Journal of Applied Entomology

WILEY

SPECIAL ISSUE The Neglected Pollinators: Understanding the Importance of Lesser-Known Insect Taxa in Pollination

JOURNAL OF APPLIED ENTOMOLOGY

ORIGINAL ARTICLE OPEN ACCESS

Ensuring Pollinator Presence in Expanding Oil Crops: The Case of *Mystrops debilis* (Nitidulidae) and the Macauba Palm (*Acrocomia aculeata*, Arecaceae)

Javier Carreño-Barrera[1] | Artur Campos Dália Maia[2,3] | Carlos Augusto Colombo[1,4] | Luis Alberto Nuñez-Avellaneda[5]

[1]Graduate Program in Tropical and Subtropical Agriculture, Instituto Agronômico de Campinas (IAC), Campinas, Brazil | [2]Graduate Program in Plant Biology, Department of Botany, Universidade Federal de Pernambuco, Recife, Brazil | [3]Graduate Program in Animal Biology, Department of Zoology, Universidade Federal de Pernambuco, Recife, Brazil | [4]Centro de Pesquisa e Desenvolvimento de Recursos Genéticos e Vegetais, Instituto Agronômico de Campinas (IAC), Campinas, Brazil | [5]Ecotonos Grupo de Investigación, Programa de Biología, Universidad de los Llanos, Villavicencio, Colombia

Correspondence: Artur Campos Dália Maia (arturmaia@gmail.com)

Received: 30 November 2024 | **Revised:** 25 April 2025 | **Accepted:** 5 May 2025

Funding: This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo, 2014/23591-7; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, 88882.444190/2019-01.

Keywords: Derelomini | flower weevil | Mystropini | neotropical palms | oleaginous fruits | palynivory | vegetable oil

ABSTRACT

The macauba palm (*Acrocomia aculeata*, Arecaceae) is a Neotropical native oil palm, increasingly important in Central and South America due to rising demand for raw materials and its potential for bioenergy. Understanding its pollinator ecology is crucial to identify new areas for cultivation. This study examines the structure of floral visitor communities, assesses pollinator abundances and variations, and highlights key pollinators across *A. aculeata* populations across different naturalization forms (wild, naturalized, and cultivated). We also projected optimal cultivation areas in Brazil and Colombia based on the presence of *Mystrops debilis* (Nitidulidae), a primary pollinator. Across all naturalization forms, Coleoptera were the dominant flower-visiting insects, with 49 species recorded in association with *A. aculeata* inflorescences. Significant differences in species richness were observed between naturalization forms. In all populations studied, *M. debilis* and *Andranthobius sp.1* (Curculionidae) consistently emerged as the dominant and most effective pollinators. Their Pollinator Importance (PI) indices, which quantifies each species' relative contribution to pollination, ranged from 14.7% to 83.2% in Brazil and 85.1% to 9.2% in Colombia. Although the two species can act as efficient pollinators, M. debilis shows greater potential adaptability to human-altered environments due to broader host preferences, being associated with 34 palm species, both native and exotic. Kernel Density Estimation (KDE) analysis identified multiple regions across a 26.6 latitudinal range in Brazil and Colombia as pollinator-sufficient areas for *A. aculeata* cultivation. In Colombia, these areas were concentrated in the Caribbean, Magdalena Medio, and Orinoquía regions. In Brazil, optimal pollination areas were predicted in the Atlantic Forest, Cerrado, and Caatinga ecoregions, spanning the states of São Paulo, Minas Gerais, Bahia, Espírito Santo, Rio de Janeiro, and Mato Grosso. Incorporating pollinator dynamics into crop planning offers a promising strategy to enhance cultivation success across diverse regions.

1 | Introduction

The macauba palm (*Acrocomia aculeata*, Arecaceae) has earned the nickname "Green Gold" in Latin American countries due to its versatility as a raw material. High-protein flour is produced from the mesocarp, while the nut is used for charcoal production. However, the oils extracted from the mesocarp (pulp) and endocarp (kernel) are the most commercially valuable (Berton

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Journal of Applied Entomology* published by Wiley-VCH GmbH.

et al. 2013; Ciconini et al. 2013; Colombo et al. 2018; de Lima et al. 2018).

Brazilian companies like Soleá Brasil and INOCAS have already established over 3000 ha of commercial *A. aculeata* plantations in the states of Minas Gerais and São Paulo (Colombo et al. 2018; INOCAS 2021). According to Berton et al. (2013) and Evaristo et al. (2016), the oil yield from plantations with 400 palms per hectare is estimated at 2.5 tons per hectare per year in a conservative scenario, with potential production reaching up to 5.0 $t.ha^{-1}$ annually. This surpasses the yield of the African oil palm (*Elaeis guineensis*) (Sierra-Márquez et al. 2017). By 2030, *A. aculeata* cultivation could expand to nearly tenfold, driven by strategies like silvopastoral systems, recovering degraded land, or integrating with crops such as maize, coffee, pumpkin, and banana. This growth positions *A. aculeata* as a promising agricultural energy alternative for Brazil and Colombia (Colombo et al. 2018; INOCAS 2021).

To fully harness the potential of *A. aculeata*, research is advancing in areas such as morpho-anatomy (Farias Neto et al. 2013; Vianna 2017), species distribution (Berton et al. 2013), fruit physico-chemical characteristics (Alfaro-Solís et al. 2020), genetic diversity (Díaz et al. 2021; Couto et al. 2024), eco-physiology (Santos Júnior et al. 2012; Resende et al. 2020), economic viability (de Carvalho Lopes et al. 2013; Colombo et al. 2018), and reproductive biology and pollination ecology (Scariot et al. 1991; Brito 2013; Carreño-Barrera et al. 2021). Regarding pollination, *A. aculeata* follows a seasonal reproductive cycle, producing inflorescences during the dry season (Montoya et al. 2016).

The species is protogynous and entomophilous, primarily pollinated by derelomine weevils (Curculionidae, Derelomini), mystropine sap beetles (Nitidulidae, Mystropini), and cyclocephaline beetles (Melolonthidae, Cyclocephalini) (Scariot et al. 1991; Carreño-Barrera et al. 2021). Pollination is highly specialised, with pollinators responding to unique phenological, chemical, and physiological cues from the inflorescences. Despite this specificity in pollination mechanisms, *A. aculeata* attracts a diverse insect community (46 species; >3000 individuals per inflorescence; Carreño-Barrera et al. 2021). During the female phase, pollen transfer to stigmas is efficient, ensuring high fruit production rates, highlighting the plant's reliance on insect pollinators.

Pollination services are crucial for maintaining the productivity of economically important palms (Henderson 1988; Borges et al. 2020). For instance, African oil palm relies exclusively on the pollinating derelomine weevil *Elaeidobius kamerunicus* to ensure large-scale fruit production worldwide (Meléndez and Ponce 2016; Yousefi et al. 2020; Gintoron et al. 2023). Locally important species like the moriche palm (*Mauritia flexuosa*) depend, among others, on mystropine sap beetles (e.g., *Mystrops dalmasi*) and derelomine weevils (e.g., *Grasidius* spp., *Phytotribus* spp.) for fruit production, as do other palms among the genera *Oenocarpus*, *Bactris*, and *Attalea* (Anderson et al. 1988; Scariot et al. 1991; Storti 1993; Küchmeister et al. 1998; Oliveira et al. 2003; Fava et al. 2011; Khorsand Rosa and Koptur 2013). In fact, various small-sized beetles contribute to the pollination of fruit crops in the neotropics, such as pumpkin (*Cucurbita mixta*) (Lattaro and Malerbo-Souza 2006), cupuaçu (*Theobroma grandiflorum*) (Maués et al. 2000), watermelon (*Citrullus lanatus*) (Malerbo-Souza et al. 1999), pear (*Pyrus communis*) (Faoro and Orth 2015), okra (*Abelmoschus esculentus*) (Malerbo-Souza et al. 2001), and *Annona* spp. (Blanche and Cunningham 2005; Kishore et al. 2012).

According to Núñez-Avellaneda and Carreño-Barrera (2013) and Núñez A. et al. (2015), the efficiency and exclusivity of pollinators for economically promising palm species like *M. flexuosa* and *Oenocarpus* spp. remain consistent across their distribution, ensuring stable fruit production under natural conditions. However, high dependence on specific pollinators can negatively impact fruit yields. For instance, in South America and Indomalaya, the introduction of *E. kamerunicus* from its native range was necessary to support large-scale African oil palm cultivation (Meléndez and Ponce 2016; Li et al. 2019). Recent studies, nonetheless, indicate that some commercial African oil palm plantations have adapted to other pollinating beetles, including *Elaeidobius subvittatus*, *Mystrops costaricensis*, *M. astrocaryi*, *M. costaricensis*, *Cyclocephala discolor*, *Orthoperus* spp. (Corylophidae), *Coproporus* spp. (Staphylinidae), and *Smicrips* spp. (Smicripidae) (Labarca and Narváez 2009; Meléndez and Ponce 2016). In some Indonesian plantations, thrips (*Trips* spp.; Thysanoptera) functioned as primary pollinators prior to the introduction of *E. kamerunicus* (Syed 1979).

The domestication of palm species for oil production poses a complex and multidisciplinary research challenge. Beyond focusing on the plants themselves, it is essential to ensure the availability of effective pollinators (Egan et al. 2018, 2020). Although domestication of pollinators is not (yet) the goal, understanding their identity, behaviour, and pollination efficiency in different environmental settings is crucial for the successful cultivation of species like the macauba palm. Our research investigates these key factors by addressing critical questions about pollination dynamics in wild, naturalised, and cultivated populations of *A. aculeata* in Brazil and Colombia. These include: (i) Do floral visitor communities vary across different regions and population forms? (ii) Are pollinators' identities and efficiency consistent among wild, naturalised, and cultivated populations of *A. aculeata*? (iii) How does *A. aculeata*'s reproductive seasonality relate to pollinator plasticity in host selection? (iv) Can pollinator distribution ranges help identify potential areas to support future commercial macauba palm plantations?

The spatial and temporal consistency of pollination services in wild populations remains under-researched, primarily due to limited knowledge of the variability in wild pollinators across space and time. Understanding the changes in floral visitors' communities and the role of pollination in economically important palm species within a geographic context can inform the development of management strategies, thus helping mitigate productivity issues.

2 | Material and Methods

2.1 | Study Areas

Between 2017 and 2024, we examined floral visitation and pollinator communities across six focal locations: four in wild populations, one in a naturalised population, and one in a cultivated setting. Three of these locations were in the Brazilian

TABLE 1 | Geographic coordinates and naturalisation forms' classification of *Acrocomia aculeata* (Arecaceae) focal populations investigated in Colombia and Brazil, where detailed pollination studies were conducted between 2017 and 2024.

Location, Municipality, Department/State	Population	Geographic coordinate
Brazil		
Agronomic Institute of Campinas (Fazenda Santa Eliza, Experimental Center), Campinas, São Paulo	Naturalised	22°51′32.22″ S—47°05′31.79″ W
Santa Rosa de Lima, Montes Claros, Minas Gerais	Wild	16°20′20.36″ S—43°57′38.54″ W
Fazenda Cachoerinha, Olaria, Minas Gerais	Cultivated	21°55′20.61″ S—43°58′12.46″ W
Colombia		
Hacienda Flor Amarillo (Mata de Gallina), Arauca, Arauca	Wild	6°52′47.18″ N—70°50′43.23″ W
La Chaparrera, Yopal, Casanare	Wild	5°28′21.60″ N—72°14′54.65″ W
Hacienda El Recuerdo, San Martín, Meta	Wild	3°46′25.86″ N—73°42′47.43″ W

states of Minas Gerais and São Paulo, while the other three were in different departments of Colombia (Table 1). Additionally, we collected data from several other sites (see below; Table S1), focusing on *A. aculeata* and various palm species, to broaden our understanding of pollinator dynamics and host selectivity across diverse ecosystems.

The investigated *A. aculeata* populations in Brazil are found in the Cerrado and Atlantic Forest ecoregions. The Brazilian Cerrado is characterised by a tropical seasonal climate with annual temperatures ranging from 22°C to 27°C and precipitation between 800 and 2000 mm. It experiences a wet season during summer months and a prolonged dry season from April to September (Ratter et al. 1997). The Atlantic Forest extends along the Brazilian Atlantic coast, featuring a humid tropical climate with annual temperatures from 22°C to 28°C and precipitation exceeding 2000 mm, with rainfall occurring throughout the year in some regions (Vancine et al. 2024). In Colombia, *A. aculeata* populations are found in the Orinoquia region, characterised by a tropical savanna climate with temperatures from 24°C to 28°C and annual precipitation ranging from 1500 to 2000 mm. It experiences a distinct rainy season from April to November, followed by a dry season from December to March (Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM) 2024).

Wild populations, found in natural environments with minimal human influence, typically display a range of reproductive adults (Harper 1977). In our study, wild populations were identified in Arauca, Casanare, and Meta in Colombia, as well as in Montes Claros, Minas Gerais, Brazil (Table 1). Naturalised populations, in contrast, are those introduced intentionally or accidentally, which have since become established and are capable of reproducing (Richardson et al. 2000; Richardson and Pyšek 2012). The naturalised population in our study is located in Campinas, São Paulo, Brazil. A cultivated population is deliberately established for commercial purposes, such as the one observed in Olaria, Minas Gerais, Brazil (Table 1, Table S1a). It consists of approximately 12,000 individuals, aged between 6 and 18 years, distributed across high escarpments, hills, riverbanks, and small tributaries. A notable characteristic of this population is its isolation—within a 200 km radius, there is no evidence of other *A. aculeata* populations. However, other palm species such as the native *Syagrus romanzoffiana* were found in the study area.

2.2 | Structural Analysis of Floral Visitor Communities Associated With *Acrocomia aculeata*

To understand the composition, richness, and abundance of insects visiting *A. aculeata* inflorescences, collections were conducted on 10 palms per each of the six aforementioned focal locations. Access to the inflorescences was facilitated using aluminium ladders, and all insects were captured after bagging and shaking the inflorescence following tried methodology (Núñez-Avellaneda and Rojas-Robles 2008; Kirejtshuk and Couturier 2010). Floral visitor collections were conducted during the female phase of anthesis, when the stigmas are receptive for fertilisation (Carreño-Barrera et al. 2021). This period specifically coincided with the evening following the opening of the peduncular bract, aligning with the peak activity of floral visitors between 18:00 and 21:00. Captured insects were preserved in alcohol and subsequently identified to the most specific taxonomic level possible, enabling the generation of a species composition table for the six study locations.

Overall similarities in the fauna of flower-visiting insects among the six focal locations were assessed by comparing their abundance and species richness using Mann–Whitney pairwise tests with Bonferroni-corrected p-values. Alpha diversity was evaluated using diversity profiles based on the exponential of the Rényi index. This approach enables robust comparisons across a continuous parameter (α), encompassing total species number ($\alpha = 0$), Shannon diversity ($\alpha \approx 1$), and Simpson diversity ($\alpha = 2$). For $\alpha > 2$, the index increasingly emphasises abundant species while minimising the influence of rare taxa. Diversity profiles were plotted with bootstrapped 95% confidence intervals from 2000 replicates to ensure interpretability.

To assess differences in flower-visiting insect community structure across *A. aculeata* naturalisation forms (wild, naturalised, cultivated) in Brazil and between Brazil and Colombia,

compositional data (individuals per species per sample) were subjected to a centered log-ratio (clr) transformation (0.001 threshold) to address compositional bias (Brückner and Heethoff 2017). Using clr-transformed data, we conducted a principal components analysis (PCA; Euclidean similarity) to visualise community patterns. Global and pairwise permutational multivariate analyses of variance (PERMANOVA; Pseudo-*F*, 9999 permutations) tested whether naturalisation form and geographic location significantly explained compositional differences, followed by permutational analysis of multivariate dispersions (PERMDISP; *F*) to evaluate homogeneity of group dispersions.

To account for potential spatial autocorrelation, we performed Mantel tests, correlating geographic distance (Haversine method; Maria et al. 2020) with ecological dissimilarity for both raw and clr-transformed data (Bray–Curtis index and Euclidean distance, respectively). Additionally, spatial clustering of key pollinator abundances (*Mystrops debilis*, *Andranthobius* sp.1) was assessed using Moran's *I* tests in R v.4.3.1 ('*ape*' package). Finally, SIMPER analysis (Bray–Curtis similarity, untransformed data) quantified species-specific contributions to compositional differences between naturalisation forms and geographic regions. All multivariate analyses, excluding Moran's *I*, were conducted in PAST v.4.15 (Hammer et al. 2001).

2.3 | Quantification of the Role of Floral Visitors in Pollination

The potential role of floral visitors in the pollination of *A. aculeata* in each focal location was determined using the Pollinator Importance value (PI) proposed by Núñez-Avellaneda and Rojas-Robles (2008), with additional methodological refinements from Carreño-Barrera et al. (2020). Based on PI values, flower-visiting species were classified as primary pollinators (PI > 10%), accessory pollinators (PI = 1%–10%), or insignificant contributors (PI < 1%).

2.4 | Presence and Spatial Variation of Primary Pollinators

We documented the presence and abundance of the primary pollinators, *M. debilis* and *Andranthobius* sp.1, throughout the natural range of *A. aculeata* across a 26.6° latitudinal span (Table S1a). Sampling involved 32 population sites across Brazil and Colombia, with five collections per site. In Brazil, we surveyed populations at 14 locations within Minas Gerais, São Paulo, and Rio de Janeiro, and included two additional published records from Distrito Federal (Scariot et al. 1991, 1995) and Minas Gerais (Brito 2013), each represented by a single collection. In Colombia, our sampling covered 16 sites across the departments of Casanare, Cesar, Norte de Santander, Meta, and Valle del Cauca. Populations at each site were characterised as wild, naturalised, or cultivated.

We generated a data matrix of the average abundances of the most important pollinators per location (Table S1b) and projected these onto histogram graphs using QGIS version 3.30. To analyse the variation in pollinator abundances across locations, we used the Kruskal–Wallis test in the software PAST v.4.15 to determine if there were significant differences between the species of the main pollinators at local and regional levels. Abundance data was tested for potential spatial autocorrelation using Matel and Moran's *I* tests (see aforementioned).

2.5 | Palm Host Preferences of the Primary Pollinator *Mystrops debilis*

We evaluated the palm host preferences of *M. debilis*, one of the two primary pollinators of *A. aculeata*, using data from extensive collections in South America and a comprehensive literature review reporting the species in 100 locations in Brazil and Colombia (Table S1c). In Brazil, we reviewed the presence of *M. debilis* and other congenerics in 41 locations, visiting wild palm populations of the genera *Acrocomia*, *Astrocaryum*, *Attalea*, and *Syagrus* in 28 locations (with 5 collections per location). Additionally, we reviewed studies related to insect communities and pollination ecology in wild palms from 13 locations in Brazil (Table S1c). In Colombia, we examined the presence of *M. debilis* and other congenerics in 59 locations, sampling wild palm populations of the genera *Attalea*, *Bactris*, *Iriartea*, *Syagrus*, and *Wettinia* in 40 locations (with 5 collections per location). We further reviewed published studies and projects related to insect communities and pollination ecology in Colombian palms from 19 locations (Table S1c).

We conducted a search for studies on insect communities and pollination ecology in palms using Google Scholar, ResearchGate, Mendeley, and the Global Biodiversity Information Facility (GBIF) database (www.gbif.org). Our search included the keywords "insect communities", "pollination", "*Mystrops*", "beetle", "Coleoptera", cross-references with the keywords "palm", "Palmae", and "Arecaceae". We applied filters to focus on peer-reviewed articles published within the last 10 years in English or Spanish, prioritising studies with geographical relevance to enhance applicability. This search documented the occurrence of *Mystrops* spp. (including *M. debilis*) across multiple palm species.

Based on presence-absence data of *Mystrops* spp. found in palm species, we produced a binary matrix (1-present; 0-absent). We assessed host palm preferences of *M. debilis* using a similarity analysis performed in PAST 4.15 software (Hammer et al. 2001) and a binary interaction network using the Bipartite library (Dormann et al. 2008) in R software v.4.0.4, coupled with RStudio Version 1.4.1106 (RStudio Team 2020).

2.6 | Ecological Activity Areas of *Mystrops debilis*

To estimate the potential occurrence areas of *M. debilis*, we generated a database of palm species distribution points that recorded any of the pollinator insects, using information from the GBIF database. We implemented Kernel Density Estimation (KDE) to examine and estimate the potential areas of pollinators using the QGIS 3.30 geographic information system software. KDE employs probability statistics (Kernel Function) to calculate the estimated density of a population

around data points, producing a smooth, conical surface that connects all data points used in the analysis (Silverman 1984; QGIS 2024).

We selected KDE because it works well with any type of data density, and the results are presented as a Utilisation Distribution (UD) (Bowman and Azzalini 1997). A UD is a grid where the value of each cell represents the probability of the taxon occurring in that cell, rather than a simple range contour (Gitzen et al. 2006). The KDE was derived from the presence data of the pollinating species *M. debilis* found in other populations of *A. aculeata* and other palm species (Table S1c,d), compiling geolocation data of palm species where some *A. aculeata* pollinators were found, along with bandwidths (smoothing parameters).

To calculate these bandwidths, we randomly measured distances between all points (total calculated data) and then averaged these distances. A bandwidth specifies the maximum distance over which data points are distributed across the study area or the search radius of the KDE function (QGIS 2024).

3 | Results

3.1 | Structural Analysis of Floral Visitor Communities Associated With *Acrocomia aculeata*

The behaviour and activity patterns of floral visitors to *A. aculeata* inflorescences were consistent across all populations in the six focal locations. Activity typically began in the late afternoon, with insects from various groups hovering around or perching on the enclosing bract. Once the inflorescences opened (around 18:00), small beetles—primarily mystropine sap beetles and derelomine weevils—along with larger cyclocephaline beetles, accessed the flowers. These initial visits generally occurred during the female phase of anthesis on the first evening when all pistillate flowers had receptive stigmas, which remained viable for several hours. On the second day, between 17:00 and 18:00, the staminate flowers opened, attracting additional flower-visiting insects. These new arrivals joined those from the previous night, waiting for anther dehiscence. The male phase lasted 2–5 days.

There were no significant differences in visitor abundances among the six focal locations. On average, inflorescences in wild, naturalised, and cultivated populations were visited by 1878–4747 ($\bar{x}=3309$), 1245–10,546 ($\bar{x}=3580$), and 1770–6782 ($\bar{x}=4268$) insects during the female phase, respectively (Figure 1a). In general, all investigated populations exhibited a similar compositional pattern of flower-visiting insects, with a few dominant species and many in low numbers (Table 2 and Table S1e).

Across all focal locations, 75 species of flower-visiting insects were recorded on female-phase inflorescences of *A. aculeata* (Table 2). Coleoptera had the highest representation with 47 species, followed by Hymenoptera (21) and smaller numbers of Hemiptera (4) and Diptera (3). Among Coleoptera, Curculionidae (19 species), Staphylinidae, Nitidulidae, and Melolonthidae (5–6 species each) were the most abundant. In Hymenoptera, Apidae (11 species) dominated, along with smaller contributions from Braconidae, Ceraphronidae, Formicidae, Halictidae, and Vespidae (1–3 species each). The taxonomic composition at the order and family levels was consistent across wild, naturalised, and cultivated populations of *A. aculeata* in Brazil and Colombia.

The total species richness of flower-visiting insects associated with *A. aculeata* was slightly higher in Brazilian populations (44 species) compared to Colombian populations (42 species), with only 15.8% of species shared between the two countries (Table 2). However, the average number of species per sampled location was significantly higher in Colombian populations (20–25 species, compared to 7–19 species in Brazil). Colombian populations also demonstrated more diverse floral visitor assemblages overall, as evidenced by consistently higher alpha diversity values. In Brazil, among different forms of naturalisation, species richness and diversity were highest in naturalised populations and lowest in cultivated populations (Figure 1b,c).

In all six focal locations, *Andranthobius* sp.1 and *Mystrops debilis* were consistently among the most abundant species associated with *A. aculeata* inflorescences, accounting for 46%–98% of all collected insects in analysed samples. Although the two species were always present in the analysed samples, they alternated dominance in populations from Brazil and Colombia, with *M. debilis* being most dominant in Brazil and *Andranthobius* sp.1 in Colombia (Table 2). A SIMPER test revealed that these two species alone contributed to 69.4% of the dissimilarity among Brazilian and Colombian populations, as well as 85.7% between different naturalisation forms in Brazil (Table S1f). Other notable floral visitors included derelomine weevils from the genera *Andranthobius*, *Phyllotrox*, and *Grasidius*, along with cyclocephaline beetles (*Cyclocephala* spp.), another species of *Mystrops*, and a species of *Diplocoelus* (Biphyllidae; Table 2).

The composition of floral visitor communities differed significantly between Brazilian and Colombian populations, as indicated by PERMANOVA results (Pseudo-$F=32.2$, $p<0.0005$) and PERMDISP analysis ($F=8.9$, $p<0.005$). In Brazil, distinct naturalisation forms also exhibited significant differences in community composition (Pseudo-$F=5.6$, $p<0.0005$; pairwise Pseudo-$F\geq 3.6$, $p<0.0005$; PERMDISP $F=86.0$, $p<0.0005$; pairwise $F\geq 22.9$, $p<0.0005$). These differences are visually represented by clear clustering patterns in the PCA plot (Figure 1d).

Within Brazilian populations, no significant correlation was found between community dissimilarity and geographic distance (Mantel test: raw abundance $r=-0.862$, $p=0.50$; clr-transformed $r=-0.393$, $p=0.83$). Likewise, Moran's I test showed no significant spatial autocorrelation in individual pollinator species' abundances ($p>0.05$).

3.2 | Quantifying the Role of Floral Visitors in Pollination

Of the 75 insect species recorded visiting *A. aculeata* inflorescences across the six study locations, only 10 were identified as effective pollen transporters (Table 3; Table S1g). The remaining species were considered of limited relevance due to not carrying pollen, appearing in low abundances, or restricting their visits and activity to the male phase of anthesis. In all naturalisation

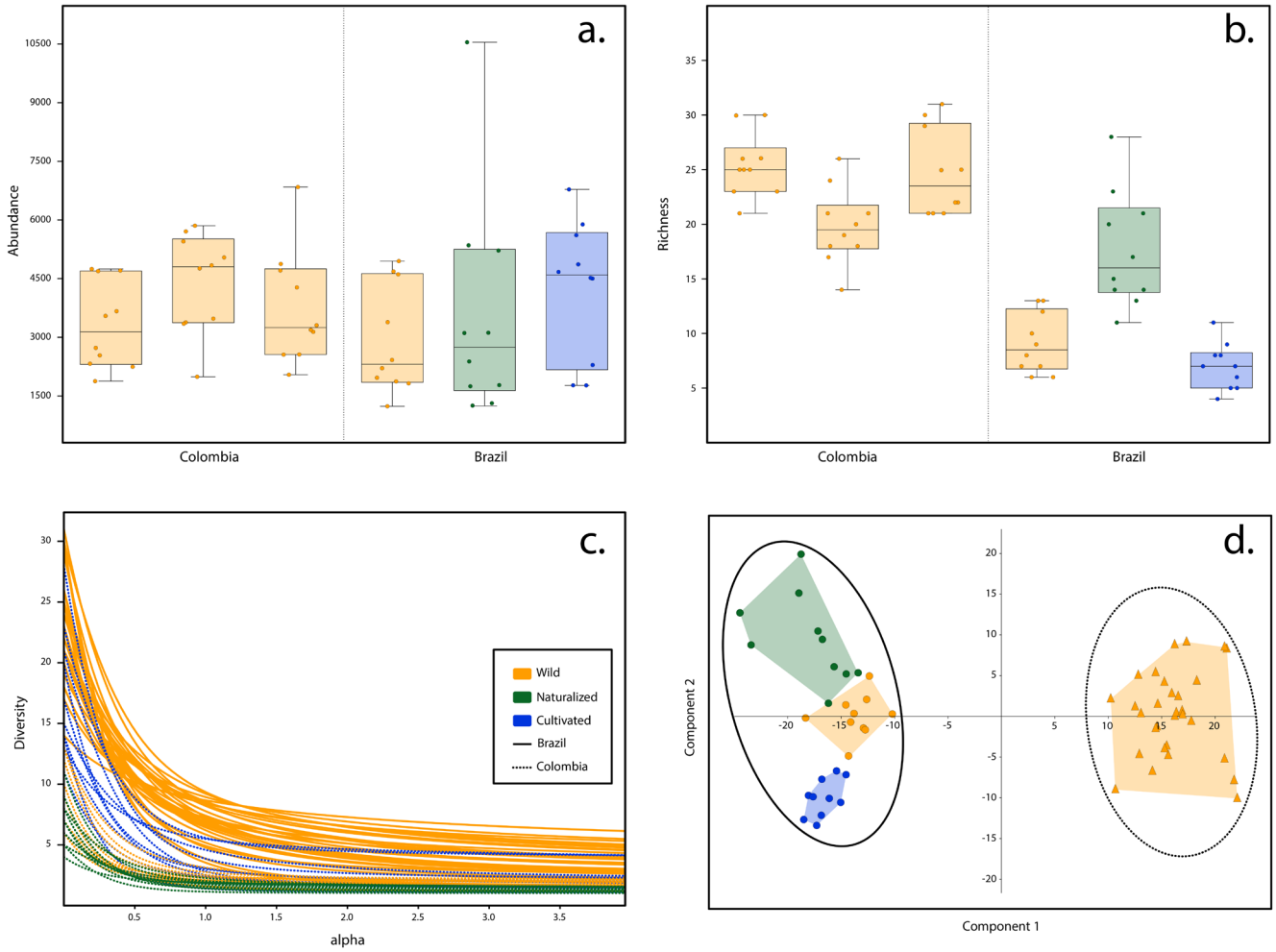


FIGURE 1 | Comparative analysis of flower-visiting insect community structure associated with different naturalisation forms of the macauba palm (*Acrocomia aculeata*, Arecaceae)—wild, naturalised, and cultivated—in Colombia and Brazil: Mean and range of (a) abundance and (b) species richness; (c) Alpha diversity profiles; and (d) PCA plot (Euclidean index, ctlr-transformed data; see Material and Methods for details), where: Circles—Brazil; triangles—Colombia. Colour coding applies to all graphs. [Colour figure can be viewed at wileyonlinelibrary.com]

forms, the species with the highest pollination importance (PI) value—and thus regarded as the main pollinators—were consistently *Andranthobius* sp.1 (PI: 14.7%–83.2%) and *Mystrops debilis* (PI: 9.2%–85.1%).

3.3 | Presence and Spatial Variation of Main Pollinators

The primary pollinators, *M. debilis* and *Andranthobius* sp.1, dominated floral visitor abundances across 31 of 32 surveyed locations in Brazil and Colombia, though their relative abundances varied regionally. In Brazil, *M. debilis* was significantly more abundant compared to *Andranthobius* sp.1 (Kruskal–Wallis $H = 16.35$, $p < 0.0001$), whereas the opposite pattern was observed in Colombia ($H = 10.37$, $p < 0.005$; Figure 2). Spatial autocorrelation analyses based on species abundance data revealed a significant spatial structure according to the Mantel test ($r = 0.299$, $p = 0.001$). However, Moran's I tests indicated no significant spatial autocorrelation for individual species (*M. debilis*: $I = 0.130$, $p = 0.072$; *Andranthobius* sp.1: $I = 0.166$, $p = 0.060$).

3.4 | Palm Host Preferences of the Primary Pollinator *Mystrops debilis*

The interactions between *Mystrops* spp. and palm species are illustrated in a bipartite network (Figure 3), which included 70,254 individuals of *Mystrops* spp. and 71 links between 25 *Mystrops* species and 53 palm species (Table S1h). Each palm species was visited by 1–3 *Mystrops* species, with a mean ± SD of 1325 ± 1658 insects per palm species. Out of 1325 potential interactions between palm species ($p = 53$) and *Mystrops* species ($I = 25$), only 71 interactions were documented, representing 5.3% of the total possible interactions. The network exhibits low specialisation, with *M. debilis* present in 34 palm species, resulting in a nested interaction pattern. The network specialisation value (H2) was 0.93, and the connectivity was 0.054, indicating a low number of interactions relative to the species richness.

The network's nestedness degree of 3.42, corroborated by the NODF index (10.92), further reflects this low specialisation. The average number of interactions per *Mystrops* species was 0.06 and per palm species 0.43. This suggests that *M. debilis* shows lower

TABLE 2 | Flower-visiting insects of the macauba palm (*Acrocomia aculeata*; Arecaceae), collected during the female phase of anthesis in populations of different naturalisation status (wild, naturalised, and cultivated) in focal locations in Brazil and Colombia (also see Table S1 for details).

	Colombia			Brazil		
	Arauca	**Casanare**	**Meta**	**Montes Claros**	**Campinas**	**Olaria**
	Wild	**Wild**	**Wild**	**Wild**	**Naturalised**	**Cultivated**
Taxon						
Diptera						
Drosophilidae						
Drosophila sp.1	2 (0.1)	2 (< 0.1)	10 (0.3)	—	—	—
Drosophila sp.2	—	—	—	1 (< 0.1)	8 (0.2)	5 (0.1)
Drosophilidae sp.	1 (< 0.1)	—	6 (0.2)	—	—	—
Coleoptera						
Carabidae						
Carabidae sp.1	—	—	4 (0.1)	—	—	—
Carabidae sp.2	—	—	—	—	1 (< 0.1)	—
Carabidae sp.3	—	—	—	1 (< 0.1)	—	—
Carabidae sp.4	—	—	—	1 (< 0.1)	—	—
Carabidae sp.5	—	—	—	—	—	12 (0.3)
Carabidae sp.6	—	—	—	—	1 (< 0.1)	—
Chrysomelidae						
Alticinae						
Alticinae sp.	2 (0.1)	—	8 (0.2)	—	—	—
Bruchinae						
Pachymerus cardo	—	—	—	—	1 (< 0.1)	0 0
Galerucinae						
Diabrotica balteata	—	—	—	1 (< 0.1)	1 (< 0.1)	—
Monolepta sp.	2 (0.1)	4 (0.1)	7 (0.2)	—	—	—
Galerucinae sp.	—	—	—	1 (< 0.1)	1 (< 0.1)	—
Curculionidae						
Curculioninae (Derelomini)						
Andranthobius sp.1	1785 (53.9)	1525 (34.8)	1432 (39.0)	885 (30.4)	1029 (28.7)	592 (13.9)
Andranthobius sp.2	210 (6.3)	503 (11.5)	387 (10.5)	—	—	—
Andranthobius sp.3	68 (2.1)	165 (3.8)	174 (4.7)	—	—	—
Celetes sp.1	2 (0.1)	5 (0.1)	11 (0.3)	1 (< 0.1)	1 (< 0.1)	1 (< 0.1)
Celetes sp.2	2 (0.1)	2 (< 0.1)	7 (0.2)	1 (< 0.1)	4 (0.1)	—
Grasidius sp.1	200 (6.0)	261 (6.0)	258 (7.0)	—	—	—
Grasidius sp.2	54 (1.6)	223 (5.1)	145 (3.9)	—	—	—
Phyllotrox sp.	267 (8.1)	552 (12.6)	400 (10.9)	61 (2.1)	159 (4.4)	19 (0.4)
Perelleschus sp.	3 (0.1)	8 (0.2)	13 (0.4)	—	—	—

(Continues)

TABLE 2 | (Continued)

	Colombia			Brazil		
	Arauca	**Casanare**	**Meta**	**Montes Claros**	**Campinas**	**Olaria**
	Wild	**Wild**	**Wild**	**Wild**	**Naturalised**	**Cultivated**
Derelomini sp.1	1 (< 0.1)	0 0	5 (0.1)	—	—	—
Derelomini sp.2	—	—	—	1 (< 0.1)	2 (0.1)	—
Derelomini sp.3	—	—	—	1 (< 0.1)	2 (0.1)	—
Derelomini sp.4	—	—	—	1 (< 0.1)	1 (< 0.1)	—
Baridinae						
Baridinae sp.1	1 (< 0.1)	7 (0.2)	5 (0.1)	—	2 (0.1)	—
Baridinae sp.2	3 (0.1)	7 (0.2)	2 (0.1)	—	2 (0.1)	—
Baridinae sp.3	—	—	—	1 (< 0.1)	2 (0.1)	—
Baridinae sp.4	—	—	—	—	1 (< 0.1)	—
Baridinae sp.5	—	—	—	—	1 (< 0.1)	—
Molytinae (Cholini)						
Cholus sp.	—	—	—	1 (< 0.1)	1 (< 0.1)	—
Biphyllidae						
Diplocoelus sp.	94 (2.8)	186 (4.2)	65 (1.8)	32 (1.1)	161 (4.5)	26 (0.6)
Melolonthidae						
Dynastinae (Cyclocephalini)						
Cyclocephala amazona	10 (0.3)	8 (0.2)	—	—	8 (0.2)	—
Cyclocephala discicollis	8 (0.2)	34 (0.8)	4 (0.1)	—	—	—
Cyclocephala forsteri	65 (2.0)	194 (4.4)	—	15 (0.5)	132 (3.79)	—
Melolonthinae						
Melolonthinae sp.1	0 0	1 (< 0.1)	3 (0.1)	—	—	—
Melolonthinae sp.2	1 (< 0.1)	—	—	—	—	—
Nitidulidae						
Nitidulinae (Mystropini)						
Mystrops debilis	389 (11.8)	505 (11.5)	410 (11.2)	1905 (65.4)	1966 (54.9)	3592 (84.1)
Mystrops sp.1	100 (3.0)	145 (3.3)	264 (7.2)	—	—	—
Mystrops sp.2	18 (0.5)	25 (0.6)	5 (0.1)	—	—	—
Mystrops sp.3	—	—	—	—	9 (0.2)	—
Nitidulinae sp.	—	7 (0.2)	3 (0.1)	—	0 0	—
Staphylinidae						
Aleocharinae (Athetini)						
Aleochara sp.	2 (0.1)	5 (0.1)	4 (0.1)	—	—	—
Athetini sp.	—	—	—	—	401 (1.1)	6 (0.1)
Tachinoporinae (Vatesini)						
Coproporus sp.	—	—	—	4 (0.1)	5 (0.1)	—
Staphylininae						

(Continues)

TABLE 2 | (Continued)

	Colombia			Brazil		
	Arauca	**Casanare**	**Meta**	**Montes Claros**	**Campinas**	**Olaria**
	Wild	**Wild**	**Wild**	**Wild**	**Naturalised**	**Cultivated**
Xanthopygus sp.1	1 (< 0.1)	5 (0.1)	12 (0.3)	—	—	—
Xanthopygus sp.2	—	—	—	—	1 (< 0.1)	—
Staphylininae sp.	—	—	—	—	1 (< 0.1)	—
Hemiptera						
Hemiptera sp.1	—	—	—	—	1 (< 0.1)	—
Hemiptera sp.2	—	—	—	—	5 (0.1)	—
Anthocoridae (Xylocorini)						
Xylocoris sp.	3 (0.1)	1 (< 0.1)	2 (0.1)	—	—	—
Hymenoptera						
Apidae						
Apis mellifera scutellata	2 (0.1)	—	5 (0.1)	1 (< 0.1)	1 (< 0.1)	—
Nogueirapis mirandula	—	—	4 (0.1)	—	—	—
Scaptotrigona sp.	1 (< 0.1)	—	—	—	—	—
Trigona ferricauda	2 (0.1)	—	3 (0.1)	—	—	—
Trigona fulviventris	2 (0.1)	—	3 (0.1)	—	—	—
Trigona silvestriana	1 (< 0.1)	—	7 (0.2)	—	—	—
Trigona sp.1	—	—	—	2 (0.1)	3 (0.1)	—
Trigona sp.2	—	—	—	1 (< 0.1)	—	—
Trigona sp.3	—	—	—	1 (< 0.1)	—	—
Trigona sp.4	—	—	—	—	—	1 (< 0.1)
Trigonisca sp.	1 (< 0.1)	—	—	—	—	—
Braconidae						
Apanteles sp.	2 (0.1)	3 (0.1)	3 (0.1)	—	—	—
Bracon sp.	1 (< 0.1)	3 (0.1)	—	—	—	—
Ceraphronidae						
Ceraphronidae sp.1	—	—	—	1 (< 0.1)	16 (0.4)	15 (0.3)
Ceraphronidae sp.2	—	—	—	—	4 (0.1)	1 (< 0.1)
Ceraphronidae sp.3	—	—	—	—	9 (0.2)	—
Formicidae						
Formicidae sp.1	—	—	—	1 (< 0.1)	—	—
Formicidae sp.2	—	—	—	1 (< 0.1)	—	—
Pseudomyrmex sp.	1 (< 0.1)	—	—	—	—	—
Halictidae						
Halictidae sp.	1 (< 0.1)	—	—	—	—	—
Vespidae						
Protopolybia acutiscutis	1 (< 0.1)	—	2 (0.1)	—	—	—

Note: Mean abundances of floral visitors per inflorescence ($n = 10$ samples per location) and their percentage of relative abundance (in parentheses) are presented. Taxa in bold were classified as effective pollinators based on their calculated Pollinator Importance (PI) values (refer to Materials and Methods section and Table 3 for details).

TABLE 3 | Percentage value indexes of pollinator importance (PI) for flower-visiting insect species with effective participation in the pollination of *Acrocomia aculeata* across populations with different naturalisation status (wild, wd; naturalised, nz; and cultivated, ct) in Brazil and Colombia.

	Colombia			Brazil		
	Arauca (wd)	Casanare (wd)	Meta (wd)	Montes Claros (wd)	Campinas (nz)	Olaria (ct)
Curculionidae, Derelomini						
[a]*Andrantobius* sp.1	83.17	74.8	77.9	31.5	74.8	77.90
Andrantobius sp.2	2.13	7.1	6	—	7.1	6
Andrantobius sp.3	0.35	1.3	1.1	—	1.3	1.1
Grasidius sp.	0.04	2.3	1.5	—	2.3	1.5
Phyllotrox sp.	1.13	2.6	0.9	0.35	2.6	0.9
Nitidulidae, Mystropini	—	—	—		—	—
[a]*Mystrops debilis*	10.45	9.2	10.1	66.1	9.2	10.1
Mystrops sp.1	0.35	0.7	1		0.7	1
Mystrops sp.2				0.02		
Biphyllidae	—	—	—		—	—
Diplocoelus sp.	0.35	1.3	0.4	0.99	1.3	0.4
Melolonthidae, Cyclocephalini	—	—	—		—	—
Cyclocephala forsteri	0.35	0.8	0.5	0.95	0.8	0.5
Others	1.69	< 0.1	0.6	0.10	< 0.1	0.6

[a]Main pollinators, or those presenting PI values > 10% across all reproductive seasons. Also refer to Carreño-Barrera et al. (2021) and Table S1 for details.

host selectivity compared to other congeneres, indicating that it is not exclusive to *A. aculeata*. *Mystrops debilis* was recorded in 34 species belonging to the following genera: *Acrocomia* (2 spp.), *Astrocaryum* (1), *Attalea* (13), *Bactris* (5), *Butia* (1), *Cocos* (1), *Syagrus* (10), and *Wettinia* (1). *Mystrops debilis* showed a marked preference for 28 of these species, as indicated by high similarity values (0.75–1). Intermediate values (0.75–0.5) were observed for associations with *Attalea maripa*, *A. pindobassu*, *Butia paraguayensis*, and *Cocos nucifera*. No association with *M. debilis* was documented in *Ceroxylon*, *Iriartea*, *Manicaria*, *Mauritia*, *Oenocarpus*, or *Socratea* (0.5–0.25) (Figure 3).

3.5 | Ecological Activity Areas of *Mystrops debilis*

The Kernel Density Estimation (KDE) analysis, based on the data gathered during this study (Table S1d), identified multiple regions across a broad latitudinal range in Colombia and Brazil as pollinator-sufficient areas concerning the presence of *M. debilis* (Figure 4).

In Brazil, optimal pollination areas were predicted in three ecoregions—the Atlantic Forest, Cerrado, and Caatinga—spanning the states of São Paulo, Minas Gerais, Bahia, Espírito Santo, Rio de Janeiro, and Mato Grosso (Figure 4a). In Colombia, these areas were concentrated in the Caribbean region, specifically in the departments of Atlántico, Cesar, Magdalena, and Sucre. Additional pollinator-sufficient regions were identified in the Magdalena Medio region, within the departments of Antioquia, Cauca, and Cundinamarca, and in the Orinoquía region, particularly in Casanare and Meta (Figure 4b).

4 | Discussion

This study highlights the contrasting patterns of species richness, abundance, and diversity of floral visitors associated with *Acrocomia aculeata* across different naturalisation forms and geographic locations in Brazil and Colombia. Wild populations consistently supported the highest species richness, while cultivated populations hosted significantly fewer species, pointing to a possible reduction in biodiversity under managed naturalisation. These findings align with previous studies showing that insect diversity and species richness suffer under land transformation pressures (Ulyshen et al. 2023). In more intact landscapes with native vegetation, floral visitor communities tend to be more diverse, benefiting from the complexity and variety of floral resources available in such habitats (Van Dulmen 2001). In wild populations of *A. aculeata*, notably in Colombia, high species richness and diverse visitor communities are likely to enhance pollination efficiency, as the presence of multiple visitors increases the probability of successful pollination (Burkle and Alarcón 2011; Beyer et al. 2022). Conversely, cultivated populations had lower richness and diversity of insect species, suggesting that these areas may rely heavily on a few key pollinators (Gaspar et al. 2022; Turo et al. 2024).

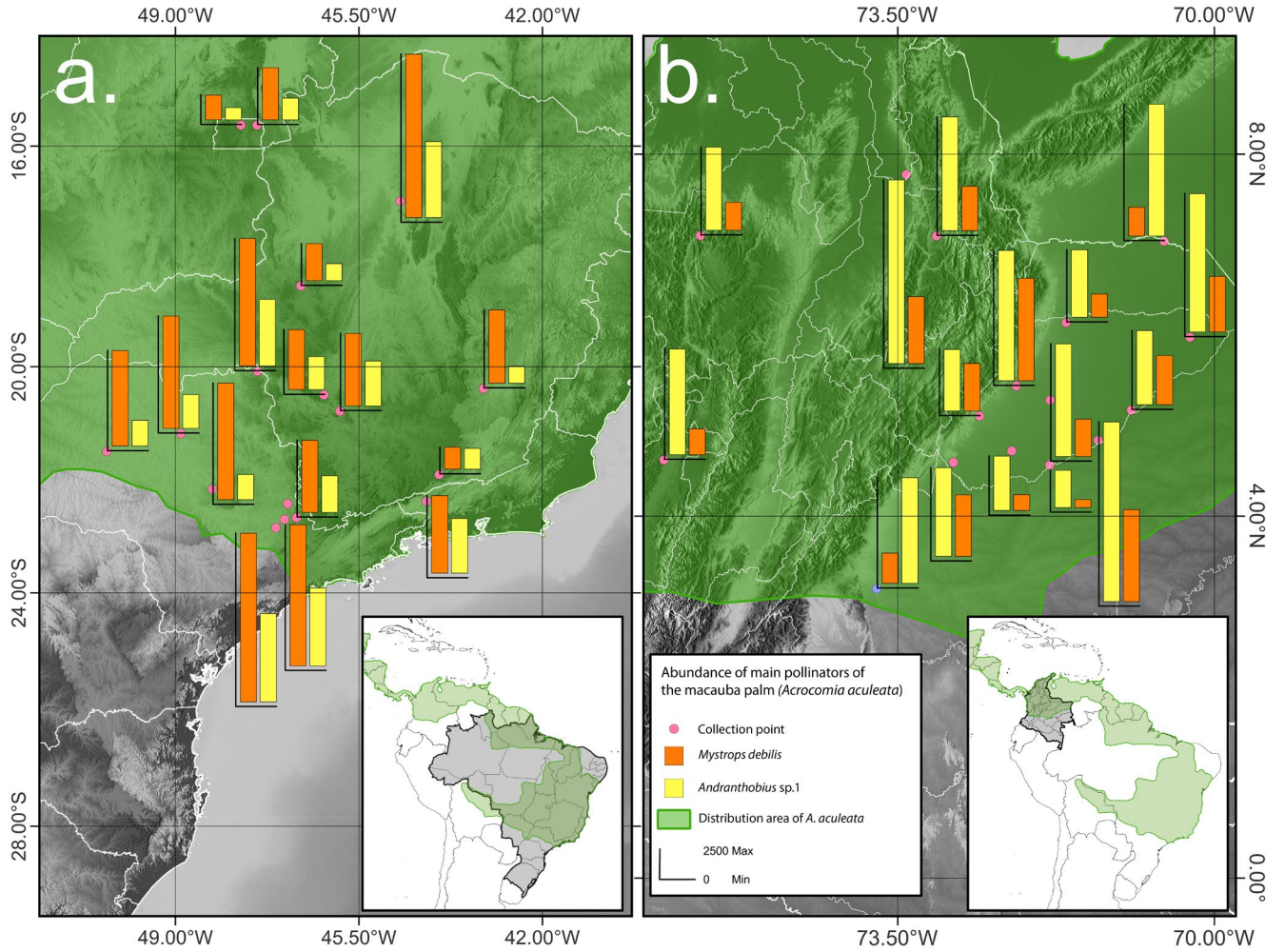


FIGURE 2 | Distribution and variation of abundances of the main pollinators of *Acrocomia aculeata*—*Mystrops debilis* (Nitidulidae, Mystropini) and *Andranthobius* sp.1 (Curculionidae, Derelomini) – in 32 localities across the species' geographic distribution range in (a) Brazil and (b) Colombia. [Colour figure can be viewed at wileyonlinelibrary.com]

Perhaps the most compelling insight from our study highlights functional redundancy's role in stabilising pollination services for *A. aculeata* within cultivated populations. Despite reduced floral visitor richness, the persistent dominance of *Andranthobius* sp.1 and *Mystrops debilis* as primary pollinators suggests these species may compensate for diversity loss in human-modified landscapes. However, since pollination success (e.g., fruit set) was not directly quantified, further work is needed to assess how reduced pollinator richness impacts reproductive outcomes—a critical consideration for conservation strategies prioritising either diversity preservation or keystone species management.

Notably, the consistent presence of pollinators across wild, naturalised, and cultivated populations of *A. aculeata* mirrors patterns observed in other palms, such as *E. guineensis*, where specialised pollinators (*Elaeidobius* spp.) support reproduction globally (Haran et al. 2020; Li et al. 2019). PI scores and abundance data indicate a clear regional shift in pollinator dominance: *Andranthobius* spp. (more specifically *Andranthobius* sp.1) predominate in wild populations, whereas *M. debilis* is more abundant in cultivated contexts. Spatial autocorrelation analyses using raw species data revealed significant geographic structuring for pollinator communities overall, but no significant spatial autocorrelation at the species level was evident. This pattern suggests geographic factors partially influence the distribution of *M. debilis*, while the lack of spatial structure for *Andranthobius* sp.1 may highlight its ecological specialisation. Future research should incorporate broader biogeographic sampling and integrate spatial analyses with direct pollination metrics to better understand ecological versus geographic influences. Such efforts will elucidate how functional redundancy and ecological specialisation together maintain pollination stability across varying landscapes.

The relationship between neotropical palms and their beetle pollinators, particularly mystropine sap beetles and derelomine weevils, highlights a strong mutualistic dependence evident across several palm genera, such as *Attalea*, *Astrocaryum*, *Ceroxylon*, *Chryosophila*, *Iriartea*, *Mauritia*, *Socratea*, and Wettinia (Núñez 2014; Henderson 2024). These beetles often rely heavily on palms as obligate pollen-feeders, displaying distinct adaptations to palm floral structures and cues, including scent and flowering timing, which facilitate their reproductive behaviours (Henderson 1986; Silberbauer-Gottsberger 1990). Although specificity varies among interactions, this close ecological association often ensures stable pollination even under

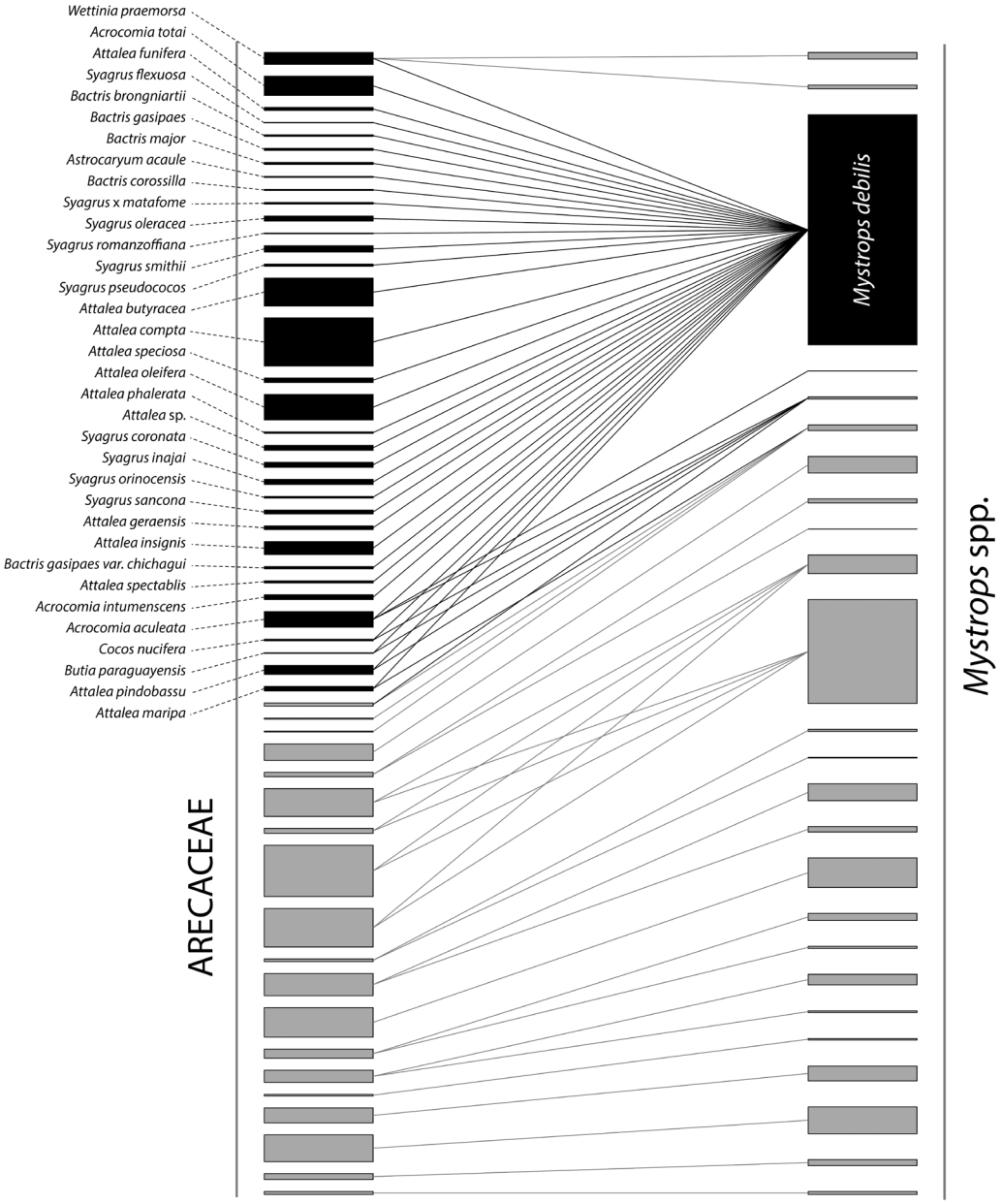


FIGURE 3 | Bipartite interaction network of 53 palm species of the genera *Acrocomia*, *Attalea*, *Bactris*, *Butia, Ceroxylon, Cocos, Iriartea, Mauritia, Manicaria, Oenocarpus*, *Socratea*, *Syagrus*, and *Wettinia*, and 25 species of the genus *Mystrops* (Nitidulidae, Mystropini) in Brazil and Colombia.

conditions of low overall insect diversity. Moreover, considering potential species-level misidentifications in previous studies, the presence and ecological roles of specific beetle species, such as *M. debilis*, across these palm genera should not be dismissed without thorough taxonomic verification. For instance, *M. dalmasi*, a primary pollinator of *Mauritia flexuosa* in the Orinoquia region of Colombia, and specific weevil genera (*Derelomus*, *Phyllotrox*, and *Anchylorhynchus*) in *Oenocarpus bataua*, maintain effective pollination under low diversity conditions when pollination systems are specialised (i.e., reliant on co-occurring partners) (Núñez A. et al. 2015; Núñez and Carreño 2017; Aguinda and Peñuela Mora 2024).

However, although Carreño-Barrera et al. (2021) already demonstrated that pollination in *A. aculeata* was primarily mediated by *M. debilis* and *Andranthobius* sp.1, they also showed that co-pollinators contribute to enhancing pollination efficiency in *A. aculeata*. In Colombian wild populations, co-pollinators play a more significant role, with contributions reaching up to 16%; in contrast, reduced co-pollinator involvement is evident in naturalised and cultivated populations in Brazil, recorded at 2.4% and 0.2% respectively. These results indicate that although *M. debilis* and *Andranthobius* sp.1 serve as primary pollinators, co-pollinators might also have an important role in maximising fruit yield in *A. aculeata*, which would align with the idea that diverse pollinator communities enhance plant reproductive success (Albrecht et al. 2012; Simpson et al. 2022).

In the scope of pollinator management for optimal *A. aculeata* productivity, *Mystrops debilis* exhibits unique characteristics compared to other pollinating species due to its adaptability and ability to utilise the floral resources of various palm species. This adaptability is

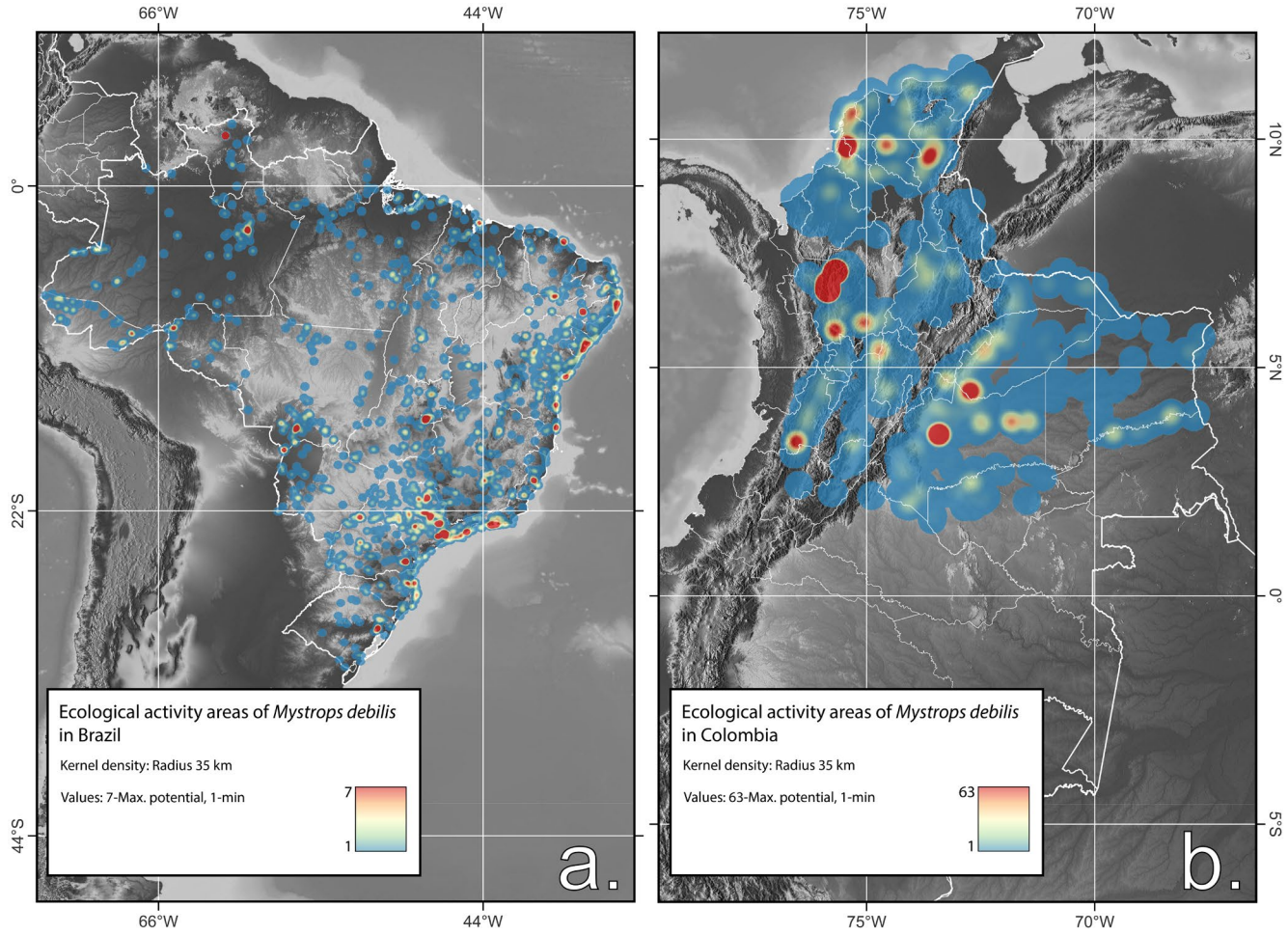


FIGURE 4 | Kernel Density Estimation (KDE) plots showing the locations where the pollinator *Mystrops debilis* (Nitidulidae, Mystropini) has been recorded in association with *Acrocomia aculeata* (Arecaceae). The plots include data from both collections and literature records (refer to Table S1d for details). The KDE plots represent the actual and predicted densities of *M. debilis*, with colour gradients indicating density levels: Blue to green represents low density, yellow to orange represents moderate density, and red indicates high density. [Colour figure can be viewed at wileyonlinelibrary.com]

particularly evident in its associations with over 30 palm species, but not without a marked preference for certain genera such as *Attalea*, *Bactris*, and especially *Syagrus*. Studies on palm pollination have documented the associations between *M. debilis*, *Andranthobius* weevils, and these palm genera (Núñez 2014; Núñez and Carreño 2016; De Medeiros et al. 2019; Brieva-Oviedo et al. 2020). The absence of *M. debilis* on other palm genera, like *Ceroxylon*, *Wettinia*, *Mauritia*, *Oenocarpus*, and *Socratea*, underscores its strong specificity within the palm family. This specificity can vary by genus—such as *Mystrops rotundula* with *Ceroxylon* palms (Carreño-Barrera et al. 2020)—or even by species, as seen with *Attalea butyracea*, *Attalea insignis*, and *Attalea maripa*, which each have unique, exclusive pollinators (Núñez 2014).

Mystrops debilis demonstrates substantial ecological plasticity, enabling its presence across diverse landscapes and a broad latitudinal range in Brazil and Colombia, thus supporting multiple regions suitable for effective pollination of *A. aculeata*. In Brazil, optimal pollination areas within the Atlantic Forest, Cerrado, and Caatinga illustrate *M. debilis*' adaptability across distinct ecoregions. This adaptability likely contributes to stable pollination services despite varying climatic and vegetative conditions.

In Colombia, the clustering of pollinator-sufficient areas within the Caribbean, Magdalena Medio, and Orinoquía regions highlights distinct biogeographical patterns linked to *M. debilis*' ecological flexibility. The concentration of suitable habitats in these Colombian departments indicates favourable ecological conditions, likely associated with specific climatic and floral characteristics. Such spatial alignment suggests a potentially significant role for *M. debilis* within pollination networks of *A. aculeata*, especially in areas where its distribution overlaps with the natural or cultivated range of the palm. However, direct studies assessing pollination efficiency and reproductive success are required to confirm its ecological importance. Identifying these spatial patterns provides a valuable foundation for targeted conservation initiatives and pollination management strategies, particularly in response to increasing pressures from land-use changes and habitat fragmentation.

Since *Acrocomia aculeata* is a seasonal species, it cannot sustain its pollinators year-round until the next reproductive event. The ability of *M. debilis* to take refuge on other palm species provides a crucial insight for agriculture companies as they expand macauba palm plantations over the next decade. For

effective pollinator support, macauba plantations should ideally be supplemented with other palm species, such as *Syagrus oleracea*, *S. coronata*, and *S. romanzoffiana*. We have already recorded *M. debilis* populations of 800 to 1500 individuals on these palms' inflorescences (J. Carreño-Barrera, A.C.D. Maia & Nunez-Avellaneda, unpublished data), which could allow *M. debilis* populations to persist between *A. aculeata* flowering events, thereby ensuring consistent fruit production through interspecific facilitation (Carreño-Barrera et al. 2020).

Based on this, landscape management strategies, such as maintaining forest corridors and preserving native palm species near commercial crops, will be critical for sustaining pollinator populations. This is especially relevant given the planned expansion of macauba palm cultivation in the Brazilian Cerrado region for biofuel production (Vargas-Carpintero et al. 2022). As macauba palm cultivation increases, understanding the dynamics of floral visitor communities and the role of key pollinators will be essential for optimising crop yields and ensuring the long-term viability of these agroecosystems.

In conclusion, the successful pollination of *Acrocomia aculeata* across its range hinges primarily on a few key pollinators, particularly *Mystrops debilis* and *Andranthobius* sp.1. While species richness and diversity of floral visitors vary across naturalisation forms and biogeographic regions, pollination success appears more closely tied to the abundance of these essential pollinators than to overall diversity. Our KDE analysis offers valuable insights into the spatial distribution of *M. debilis*, underscoring the importance of conserving native vegetation and alternative floral resources near macauba palm plantations to support these pollinators. This study, as the first to propose crop expansion areas based on critical pollinator management factors, will serve as an essential reference for research on domesticated Neotropical palms. By integrating considerations of host palm dynamics, pollinator distribution, biological traits, and pollinator significance, it challenges the traditional approach of prioritising agronomic factors and relegating pollination to a secondary concern. Given that palms often require several years to mature and produce fruit, overlooking pollinator availability and ecosystem interactions could pose significant risks to crop productivity in the long term. Therefore, future efforts to expand *A. aculeata* cultivation must address the ecological needs of its pollinators to ensure sustainable fruit production and yield stability.

Author Contributions

Javier Carreño-Barrera: conceptualisation, data curation, investigation, original draft, formal analysis, visualisation, methodology, review, and writing. **Artur Campos Dália Maia:** conceptualisation, investigation, data curation, original draft, editing, review, formal analysis, methodology, and writing. **Carlos Augusto Colombo:** resources, review, formal analysis, visualisation, and writing. **Luis Alberto Nuñez-Avellaneda:** conceptualisation, resources, methodology, data curation, formal analysis, investigation, original draft, visualisation, review, validation, editing, and writing.

Acknowledgements

This work was supported by the São Paulo Research Foundation (FAPESP) [grant number 2014/23591-7] and the Coordination for the Improvement of Higher Education Personnel (CAPES). We thank CAPES for the doctoral scholarship (process 88882.444190/2019-01) and the Center for Genetic Resources of the Agronomic Institute (IAC) for logistical support. The collections conducted in Brazil and Colombia are part of the doctoral thesis project "Evaluation of the Biological, Ecological, and Functional Aspects of Floral Visitors and Pollinators in Natural and Cultivated Populations of the Macaúba Palm in Brazil and Colombia (*Acrocomia aculeata* Jacq. Lodd ex Mart.)" and the ongoing project titled "Generation of Scientific Bases on Pollinating Insects of Acrocomia aculeata (Arecaceae) as a Contribution to the Domestication, Increased Productivity, and Sustainability of Crops of a High-Impact Oil Palm in the Colombian Orinoquia," code C03-F02-013-2022. We also acknowledge the assistance of ChatGPT, an AI language model by OpenAI, for English review of orthography, grammar, and style. No direct funding was received for the research, authorship, or publication of this article. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors confirm that the data supporting the findings of this study are available within the article and its Supporting Information. The raw data underlying these findings have also been deposited in Dryad and are publicly accessible under DOI 10.5061/dryad.4xgxd25n6. These data can be retrieved directly at https://doi.org/10.5061/dryad.4xgxd25n6.

References

Aguinda, J. G. T., and M. C. Peñuela Mora. 2024. "Diversity of Visitors to the Flowers of Two Palm Species of the Genus *Oenocarpus* in the Province of Napo, Ecuador." *Trees* 38: 915–926.

Albrecht, M., B. Schmid, Y. Hautier, and C. B. Müller. 2012. "Diverse Pollinator Communities Enhance Plant Reproductive Success." *Proceedings of the Royal Society B: Biological Sciences* 279: 4845–4852.

Alfaro-Solís, J. D., A. Montoya-Arroyo, V. M. Jiménez, et al. 2020. "*Acrocomia aculeata* Fruits From Three Regions in Costa Rica: An Assessment of Biometric Parameters, Oil Content and Oil Fatty Acid Composition to Evaluate Industrial Potential." *Agroforestry Systems* 94: 1913–1927.

Anderson, A. B., W. L. Overal, and A. Henderson. 1988. "Pollination Ecology of a Forest-Dominant Palm (*Orbignya phalerata* Mart.) in Northern Brazil." *Biotropica* 20: 192–205.

Berton, L. H., J. A. de Azevedo Filho, W. J. Siqueira, W. J. Siqueira, and C. Colombo. 2013. "Seed Germination and Estimates of Genetic Parameters of Promising Macaw Palm (*Acrocomia aculeata*) Progenies for Biofuel Production." *Industrial Crop and Prodution* 51: 258–266.

Beyer, N., D. Gabriel, and C. Westphal. 2022. "Landscape Composition Modifies Pollinator Densities, Foraging Behavior and Yield Formation in Faba Beans." *Basic and Applied Ecology* 61: 30–40.

Blanche, R., and S. A. Cunningham. 2005. "Rain Forest Provides Pollinating Beetles for Atemoya Crops." *Journal of Economic Entomology* 98: 1193–1201.

Borges, R. C., R. M. Brito, V. L. Imperatriz-Fonseca, and T. C. Giannini. 2020. "The Value of Crop Production and Pollination Services in the Eastern Amazon." *Neotropical Entomology* 49: 545–556.

Bowman, A. W., and A. Azzalini. 1997. *Applied Smoothing Techniques for Data Analysis: The Kernel Approach With S-Plus Illustrations (Vol. 18)*. Oxford University Press.

Brieva-Oviedo, E., A. C. D. Maia, and L. A. Núñez-Avellaneda. 2020. "Pollination of *Bactris guineensis* (Arecaceae), a Potential Economically Exploitable Fruit Palm From the Colombian Caribbean." *Flora* 269: 151628.

Brito, A. C. 2013. *Biologia reprodutiva de macaúba: Floração, polinizadores, frutificação e conservação de pólen*. PhD thesis, Universidade Federal de Viçosa.

Brückner, A., and M. Heethoff. 2017. "A Chemo-Ecologists' Practical Guide to Compositional Data Analysis." *Chemoecology* 27: 33–46.

Burkle, L. A., and R. Alarcón. 2011. "The Future of Plant–Pollinator Diversity: Understanding Interaction Networks Across Time, Space, and Global Change." *American Journal of Botany* 98: 528–538.

Carreño-Barrera, J., A. C. D. Maia, C. Colombo, and L. A. Núñez-Avellaneda. 2021. "Co-Pollination, Fidelity and Efficiency Over Time: Small Beetles and the Reproductive Success of *Acrocomia aculeata* (Arecaceae) in the Colombian Orinoquia." *Botanical Letters* 168: 395–407.

Carreño-Barrera, J., L. A. Núñez-Avellaneda, M. J. Sanín, and A. C. D. Maia. 2020. "Orchestrated Flowering and Interspecific Facilitation: Key Factors in the Maintenance of the Main Pollinator of Coexisting Threatened Species of Andean Wax Palms (*Ceroxylon* spp.)." *Annals of the Missouri Botanical Garden* 105: 281–299.

Ciconini, G., S. P. Favaro, R. Roscoe, et al. 2013. "Biometry and Oil Contents of *Acrocomia aculeata* Fruits From the Cerrados and Pantanal Biomes in Mato Grosso Do Sul, Brazil." *Industrial Crop Production* 45: 208–214.

Colombo, C. A., L. H. C. Berton, B. G. Diaz, and R. A. Ferrari. 2018. "Macaúba: A Promising Tropical Palm for the Production of Vegetable Oil." *OCL* 25: D108.

Couto, E. G. D. O., J. Morales-Marroquin, A. Alves-Pereira, et al. 2024. "Genome-Wide Association Insights Into the Genomic Regions Controlling Oil Production Traits in *Acrocomia aculeata* (Neotropical Native Palm)." *bioRxiv*. https://doi.org/10.1101/2024.01.17.576138.

de Carvalho Lopes, D., A. J. S. Neto, A. A. Mendes, and D. T. V. Pereira. 2013. "Economic Feasibility of Biodiesel Production From Macauba in Brazil." *Energy Economics* 40: 819–824. https://doi.org/10.1016/j.eneco.2013.10.003.

de Lima, N. E., A. A. Carvalho, A. W. Meerow, and M. H. Manfrin. 2018. "A Review of the Palm Genus *Acrocomia*: Neotropical Green Gold." *Organisms Diversity & Evolution* 18, no. 2: 151–161. https://doi.org/10.1007/s13127-018-0362-x.

De Medeiros, B. A., L. A. Núñez-Avellaneda, A. M. Hernandez, and B. D. Farrell. 2019. "Flower Visitors of the Licuri Palm (*Syagrus coronata*): Brood Pollinators Coexist With a Diverse Community of Antagonists and Mutualists." *Biological Journal of the Linnean Society* 126: 666–687.

Díaz, B. G., M. I. Zucchi, A. Alves-Pereira, et al. 2021. "Genome-Wide SNP Analysis to Assess the Genetic Population Structure and Diversity of *Acrocomia* Species." *PLoS One* 16: e0241025.

Dormann, C., B. Gruber, and J. Fruend. 2008. "Introducing the Bipartite Package: Analysing Ecological Networks." *R News* 8: 8–11.

Egan, P. A., L. S. Adler, R. E. Irwin, I. W. Farrell, E. C. Palmer-Young, and P. C. Stevenson. 2018. "Crop Domestication Alters Floral Reward Chemistry With Potential Consequences for Pollinator Health." *Frontiers in Plant Science* 9: 1357.

Egan, P. A., L. V. Dicks, H. M. Hokkanen, and J. A. Stenberg. 2020. "Delivering Integrated Pest and Pollinator Management (IPPM)." *Trends in Plant Science* 25: 577–589.

Evaristo, A. B., D. C. Martino, A. H. Ferrarez, D. B. Donato, A. D. C. O. Carneiro, and J. A. S. Grossi. 2016. "Potencial energético dos resíduos do fruto da macaúba e sua utilização na produção de carvão vegetal." *Ciência Florestal* 26: 571–577.

Faoro, I. D., and A. I. Orth. 2015. "Occurrence of Melitophilly and Cantarophilly on Pear Trees Pollination in Brazil." *Acta Horticulturae* 1094: 269–274. https://doi.org/10.17660/ActaHortic.2015.1094.34.

Farias Neto, J. T. D., C. R. Clement, and M. D. V. D. Resende. 2013. "Estimativas de parâmetros genéticos e ganho de seleção para produção de frutos em progênies de polinização aberta de pupunheira no Estado do Pará, Brasil." *Bragantia* 72: 122–126.

Fava, W. S., W. da Silva Covre, and M. R. Sigrist. 2011. "*Attalea phalerata* and *Bactris glaucescens* (Arecaceae, Arecoideae): Phenology and Pollination Ecology in the Pantanal, Brazil." *Flora* 206: 575–584.

Gaspar, H., J. Loureiro, H. Castro, et al. 2022. "Impact of Local Practices and Landscape on the Diversity and Abundance of Pollinators in an Insect-Dependent Crop." *Agriculture, Ecosystems & Environment* 326: 107804.

Gintoron, C. S., M. A. Mohammed, S. N. Sazali, et al. 2023. "Factors Affecting Pollination and Pollinators in Oil Palm Plantations: A Review with an Emphasis on the *Elaeidobius kamerunicus* Weevil (Coleoptera: Curculionidae)." *Insects* 14, no. 5: 454.

Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. "Bandwidth Selection for Fixed-Kernel Analysis of Animal Utilization Distributions." *Journal of Wildlife Management* 70: 1334–1344.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. "PAST: Paleontological Statistics Software Package for Education and Data Analysis." *Palaeontologica Electronica* 4: 1–9.

Haran, J., L. Beaudoin-Ollivier, L. Benoit, and G. Kuschel. 2020. "Revision of the Palm-Pollinating Weevil Genus *Elaeidobius* Kuschel, 1952 (Curculionidae, Curculioninae, Derelomini) With Descriptions of Two New Species." *European Journal of Taxonomy* 684: 1–32.

Harper, J. L. 1977. *Population Biology of Plants*. Academic Press.

Henderson, A. 1986. "A Review of Pollination Studies in the Palmae." *Botanical Review* 52: 221–259.

Henderson, A. 1988. "Pollination Biology of Economically Important Palms." *Advances in Economic Botany* 6: 36–41.

Henderson, A. 2024. "Pollination Systems of Palms (Arecaceae)." *Journal of Pollination Ecology* 35: 144–248.

INOCAS. 2021. "Innovative Oil and Carbon Solutions. [Macauba Project Brazil]." http://www.inocas.com/projects.html.

Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM). 2024. "Metereological Data." http://dhime.ideam.gov.co/atencionciudadano/.

Khorsand Rosa, R., and S. Koptur. 2013. "New Findings on the Pollination Biology of *Mauritia flexuosa* (Arecaceae) in Roraima, Brazil: Linking Dioecy, Wind, and Habitat." *American Journal of Botany* 100: 613–621.

Kirejtshuk, A. G., and G. Couturier. 2010. "Sap Beetles of the Tribe Mystropini (Coleoptera: Nitidulidae) Associated With South American Palm Inflorescences." *Annales de la Societe Entomologique de France* 46: 367–421.

Kishore, K., A. K. Shukla, N. Babu, D. N. Sarangi, and S. Patanayak. 2012. "Pollination Biology of *Annona squamosa* L. (Annonaceae): Evidence for Pollination Syndrome." *Scientia Horticulturae* 144: 212–217.

Küchmeister, H., A. Webber, I. Silberbauer-Gottsberger, and G. Gottsberger. 1998. "A polinização e sua relação com a termogênese em espécies de Arecaceae e Annonaceae da Amazônia Central." *Acta Amazonica* 28: 217–245.

Labarca, M. V., and Z. Narváez. 2009. "Identificación y fluctuación poblacional de insectos polinizadores en palma aceitera (*Elaeis guineensis* Jacquin) en el sur del lago de Maracaibo, estado Zulia, Venezuela." *Revista de la Facultad de Agronomía* 26: 305–324.

Lattaro, L. H., and D. T. Malerbo-Souza. 2006. "Polinização entomófila em abóbora caipira, *Cucurbita mixta* (Curcubitaceae)." *Acta Scientiarum Agronomy* 28: 563–568.

Li, K., T. Tscharntke, B. Saintes, D. Buchori, and I. Grass. 2019. "Critical Factors Limiting Pollination Success in Oil Palm: A Systematic Review." *Agriculture, Ecosystems & Environment* 280: 152–160.

Malerbo-Souza, D. T., V. D. A. A. de Toledo, A. C. Stuchi, and J. D. O. A. de Toledo. 2001. "Estudo sobre a polinização do quiabeiro, *Abelmoschus esculentus* (L.) Moench." *Acta Scientiarum* 23: 1281–1285.

Malerbo-Souza, D. T., A. M. Tadeu, P. C. Bettini, and V. D. A. A. de Toledo. 1999. "Importância dos insetos na produção de melancia (*Citrullus lanatus* Thunb.)—Cucurbitaceae." *Acta Scientiarum* 21: 579–583.

Maria, E., E. Budiman, and M. Taruk. 2020. "Measure Distance Locating Nearest Public Facilities Using Haversine and Euclidean Methods." *Journal of Physics: Conference Series* 1450: 12080.

Maués, M. M., L. A. Souza, and R. Miyanaga. 2000. *Insetos polinizadores do cupuaçuzeiro (Theobroma grandiflorum Willd. Ex. Sprengel) no Estado da Pará, Brasil*. Embrapa Amazonia Oriental, Circular Técnica Vol. 12.

Meléndez, M. R., and W. P. Ponce. 2016. "Polinização em palma azeiteira *Elaeis guineensis*, *E. oleifera* e seus híbridos (OxG), na América Tropical." *Pesquisa Agropecuária Tropical* 46: 102–110.

Montoya, S. G., S. Y. Motoike, K. N. Kuki, and A. D. Couto. 2016. "Fruit Development, Growth, and Stored Reserves in Macauba Palm (*Acrocomia aculeata*), an Alternative Bioenergy Crop." *Planta* 244: 927–938.

Núñez A., L. A., C. Isaza, and G. Galeano. 2015. "Ecología de la polinización de tres especies de *Oenocarpus* (Arecaceae) simpátricas en la Amazonia Colombiana." *Revista de Biología Tropical* 63: 35–55.

Núñez, L. A. 2014. *Patrones de asociación entre insectos polinizadores y palmas silvestres en Colombia con énfasis en palmas de importancia económica*. PhD thesis, Universidad Nacional de Colombia.

Núñez, L. A., and J. Carreño. 2016. *Análisis espacial de los visitantes florales y polinizadores del moriche (Mauritia flexuosa: Arecaceae) en Colombia*. XIV. Morichales, cananguchales y otros palmares inundables de Suramérica.

Núñez, L. A., and J. Carreño. 2017. "Análisis espacial de los visitantes florales y polinizadores del Moriche (*Mauritia flexuosa*: Arecaceae) en Colombia." In *XIV: Morichales, cananguchales y otros palmares de Suramérica Parte II. Serie Editorial Recursos Hidrobiológicos y pesqueros Continentales de Colombia*, edited by C. A. Lasso, G. Colonello, and M. Moraes, 131–155. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Núñez-Avellaneda, L. A., and J. Carreño-Barrera. 2013. "Biologia reproductiva de *Mauritia flexuosa* en Casanare, Orinoquia Colombiana." In *VII. Morichales y cananguchales de la Orinoquia y Amazonia: Colombia—Venezuela. Parte I. Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia*, edited by C. A. Lasso, A. Rial, and V. González-B, 119–151. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Núñez-Avellaneda, L. A., and R. Rojas-Robles. 2008. "Biología reproductiva y ecología de la polinización de la palma milpesos *Oenocarpus bataua* en los Andes colombianos." *Caldasia* 30: 101–125.

Oliveira, M. S. P., G. Couturier, and P. Beserra. 2003. "Biologia da polinização da palmeira tucumã (*Astrocaryum vulgare* Mart.) em Belém, Pará, Brasil." *Acta Botânica Brasílica* 17: 343–353.

QGIS. 2024. *QGIS Geographic Information System*. QGIS Association. http://www.qgis.org.

Ratter, J. A., J. F. Ribeiro, and S. Bridgewater. 1997. "The Brazilian Cerrado Vegetation and Threats to Its Biodiversity." *Annals of Botany* 80: 223–230.

Resende, R. T., K. N. Kuki, T. R. Correa, et al. 2020. "Data-Based Agroecological Zoning of *Acrocomia aculeata*: GIS Modeling and Ecophysiological Aspects Into a Brazilian Representative Occurrence Area." *Industrial Crops and Products* 154: 112749.

Richardson, D. M., and P. Pyšek. 2012. "Naturalization of Introduced Plants: Ecological Drivers of Biogeographical Patterns." *New Phytologist* 196: 383–396.

Richardson, D. M., P. Pyšek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. "Naturalization and Invasion of Alien Plants: Concepts and Definitions." *Diversity and Distributions* 6: 93–107.

RStudio Team. 2020. "RStudio: Integrated development for R." http://www.rstudio.com/.

Santos Júnior, J. F., V. Spacki, F. P. Santana, D. C. Costa, and G. M. A. C. Lorenzi. 2012. *Bocaiuva, macaúva, macaúba, bocajá: Técnicas e dicas de aproveitamento*. ECOA.

Scariot, A., E. Lleras, and J. D. Hay. 1995. "Flowering and Fruiting Phenologies of the Palm *Acrocomia aculeata*: Patterns and Consequences." *Biotropica* 27: 168–173.

Scariot, A. O., E. Lleras, and J. D. Hay. 1991. "Reproductive Biology of the Palm *Acrocomia aculeata* in Central Brazil." *Biotropica* 23: 12–22. https://doi.org/10.2307/2388683.

Sierra-Márquez, J., L. Sierra-Márquez, and J. Olivero-Verbel. 2017. "Potencial económico de la palma aceitera (*Elaeis guineensis* Jacq)." *Agronomía Mesoamericana* 28: 523–534.

Silberbauer-Gottsberger, I. 1990. "Pollination and Evolution in Palms." *Phyton* 30, no. 2: 213–233.

Silverman, B. W. 1984. "Spline Smoothing: The Equivalent Variable Kernel Method." *Annals of Statistics* 12: 898–916.

Simpson, D. T., L. R. Weinman, M. A. Genung, M. Roswell, M. MacLeod, and R. Winfree. 2022. "Many Bee Species, Including Rare Species, Are Important for Function of Entire Plant–Pollinator Networks." *Proceedings of the Royal Society B* 289: 20212689.

Storti, E. F. 1993. "Biologia floral de Mauritia flexuosa Lin. fil, na região de Manaus, AM, Brasil." *Acta Amazonica* 23: 371–381.

Syed, R. A. 1979. "Studies on Oil Palm Pollination by Insects." *Bulletin of Entomological Research* 69: 213–224.

Turo, K. J., J. R. Reilly, T. P. Fijen, A. Magrach, and R. Winfree. 2024. "Insufficient Pollinator Visitation Often Limits Yield in Crop Systems Worldwide." *Nature Ecology & Evolution* 8: 1612–1622.

Ulyshen, M., K. R. Urban-Mead, J. B. Dorey, and J. W. Rivers. 2023. "Forests Are Critically Important to Global Pollinator Diversity and Enhance Pollination in Adjacent Crops." *Biological Reviews* 98: 1118–1141.

Van Dulmen, A. 2001. "Pollination and Phenology of Flowers in the Canopy of Two Contrasting Rain Forest Types in Amazonia, Colombia." *Plant Ecology* 158: 73–85.

Vancine, M. H., R. L. Muylaert, B. B. Niebuhr, et al. 2024. "The Atlantic Forest of South America: Spatiotemporal Dynamics of the Vegetation and Implications for Conservation." *Biological Conservation* 291: 110499. https://doi.org/10.1016/j.biocon.2024.110499.

Vargas-Carpintero, R., T. Hilger, K. Tiede, et al. 2022. "A Collaborative, Systems Approach for the Development of Biomass-Based Value Webs: The Case of the *Acrocomia* Palm." *Land* 11: 1748.

Vianna, S. A. 2017. "A New Species of *Acrocomia* (Arecaceae) From Central Brazil." *Phytotaxa* 314: 45–54. https://doi.org/10.11646/phytotaxa.314.1.2.

Yousefi, M., A. S. M. Rafie, S. Abd Aziz, and S. Azrad. 2020. "Introduction of Current Pollination Techniques and Factors Affecting Pollination Effectiveness by *Elaeidobius kamerunicus* in Oil Palm Plantations on Regional and Global Scale: A Review." *South African Journal of Botany* 132: 171–179.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.