records of wasp visitation were grouped according to their attraction to floral visitors in terms of accessibility, resource or visibility (Faegri and Van Der Pijl 1979; Fenster et al. 2004; Table 1). The accessibility group encompassed: (i) the symmetry of the corolla, which was classified as actinomorphic (radial), asymmetric or zygomorphic (bilateral); and (ii) the time of anthesis, understood as the time of the day in which floral rewards are first available to visitors, and categorised as diurnal, crepuscular or nocturnal. The resource includes the primarily floral reward targeted by floral visitors and was classified as nectar, pollen, oil or tissue. Finally, the visibility group included the overall flower colour and size, and the type of inflorescence. The flower colour category refers to human vision, with violet also including blue tones (Machado and Lopes 2004). The flower size (mm) was designated as small (< 10), medium (10–20), large (20–30) or very large (> 30) (adapted from Machado and Lopes 2004). The inflorescences were categorised according to their architecture as corymb, cymes, glomerule, head, panicle, racemes, spike or thyrse following Simpson (2006). Details of the categories and functionality are given in Table 1.

2.3 | Flower–Wasp Network Structure and Species' Centrality and Importance

To visually explore the role of wasps as floral visitors with pollination potential, we built an unweighted qualitative interaction network, linking plant species and wasp floral visitors based on literature records of interactions. In an unweighted network the plant–wasp interactions are represented by 0 when absent, and 1 when present. The network was created using Pajek 5.19 (Batagelj and Mrvar 1998). We assessed the contribution of each plant species to the structure, dynamics and stability of the flower–wasp interaction network using centrality metrics within a bipartite network approach, with plants as rows (i) and wasps as columns (j). Each species was treated as a node within the network (Martín González et al. 2010; Gélvez-Zúñiga et al. 2024).

Species centrality reflects the relative importance of a species within the network, determined by its connectivity (the

TABLE 1 | Categorisation of floral traits used for each plant species within the literature review of flower–wasp interactions in neotropical savannas of Brazil.

Group	Trait	Categories	Function	References
Accessibility	Corolla symmetry	Actinomorphic Asymmetric Zygomorphic	Species pollinated by diverse insect groups are often visited by wasps. Wasps often visit flowers with freely exposed rewards (generalist type). Plants pollinated by deception may exhibit restrictive morphologies with bilateral or asymmetric corollas	Shuttleworth and Johnson (2009), Mello et al. (2011), Borchardt et al. (2024), Pereira (2024)
	Time of anthesis	Diurnal Crepuscular Nocturnal	Several wasp species are among the insects which performs diurnal pollination, but they are also recorded as secondary pollinators of plants with crepuscular anthesis. There are also records of night vision adaptations in some wasp clades	Warrant et al. (2006), Greiner (2006), Warrant (2008), Souza et al. (2016), Soares and Morellato (2018), Souza et al. (2022)
Resource	Reward	Nectar Pollen Oil Tissue	Adult wasps forage for nectar to feed or to sustain the colony (when social). Some wasp species (e.g., Masarinae) exhibit bristles adapted for pollen collection. Wasps rob nectar and consume floral tissues	O'Neill (2001), Gélvez-Zúñiga et al. (2018), Pereira (2024)
Visibility	Colour	Red Orange Rose Violet (blue) Yellow White Greenish	Wasps' visitation on flowers respond to generalised floral cues which are present in a variety of plant taxa. Colour saturation (contrast against the background) may act as a crucial factor to favour pollinator visitation in natural communities Pollinator wasp visits are present in less conspicuous flowers such as greenish and yellow corollas, while wasps acting as robbers or secondary pollinators are present in species associated to hummingbird (red, orange) and bees (rose, white, violet) corollas	Souza et al. (2016), Gélvez-Zúñiga et al. (2018), Soares and Morellato (2018), Camargo et al. (2019), Borchardt et al. (2024)
	Size (mm)	Small < 10 Medium 10–20 Large 20–30 Very large > 30	Larger flowers are widely associated with greater flower visitation by both pollinators and floral antagonist (robbers, thieves and florivores), including wasp species collecting nectar, pollen for feeding adults or larvae	Fenster et al. (2004), Souza et al. (2016), Gélvez-Zúñiga et al. (2018, 2024), Caruso et al. (2019)
	Type of inflorescence	Corymb Cymes Glomerule Head Panicle Racemes Spike Thyrse	Multiple flowers displayed in inflorescences can increase the plant's attractiveness to floral visitors. Inflorescences offer dense floral resources with free access to nectar which can increase visits by wasps. The architecture of the inflorescences may benefit the foraging of multiple flowers in short periods of time	Fenster et al. (2004), Harder et al. (2004), Mello et al. (2011), Caruso et al. (2019), Pereira (2024)

Note: Literature review comprised studies available until May 2024. Categories adapted from Machado and Lopes (2004).

number of links it has) and how these links are distributed throughout the network (Nooy et al. 2011). We calculated four centrality metrics commonly used to assess species importance to network cohesion and structure (Sazima et al. 2010; Vidal et al. 2014; Maruyama et al. 2019): Normalised degree (ND) that measures species generalisation as the proportion of interactions out of the total possible interactions in the network (Martín González et al. 2010); Closeness centrality (CC) that estimates the proximity of a species to all others in the network, based on the shortest path between species pairs; Betweenness centrality (BC) describes a species' importance as a connector linking distinct parts of the network, acting as a bridge (Mello et al. 2015; Gélvez-Zúñiga et al. 2024); and SS that is the sum of the proportions of interactions between a species from different trophic levels, quantifying their mutual dependence (Bascompte et al. 2006). All centrality metrics were calculated using the *bipartite* package (Dormann et al. 2014) in R 4.4.0 (R Core Team 2024).

2.4 | Statistical Analysis

To test whether the observed proportions of each wasp and floral traits' categories differ from a uniform (or expected) distribution, we performed a Chi-square goodness-of-fit test. Furthermore, to test whether these wasp and floral traits influenced plant centrality in the network, we performed generalised linear models (GLMs) using wasp sociality, wasp life form, wasp size, the time of anthesis, flower symmetry, floral reward, flower colour and flower size as explanatory variables. The ND, CC, BC and SS were used as response variables for both wasps and plants models, respectively. We assumed a quasi-Poisson error distribution (link: log) for all the response variables due to data overdispersion. To evaluate the relationship between wasp and floral traits and the species' centrality as response variables, we calculated pseudocoefficients of determination as $R^2 = 1 - (D_{model}/D_{null})$, where D_{model} and D_{null} represent the residual deviances of the regression model and the corresponding null model, respectively. For all the significant models, we used the "LSMeans" package with Tukey-adjusted to make comparisons and detect statistical differences between the traits categories. All the GLMs were performed using the *glm* function in R 4.4.0.

3 | Results

We reviewed 23 papers that contained information on flower–wasp interactions as potential pollination events (Table S1). These studies were primarily conducted in central Brazil (Figure 1), mostly within the Cerrado domain, with one exception located in a significant Brazilian mountainous grassland (*campo de altitude*) (Freitas and Sazima 2006; Table S1). The flower–wasp interaction network comprised 185 wasp species and 144 plant species, performing 728 interactions (Figure 2, Tables S2 and S3). Of these interactions, 97% (708 out of 728) were considered potential pollination events, as the wasps made contact with the reproductive parts of the flowers. The other 3% of interactions reported by the revision were indicated as florivory.

Flower visits were made by wasps from 14 families, primarily Vespidae (mainly the Polistinae and Eumeninae subfamilies), which accounted for 77% (558 out of 728) of the interactions, followed by Sphecidae and Pompilidae, with 6% and 5%, respectively

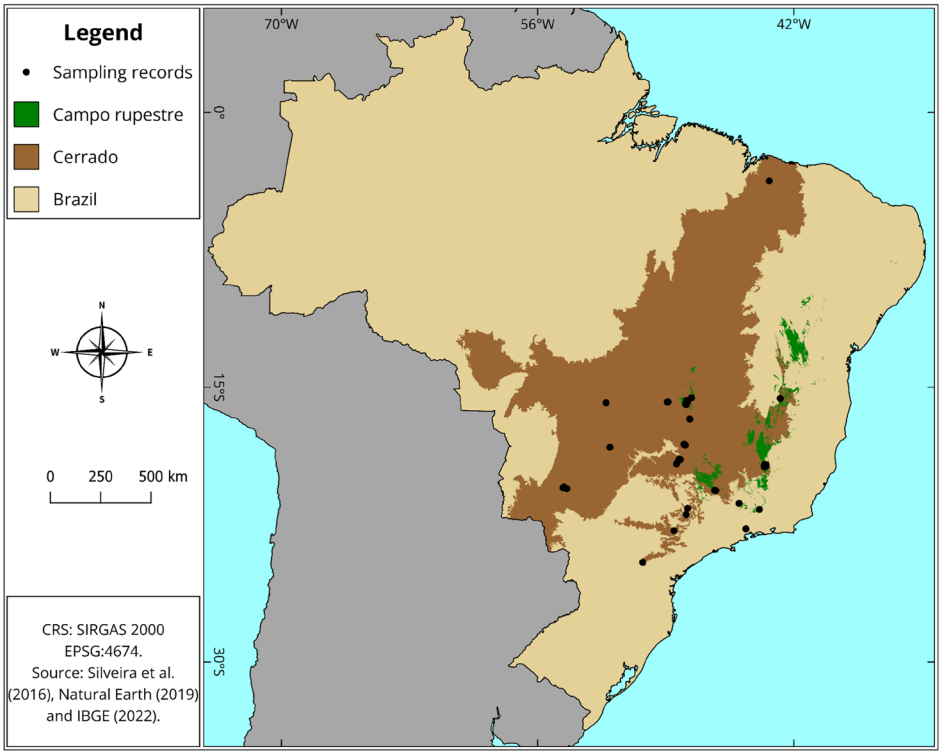

FIGURE 1 | Location of the studies assessing flower–wasp interactions in the Cerrado, a neotropical savanna of Brazil. [Colour figure can be viewed at wileyonlinelibrary.com]

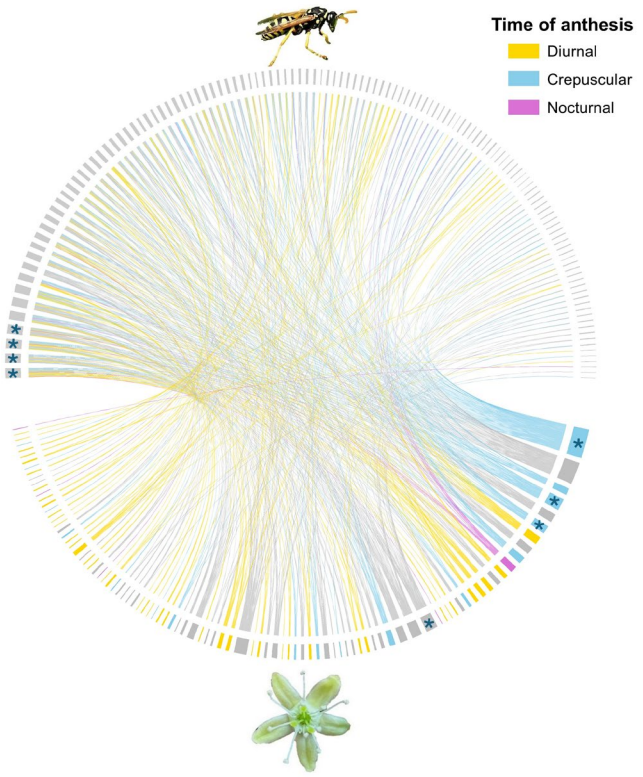

FIGURE 2 | Bipartite network of interactions between wasp species (top semicircle) and plant species (bottom semicircle) in the Cerrado, a neotropical savanna of Brazil. Each line represents a unique floral visitation event gathered by the systematic literature review. Asterisks (*) highlight the most frequently interacting species: The plants *Stryphnodendron adstringens* (Fabaceae; 65 interactions), *Baccharis retusa* (Asteraceae; 25), *Echinolaena inflexa* (Poaceae; 18), and *Erythroxylum suberosum*; and the wasps *Brachygastra lecheguana* (23 interactions), *Polybia ignobilis* (22), *P. fastidiosuscula*, and *P. sericea*. [Colour figure can be viewed at wileyonlinelibrary.com]

(Table S2). The most frequent wasp species in the interaction network were *Brachygastra lecheguana*, which performed 23 out of 728 interactions, followed by three species of *Polybia*: *P. ignobilis*, with 22 interactions, *P. fastidiosuscula*, and *P. sericea*, both with 21 interactions each. Regarding the wasp traits, sociality increased all wasp centrality indices, while life form boosted the SS in the network (Table 2). Despite solitary wasps representing the highest number of species in the network (Figure S1A), social wasps boosted the centrality and SS in the network (Figure 3A–C). For instance, social wasp species enhance network cohesion by visiting a greater number of plant species, since sociality affected wasp ND (Figure 3A, Table 2). In addition, social wasps act as important network connectors due to greater BC (Figure 3B, Table 2). We also observed that social wasps increased wasp CC, that is, their proximity to all other wasps in the network (Figure 3C, Table 2). Social wasps also showed greater SS, resulting in a greater diversity of plants visited by this wasp category (Table 2). Finally, the wasp life form boosted the SS by prompting a greater diversity of plants visited by predator wasps when compared with herbivore or parasite ones (Figure 3D, Table 2).

The plant species in the interaction network were distributed across 40 different botanical families, with the Asteraceae family accounting for 36% (265 out of 728) of the interactions, followed by species from the Fabaceae and Erythroxylaceae families, with 11% and 9% of the interactions, respectively (Table S3). The plant genera most frequently visited by wasps were *Stryphnodendron* (Fabaceae), with 65 interactions, *Erythroxylum* (Erythroxylaceae), with 63, and *Baccharis* (Asteraceae), with 61. The plant species most frequently visited by wasps were *Stryphnodendron adstringens* (Fabaceae) with 65 interactions, *Baccharis retusa* (Asteraceae) with 25, *Echinolaena inflexa* (Poaceae) with 18, and *Erythroxylum suberosum* (Erythroxylaceae), with 17. Regarding the plant's floral traits we found significant deviations from a uniform distribution

TABLE 2 | Results of the generalised linear models (GLMs) testing the effects of wasp traits on wasp centrality metrics in a flower–wasp interaction network.

Wasp trait	Response variable	Deviance	df	*F*	*p*	Pseudo-R^2
Sociability	Normalised degree	1.23	140	58.21	**0.01**	0.32
Life form		0.04	84	1.52	0.22	0.05
Size		0.13	113	1.14	0.34	0.04
Sociability	Betweenness centrality	0.54	140	15.99	**0.01**	0.19
Life form		0.01	84	0.13	0.88	0.01
Size		0.01	113	0.05	0.98	0
Sociability	Closeness centrality	0	140	6.31	**0.01**	0.03
Life form		0	84	0.33	0.72	0.01
Size		0	113	0.53	0.66	0.01
Sociability	Species strength	50.19	140	45.32	**0.01**	0.28
Life form		4.5	84	3.28	**0.04**	0.11
Size		6.87	113	1.47	0.23	0.05

Note: Pseudocoefficients of determination (R^2) were calculated as $1-(D_{model}/D_{null})$, where D_{model} and D_{null} are the residual deviances of the regression model and of the corresponding null model, respectively. Significant *p*-values are marked in bold ($p<0.05$).

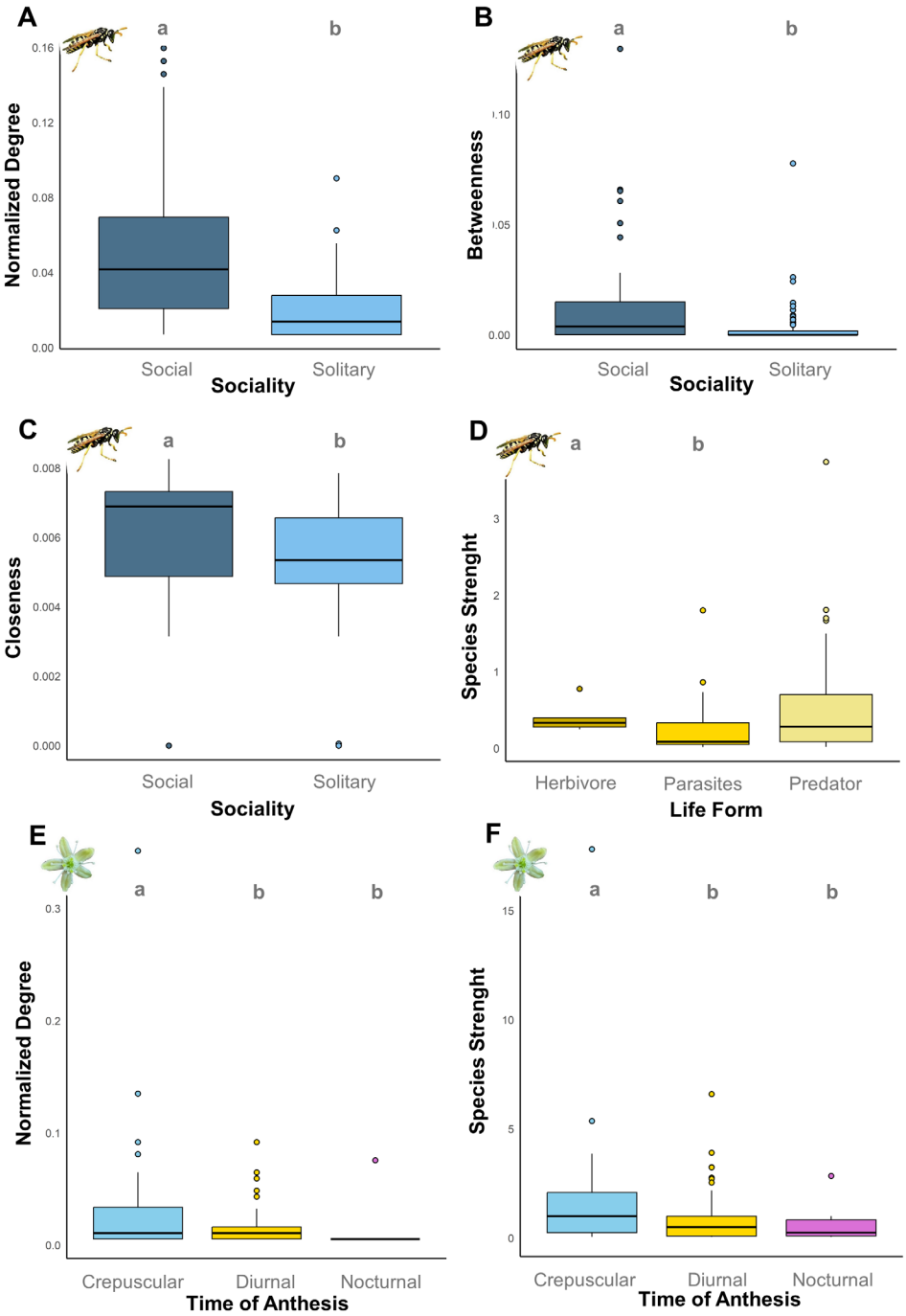

FIGURE 3 | Relationship between wasp sociality and life form, and plant time of anthesis and species centrality indices in a plant–wasp interaction network in the Cerrado, a neotropical savanna in Brazil. Wasp sociality is higher when evaluating (A) normalised degree, (B) betweenness, and (C) closeness centrality of social wasps. Wasp life shows higher values in (D) species strenght of predatory wasps. Plant species centrality is greater when evaluating (E) normalised degree across plant species with crepuscular anthesis and (F) species strength also with crepuscular anthesis. Different letters above each boxplot indicate significant differences among trait categories. See Table 3 for statistical outcomes. [Colour figure can be viewed at wileyonlinelibrary.com]

across all traits (Figure S2). We highlight some traits such as array (Figure S2C), size (Figure S2D), and reward (Figure S2E) showing extreme skewness towards particular categories, such as inflorescences, small flowers which offer nectar, respectively. Regarding the floral traits with the highest number of interactions were those with actinomorphic symmetry, accounting for 41% of the interactions (300 out of 728), followed by 27% with crepuscular anthesis and 26% with diurnal anthesis (200 and 195 interactions, respectively). Additionally, 75% of the flowers interacting in the network offered nectar as a reward (543 interactions), 20% were white or greenish flowers (143 and 154, respectively), and 41% were small-sized (302).

Among the floral traits, the time of anthesis and type of inflorescence were the only that influenced plant centrality. The time of anthesis boosted plant centrality, since the ND

TABLE 3 | Results of the generalised linear models (GLMs) testing the effects of flower traits on plant centrality metrics in a flower–wasp interaction network.

Plant trait	Response variable	Deviance	df	*F*	*p*	Pseudo-R^2
Time of anthesis	Normalised degree	0.38	2	3.77	**0.03**	0.11
Flower symmetry		0.20	2	1.64	0.20	0.06
Floral reward		0.08	2	0.52	0.59	0.02
Colour		0.49	6	1.60	0.16	0.15
Size		0.05	3	0.26	0.86	0.01
Inflorescence type		0.40	7	1.12	0.36	0.12
Time of anthesis	Betweenness centrality	0.14	2	2.22	0.11	0.07
Flower symmetry		0.00	2	0.88	0.42	0.01
Floral reward		0.04	2	0.57	0.57	0.02
Colour		0.32	6	2.00	0.07	0.16
Size		0.05	3	0.50	0.68	0.02
Inflorescence type		0.43	7	2.84	**0.01**	0.21
Time of anthesis	Closeness centrality	0.00	2	0.20	0.82	0.02
Flower symmetry		0.10	2	1.40	0.25	0.05
Floral reward		0.00	2	0.22	0.80	0.01
Colour		0.02	6	1.35	0.24	0.05
Size		0.04	3	0.98	0.40	0.02
Inflorescence type		0.01	7	0.99	0.44	0.04
Time of anthesis	Species strength	18.30	2	1.35	**0.04**	0.09
Flower symmetry		6.06	2	0.90	0.41	0.03
Floral reward		3.50	2	0.37	0.69	0.01
Colour		29.92	6	1.74	0.11	0.16
Size		29.91	3	2.06	0.07	0.21
Inflorescence type		21.35	7	1.15	0.34	0.11

Note: Pseudocoefficients of determination (R^2) were calculated as $1 - (D_{model}/D_{null})$, where D_{model} and D_{null} are the residual deviances of the regression model and of the corresponding null model, respectively. Significant *p*-values are marked in bold ($p < 0.05$).

was positively related to crepuscular anthesis (Figure 3E, Table 3). In other words, plant species with crepuscular flowers enhance network cohesion by supporting a higher number of wasp visits. In addition, crepuscular anthesis also showed greater SS (Figure 3F, Table 3), resulting in a greater diversity of wasps attracted to floral rewards at this time of the day. Furthermore, the architecture of the inflorescences are relevant as network connectors among plants since the inflorescence type determined the BC ($p = 0.0097$, Table 3). However, despite the greater betweenness values being found in species with thyrse inflorescences, no differences were detected across the inflorescence types.

4 | Discussion

In this study, we elucidated flower–wasp interactions, focusing on the often-overlooked behaviour of wasps as potential pollinators in mutualistic flower–wasp networks. By analysing data from a literature review and our own data on flower–wasp interactions in a highly diverse tropical ecosystem, we demonstrated that wasps are common visitors to the flowers of Asteraceae, Fabaceae and Erythroxylaceae species, particularly those with crepuscular, actinomorphic and nectar-rewarding blooms. Additionally, the social wasp species *Brachygastra lecheguana*, *Polybia ignobilis*, *P. fastidiosusculaand* *P. sericea* played key roles in the network as the most frequent potential pollinators, exhibiting high centrality indices. Wasps from the Vespidae family, specifically the *Polybia* and *Polistes* genera, also warrant further study regarding their behaviour while interacting with floral resources, as they show high network centrality and are commonly reported as physically contacting the reproductive floral parts (e.g., by visiting a greater number of plant species, acting as important network connectors, and in a greater diversity of plants visited by this wasp category; Carstensen et al. 2014, 2016). Moreover,

social wasp species boosted network centrality by visiting a greater diversity of plants and acting as network connectors in this interaction network. Furthermore, plant species with crepuscular flowers increased plant cohesion in the network and supported a higher diversity of interactions with wasps. Our results provide new insights into wasps, especially social species, which are often overlooked as pollinators, highlighting their potential role in pollination within tropical communities through numerous interactions and significant network centrality. Additionally, we highlight the potential of flower–wasp interactions as a research opportunity to assess wasp efficiency as pollinators, a behaviour that remains understudied.

The majority of wasp species reported here interacting with flowers were Vespids from the social Polistinae and solitary Eumeninae subfamilies. Social wasps tend to visit a wide variety of flowers from similar plants while foraging for nectar, and accordingly, wasp-flower networks have shown to be less specialised when compared with pollination networks including several animal taxa, thus exhibiting a low level of mutual dependence in this wasp–plant interactions (Santos et al. 2010; Mello et al. 2011). This limited dependence between wasps and the plants they pollinate may be linked to the fact that, although nectar is an important resource for adult wasps to support the colony, their nestmates when social and to feed the larvae, many wasp groups also feed their larvae with captured preys (Mello et al. 2011; Rafael et al. 2024). In parallel, we found that floral traits associated with potential pollination by wasps align with the characteristics of generalist flowers, arranged in inflorescences, usually of the thryse type, with greenish and white, actinomorphic (radial) corollas, the last one is usually associated to freely exposed rewards and generalist pollination systems. In this regard, some studies indicate that wasps play an important role in generalist plant pollination systems worldwide, including in the Brazilian Cerrado and Caatinga (Santos et al. 2010; Mello et al. 2011), preserved areas in France (Descamps et al. 2015), and in species from the Asclepiadoideae (Apocynaceae) subfamily from Japan (Yamashiro et al. 2008), as well as for melon and watermelon crops (Shaik et al. 2017; Campbell et al. 2019) and agroforestry systems (Dag 2009; Taki et al. 2009; Latif et al. 2019; Kilian et al. 2023). These examples provide potential study systems to test pollination by wasps, underscoring the key role of both social and solitary wasps in sustainable crop production, as they may serve both as pollinators and as providers of biological pest control (Fabian et al. 2013).

Our results showed that wasps play a significant role in the pollination network while interacting with *Stryphnodendron* (Fabaceae), *Erythroxylum* (Erythroxylaceae), and *Baccharis* (Asteraceae) genera. Social wasps have already been reported as the main and most effective pollinators in three species of *Erythroxylum* (Erythroxylaceae) in the Cerrado and Atlantic Rainforest domains (Barros 1998; Sühs et al. 2021). Similarly, studies on species pollinated by several functional groups, such as *Croton sarcopetalus* and *C. suberosus* (Euphorbiaceae), have indicated both social and solitary wasp species as one of the most frequent and significant pollinators (Freitas et al. 2001; Narbona and Dirzo 2010). These results suggest that although wasps are best known as pollinators in a few highly specialised pollination systems (e.g., figs and a few orchid genera), they are consistent floral visitors, capable of carrying pollen grains and being as effective as other functional groups of floral visitors (Borchardt et al. 2024). This reinforces the need for a deeper understanding of the role of wasps in generalist pollination systems, their effectiveness as pollinators in these systems, and the potential dependence of plant species on wasp pollination.

The time of anthesis and inflorescence type were the floral traits that affected plant centrality in the network, where crepuscular flowers enhanced wasp visitation and supported a greater diversity of wasp species (Table 3). Since the production and maintenance of floral resources demands high water regulation, especially in seasonal environments such as the Cerrado (Fernandes et al. 2020), some species might produce greater nectar amounts during crepuscular periods to avoid water loss through evapotranspiration, thus resulting in flowers which may support greater pollinator visits during dawn and dusk periods (Borges et al. 2016). This may suggest that wasp species may be foraging for nectar in crepuscular species despite having diurnal activity peaks, which could be associated with other floral traits associated with these plant species. Additionally, studies in the *campo rupestre* indicate that crepuscular insects are the main pollinators of two Melastomataceae species, *Cambessedesia wurdackii* and *Microlicia laniflora*, although exhibiting traits associated with diurnal pollination (Franco and Gimenes 2011; Soares and Morellato 2018). These records support the potential for wasp-pollinated systems in these diverse environments, suggesting that wasps may play a much more significant role in pollination than previously recognised. Nevertheless, we did not find any relationship between the large flowers, nectar-rewarded, with actinomorphic (radial) corollas, as expected. This could be due to a limitation of the secondary data accessed in this review. Furthermore, it reinforces the need to address floral traits associated with wasp visitation in the field, such as the type and amount of resource used and the pollen adhered to the wasp body (Borchardt et al. 2024).

Although the aim of this study was to synthesise records of mutualistic interactions, we acknowledge that wasps may frequently behave as floral antagonists by damaging floral structures when collecting rewards (McCall and Irwin 2006). However, identifying such behaviours on flowers was only possible in 3% of the interactions, due to a lack of detailed information reported by the authors regarding wasp behaviour during flower interactions (but see Gélvez-Zúñiga et al. 2018; Gélvez-Zúñiga et al. 2025). Records of both mutualistic and antagonistic interactions between flowers and their visitors allow a deeper understanding of the complexity of insect-flower interactions in natural communities (Gélvez-Zúñiga et al. 2024). Although wasps have historically been considered floral antagonists (Faegri and Van Der Pijl 1979; Endress 1994) and despite the general lack of detailed behavioural observation of floral visitors in interaction network studies (Burkle and Knight 2012), our results reinforce the high frequency of wasps as floral visitors and highlight their potential as pollinators in generalist flowers. We encourage researchers to report the nature of wasp behaviour on flowers to deepen our understanding of wasps as floral visitors, their effectiveness as pollinators, and their potential consequences for plant reproduction.

5 | Conclusion

In conclusion, our study highlights the significant yet often-overlooked role of wasps as potential pollinators in the cerrado, a highly diverse tropical ecosystem. By analysing interactions between wasps and plants, it becomes clear that wasps are frequent flower visitors and their role as effective pollinators is promising and deserves further study. Our results underscore the importance of wasp sociality and floral traits, such as crepuscular anthesis, which increase plant centrality and seem to attract a higher diversity of wasps. This insight sets the stage for future research on wasp pollination efficiency and emphasises the need to reconsider the ecological roles of wasps, especially in biodiversity hotspots and tropical ecosystems. Our findings have important implications for the conservation and management of pollinators in rapidly changing and threatened environments.

Author Contributions

Beatriz Lopes Monteiro: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing – original draft, writing – review and editing. **Julio Cesar Lopes Santiago:** conceptualization, data curation, investigation, writing – original draft. **Leonor Patricia Cerdeira Morellato:** funding acquisition, methodology, project administration, resources, validation, writing – review and editing. **Geraldo Wilson Fernandes:** funding acquisition, project administration, resources, validation, writing – review and editing. **Irene Gélvez-Zúñiga:** conceptualization, data curation, formal analysis, investigation, methodology, software, supervision, validation, visualization, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available as Supporting Information and openly available in Figshare.com at https://figshare.com/s/db8e56fe2077374ed10c.

References

Armbruster, W. S. 2017. "The Specialization Continuum in Pollination Systems: Diversity of Concepts and Implications for Ecology, Evolution and Conservation." *Functional Ecology* 31, no. 1: 88–100.

Barros, M. G. E. 1998. "Sistemas reprodutivos e polinização em espécies simpátricas de *Erythroxylum* P. Br. (Erythroxylaceae) do Brasil." *Revista Brasileira de Botânica* 21, no. 2: 159–166.

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. "Asymetric Coevolutionary Networks Facilitate Biodiversity Maintenance." *Science* 312, no. 5772: 431–433.

Batagelj, V., and A. Mrvar. 1998. "Pajek – A Program for Large Network Analysis." *Connect* 21: 47–57.

Bernhardt, P., and P. Goldblatt. 2006. "The Role of Phylogenetic Constraints in the Evolution of Pollination Mechanisms in Iridaceae of Sub-Saharan Africa." *Aliso* 22: 434–444.

BFG. 2020. "The Brazil Flora Group. Brazilian Flora. 2020 Project – Instituto de Pesquisas Jardim Botânico do Rio de Janeiro." http://floradobrasil.jbrj.gov.br.

Borchardt, K. E., D. Holthaus, P. A. Soto Méndez, and A. L. Toth. 2024. "Debunking Wasp Pollination: Wasps Are Comparable to Bees in Terms of Plant Interactions, Body Pollen and Single-Visit Pollen Deposition." *Ecological Entomology* 49: 1–584.

Borges, R. M., H. Somanathan, and A. Kelber. 2016. "Patterns and Processes in Nocturnal and Crepuscular Pollination Services." *Quarterly Review of Biology* 91: 389–418.

Bower, C. C. 1996. "Demonstration of Pollinator-Mediated Reproductive Isolation in Sexually Deceptive Species of *Chiloglottis* (Orchidaceae: Caladeniinae)." *Australian Journal of Botany* 44, no. 1: 15–33.

Burkle, L. A., and T. M. Knight. 2012. "Shifts in Pollinator Composition and Behavior Cause Slow Interaction Accumulation With Area in Plant–Pollinator Networks." *Ecology* 93, no. 11: 2329–2335.

Camargo, M. G. G., K. Lunau, M. A. Batalha, S. Brings, V. L. G. Brito, and L. P. C. Morellato. 2019. "How Flower Colour Signals Allure Bees and Hummingbirds: A Community-Level Test of the Bee Avoidance Hypothesis." *New Phytologist* 222: 1112–1122.

Campbell, J. W., C. Stanley-Stahr, M. Bammer, J. C. Daniels, and J. D. Ellis. 2019. "Contribution of Bees and Other Pollinators to Watermelon (*Citrullus lanatus* Thunb.) Pollination." *Journal of Apicultural Research* 58, no. 4: 597–603.

Carstensen, D. W., M. Sabatino, and L. P. C. Morellato. 2016. "Modularity, Pollination Systems, and Interaction Turnover in Plant-Pollinator Networks Across Space." *Ecology* 97, no. 5: 1298–1306.

Carstensen, D. W., M. Sabatino, K. Trøjelsgaard, and L. P. C. Morellato. 2014. "Beta Diversity of Plant-Pollinator Networks and the Spatial Turnover of Pairwise Interactions." *PLoS One* 9, no. 11: e112903.

Caruso, C. M., K. E. Eisen, R. A. Martin, and N. Sletvold. 2019. "A Meta-Analysis of the Agents of Selection on Floral Traits." *Evolution* 73: 4–14.

Carvalho, G. H., M. V. Cianciaruso, and M. A. Batalha. 2010. "Plantminer: A Web Tool for Checking and Gathering Plant Species Taxonomic Information." *Environmental Modelling & Software* 25, no. 6: 815–816.

Ciotek, L., P. Giorgis, S. Benitez-Vieyra, and A. A. Cocucci. 2006. "First Confirmed Case of Pseudocopulation in Terrestrial Orchids of South America: Pollination of *Geoblasta pennicillata* (Orchidaceae) by *Campsomeris bistrimacula* (Hymenoptera, Scoliidae)." *Flora-Morphology, Distribution, Functional Ecology of Plants* 201, no. 5: 365–369.

Clemente, M. A., D. Lange, K. Del-Claro, F. Prezoto, N. R. Campos, and B. C. Barbosa. 2012. "Flower-Visiting Social Wasps and Plants Interaction: Network Pattern and Environmental Complexity." *Psyche (Cambridge, Mass.)* 2012, no. 1: 478431.

Coombs, G., C. I. Peter, and S. D. Johnson. 2009. "A Test for Allee Effects in the Self-Incompatible Wasp-Pollinated Milkweed *Gomphocarpus physocarpus*." *Austral Ecology* 34: 688–697.

Cowie, R. H., P. Bouchet, and B. Fontaine. 2022. "The Sixth Mass Extinction: Fact, Fiction or Speculation?" *Biological Reviews* 97, no. 2: 640–663.

da Silva, V. H. D., M. T. Baumgartner, M. G. Hermes, and L. D. B. Faria. 2022. "How Short Are We on the Goal Line of Estimating Insect-Plant Interaction in a Hyperdiverse Tropical Environment?" *Journal of Insect Conservation* 26, no. 5: 809–821.

Dag, A. 2009. "Interaction Between Pollinators and Crop Plants: The Israeli Experience." *Israel Journal of Plant Sciences* 57, no. 3: 231–242.

Descamps, C., L. Moquet, M. Migon, and A. L. Jacquemart. 2015. "Diversity of the Insect Visitors on *Calluna vulgaris* (Ericaceae) in Southern France Heathlands." *Journal of Insect Science* 15, no. 1: 130.

Dormann, C. F., J. Fruend, and B. Gruber. 2014. "Package 'Bipartite'. Visualizing Bipartite Networks and Calculating Some (Ecological) Indices (Version 2.04). (R Foundation for Statistical Computing)." https://cran.r-project.org/web/packages/bipartite/index.html.

Endress, P. K. 1994. *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge University Press.

Fabian, Y., N. Sandau, O. T. Bruggisser, et al. 2013. "The Importance of Landscape and Spatial Structure for Hymenopteran-Based Food Webs in an Agro-Ecosystem." *Journal of Animal Ecology* 82, no. 6: 1203–1214.

Faegri, K., and L. Van Der Pijl. 1979. *Principles of Pollination Ecology*. Pergamon Press.

Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. "Pollination Syndromes and Floral Specialization." *Annual Review of Ecology, Evolution, and Systematics* 35, no. 1: 375–403.

Fernandes, G. W., L. Arantes-Garcia, M. Barbosa, et al. 2020. "Biodiversity and Ecosystem Services in the Campo Rupestre: A Road Map for the Sustainability of the Hottest Brazilian Biodiversity Hotspot." *Perspectives in Ecology and Conservation* 18: 213–222.

Franco, E. L., and M. Gimenes. 2011. "Pollination of *Cambessedesia wurdackii* in Brazilian Campo Rupestre Vegetation, With Special Reference to Crepuscular Bees." *Journal of Insect Science* 11, no. 97: 1–13.

Freitas, L., G. Bernardello, L. Galetto, and A. A. Paoli. 2001. "Nectaries and Reproductive Biology of *Croton sarcopetalus* (Euphorbiaceae)." *Botanical Journal of the Linnean Society* 136, no. 3: 267–277.

Freitas, L., and M. Sazima. 2006. "Pollination Biology in a Tropical High-Altitude Grassland in Brazil: Interactions at the Community Level." *Annals of the Missouri Botanical Garden* 93, no. 3: 465–516.

Gama, L. U., A. A. A. Barbosa, and P. E. A. M. Oliveira. 2011. "Sistema sexual e biologia floral de *Pouteria ramiflora* e *P. torta* (Sapotaceae)." *Revista Brasileira de Botânica* 34, no. 3: 375–387.

Gélvez-Zúñiga, I., M. Beirão, S. Novais, J. C. Santiago, and G. W. Fernandes. 2025. "Floral Resource Availability Declines and Florivory Increases Along an Elevation Gradient in a Highly Biodiverse Community." *Annals of Botany* 135: 199–210.

Gélvez-Zúñiga, I., F. V. Costa, A. L. Teixido, L. Ashworth, A. Aguilar, and G. W. Fernandes. 2024. "Flower Visitor Networks: Reduced Reproductive Success Driven by Antagonists in a Hummingbird-Pollinated Species." *Biotropica* 56, no. 4: e13342.

Gélvez-Zúñiga, I., A. C. Neves, A. L. Teixido, and G. W. Fernandes. 2018. "Reproductive Biology and Floral Visitors of *Collaea cipoensis* (Fabaceae), an Endemic Shrub of the Rupestrian Grasslands." *Flora* 238: 129–137.

Gess, S. K., and F. W. Gess. 2010. "Pollen Wasps and Flowers in Southern Africa." In *South African National Biodiversity Institute*. 147.

Goldblatt, P., and J. C. Manning. 2006. "Radiation of Pollination Systems in the Iridaceae of Sub-Saharan Africa." *Annals of Botany* 97: 317–344.

Greiner, B. 2006. "Visual Adaptations in the Night-Active Wasp Apoica Pallens." *Journal of Comparative Neurology* 495, no. 3: 255–262.

Harder, L. D., C. Y. Jordan, W. E. Gross, and M. B. Routley. 2004. "Beyond Floricentrism: The Pollination Function of Inflorescences." *Plant Species Biology* 19, no. 3: 137–148.

Herre, E. A., K. C. Jandér, and C. A. Machado. 2008. "Evolutionary Ecology of Figs and Their Associates: Recent Progress and Outstanding Puzzles." *Annual Review of Ecology, Evolution, and Systematics* 39, no. 1: 439–458.

Kilian, I. C., S. J. Swenson, X. Mengual, et al. 2023. "More Complex Than You Think: Taxonomic and Temporal Patterns of Plant–Pollinator Networks of Caraway (*Carum carvi* L.)." *Molecular Ecology* 32, no. 13: 3702–3717.

Latif, A., S. A. Malik, S. Saeed, et al. 2019. "Diversity of Pollinators and Their Role in the Pollination Biology of Chickpea, *Cicer arietinum* L.(Fabaceae)." *Journal of Asia-Pacific Entomology* 22, no. 2: 597–601.

Machado, I. C., and A. V. Lopes. 2004. "Floral Traits and Pollination Systems in the Caatinga, a Brazilian Tropical Dry Forest." *Annals of Botany* 94, no. 3: 365–376.

Martín González, A. M., B. Dalsgaard, and J. M. Olesen. 2010. "Centrality Measures and the Importance of Generalist Species in Pollination Networks." *Ecological Complexity* 7, no. 1: 36–43.

Maruyama, P. K., C. Bonizário, A. P. Marcon, et al. 2019. "Plant-Hummingbird Interaction Networks in Urban Areas: Generalization and the Importance of Trees With Specialized Flowers as a Nectar Resource for Pollinator Conservation." *Biological Conservation* 230: 187–194.

Maruyama, P. K., C. E. P. Nunes, J. Vizentin-Bugoni, S. Gustafsson, and L. P. C. Morellato. 2018. "Are Native Bees and *Apis mellifera* Equally Efficient Pollinators of the Rupestrian Grassland Daisy *Aspilia jolyana* (Asteraceae)?" *Acta Botânica Brasílica* 32, no. 3: 386–391.

McCall, A. C., and R. E. Irwin. 2006. "Florivory: The Intersection of Pollination and Herbivory." *Ecology Letters* 9: 1351–1365.

Mello, M. A. R., G. M. de Mendonça Santos, M. R. Mechi, and M. G. Hermes. 2011. "High Generalization in Flower-Visiting Networks of Social Wasps." *Acta Oecologica* 37: 37–42.

Mello, M. A. R., F. A. Rodrigues, L. F. Costa, et al. 2015. "Keystone Species in Seed Dispersal Networks Are Mainly Determined by Dietary Specialization." *Oikos* 124: 1031–1039.

Monteiro, B. L., M. G. G. Camargo, P. P. Loiola, D. W. Carstensen, S. Gustafson, and L. P. C. Morellato. 2021. "Pollination of the Campo Rupestre: A Test of Hypothesis for an Ancient Tropical Mountain Vegetation." *Biological Journal of the Linnean Society* 133, no. 2: 512–530.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, and J. Kent. 2000. "Biodiversity Hotspots for Conservation Priorities." *Nature* 403, no. 6772: 853–858.

Narbona, E., and R. Dirzo. 2010. "A Reassessment of the Function of Floral Nectar in *Croton suberosus* (Euphorbiaceae): A Reward for Plant Defenders and Pollinators." *American Journal of Botany* 97, no. 4: 672–679.

Nooy, W., A. Mrvar, and V. Batagelj. 2011. *Exploratory Social Network Analysis With Pajek*. Cambridge University Press, 420 pp.

Oi, C. A., R. L. Brown, and S. Sumner. 2024. "Bee-Ing Positive About Wasp-Negative Media Reporting: The Opinions of Scientists and Their Influence on the Media." *Insectes Sociaux* 71, no. 1: 29–42.

Oliveira, P. E., and P. E. Gibbs. 2000. "Reproductive Biology of Woody Plants in a Cerrado Community of Central Brazil." *Flora* 195, no. 4: 311–329.

Ollerton, J., R. Alarcón, N. M. Waser, et al. 2009. "A Global Test of the Pollination Syndrome Hypothesis." *Annals of Botany* 103, no. 9: 1471–1480.

Ollerton, J., S. D. Johnson, L. Cranmer, and S. Kellie. 2003. "The Pollination Ecology of an Assemblage of Grassland Asclepiads in South Africa." *Annals of Botany* 92: 807–834.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. "How Many Flowering Plants Are Pollinated by Animals?" *Oikos* 120, no. 3: 321–326.

O'Neill, K. M. 2001. *Solitary Wasps: Behavior and Natural History*. Cornell University Press.

O'Neill, K. M. 2019. "Solitary Wasps: Behavior and Natural History." In *Solitary Wasps, Cornell Series in Anthropod Biology*. Cornell University Press.

Pereira, R. A. S. 2024. "Wasp Pollination: Mechanisms, Evolution and Ecological Significance in Neglected Pollinator Groups." *Journal of Applied Entomology* 149: 866–881. https://doi.org/10.1111/jen.13386.

Peters, R. S., L. Krogmann, C. Mayer, et al. 2017. "Evolutionary History of the Hymenoptera." *Current Biology* 27, no. 7: 1013–1018.

Pilosof, S., M. A. Porter, M. Pascual, and S. Kéfi. 2017. "The Multilayer Nature of Ecological Networks." *Nature Ecology & Evolution* 1: 0101.

R Core Team. 2024. R: A Language and Environment for Statistical Computing.

Rafael, J. A., G. A. R. D. Melo, C. J. B. D. Carvalho, S. A. Casari, and R. Constantino. 2024. *Insetos do Brasil: diversidade e taxonomia*. Editora INPA.

Richter, M. R. 2000. "Social wasp (Hymenoptera: Vespidae) foraging behavior." *Annual review of entomology* 45, no. 1: 121–150.

Rosas-Guerrero, V., R. Aguilar, S. Martén-Rodríguez, et al. 2014. "A Quantitative Review of Pollination Syndromes: Do Floral Traits Predict Effective Pollinators?" *Ecology Letters* 17, no. 3: 388–400.

Santos, G. M. M., C. M. L. Aguiar, and M. A. M. Mello. 2010. "Flower-Visiting Guild Associated With the Caatinga Flora: Trophic Interaction Networks Formed by Social Bees and Social Wasps With Plants." *Apidologie* 41: 466–475.

Santos, N., J. F. D. Andrade, R. A. S. Pereira, and F. H. A. Farache. 2022. "Community Structure and Specialization in Fig Wasps (Hymenoptera: Chalcidoidea) in a Region of Cerrado." *Revista Brasileira de Entomologia* 66, no. 1: e20210101.

Sazima, C., P. R. Guimarães Jr., S. F. Dos Reis, and I. Sazima. 2010. "What Makes a Species Central in a Cleaning Mutualism Network?" *Oikos* 119, no. 8: 1319–1325.

Shaik, R. S., G. E. Burrows, N. A. Urwin, D. Gopurenko, B. J. Lepschi, and L. A. Weston. 2017. "The Biology and Management of Prickly Paddy Melon (*Cucumis myriocarpus* L.), an Important Summer Annual Weed in Australia." *Crop Protection* 92: 29–40.

Shuttleworth, A., and S. D. Johnson. 2009. "The Importance of Scent and Nectar Filters in a Specialized Wasp-Pollination System." *Functional Ecology* 23, no. 5: 931–940.

Simpson, M. G. 2006. *Plant Systematics*. Elsevier Academic Press.

Soares, N. C., and L. P. C. Morellato. 2018. "Crepuscular Pollination and Reproductive Ecology of *Trembleya laniflora* (Melastomataceae), an Endemic Species in Mountain Rupestrian Grasslands." *Flora* 238: 138–147.

Souza, C. S., C. Aoki, A. Ribas, A. Pott, and M. R. Sigrist. 2016. "Floral Traits as Potential Indicators of Pollination vs. Theft." *Rodriguésia* 67: 309–320.

Souza, C. S., P. K. Maruyama, C. Aoki, et al. 2018. "Temporal Variation in Plant–Pollinator Networks From Seasonal Tropical Environments: Higher Specialization When Resources Are Scarce." *Journal of Ecology* 106, no. 6: 2409–2420.

Souza, C. S., P. O. Oliveira, B. B. Rosa, and P. K. Maruyama. 2022. "Integrating Nocturnal and Diurnal Interactions in a Neotropical Pollination Network." *Journal of Ecology* 110: 2145–2155.

Sühs, R. B., A. Somavilla, and E. L. H. Giehl. 2021. "Weather Variables Affecting the Behaviour of Insect Flower Visitors and Main Pollinators of *Erythroxylum myrsinites* Martius (Erythroxylaceae)." *Sociobiology* 68, no. 1: e5451.

Sumner, S. 2022. *Endless Forms: The Secret World of Wasps*. HarperCollins Publishers.

Sumner, S., G. Law, and A. Cini. 2018. "Why We Love Bees and Hate Wasps." *Ecological Entomology* 43: 836–845.

Taki, H., K. Okabe, S. I. Makino, Y. Yamaura, and M. Sueyoshi. 2009. "Contribution of Small Insects to Pollination of Common Buckwheat, a Distylous Crop." *Annals of Applied Biology* 155, no. 1: 121–129.

Vidal, M. M., E. Hasui, M. A. Pizo, J. Y. Tamashiro, W. R. Silva, and P. R. Guimarães Jr. 2014. "Frugivores at Higher Risk of Extinction Are the Key Elements of a Mutualistic Network." *Ecology* 95, no. 12: 3440–3447.

Warrant, E. J. 2008. "Review: Seeing in the Dark: Vision and Visual Behaviour in Nocturnal Bees and Wasps." *Journal of Experimental Biology* 211: 1737–1746.

Warrant, E. J., A. Kelber, R. Wallen, and W. Wcislo. 2006. "Ocellar Optics in Diurnal and Nocturnal Bees and Wasps." *Arthropod Structure & Development* 35: 293–305.

Weiblen, G. D. 2002. "How to Be a Fig Wasp." *Annual Review of Entomology* 47, no. 1: 299–330.

Yamashiro, T., A. Yamashiro, J. Yokoyama, and M. Maki. 2008. "Morphological Aspects and Phylogenetic Analyses of Pollination Systems in the *Tylophora–Vincetoxicum* Complex (Apocynaceae-Asclepiadoideae) in Japan." *Biological Journal of the Linnean Society* 93, no. 2: 325–341.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1 Figure S1 Figure S2**