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Mangrove Pollinator Functional Diversity Decreases With Patch Size and Landscape Anthropization

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ABSTRACT

The impact of land use changes on pollinator diversity can vary depending on factors such as the size of remaining natural habitat patches, the type and intensity of anthropogenic activities, and the functional composition of pollinator communities. This understanding is particularly crucial for mangrove ecosystems, which are critically endangered by human activities and prioritized in global conservation strategies. This study investigates how anthropization affects mangrove pollinator diversity by examining how pollinators with different functional traits respond to variations in mangrove patch size and anthropogenic changes in the surrounding landscape matrix. We found that overall pollinator abundance, richness, and diversity increased in smaller mangrove patches, potentially helping to mitigate negative effects such as inbreeding and genetic drift—common in naturally patchy and isolated mangrove populations. However, these pollinator metrics declined with increasing landscape anthropization, with notably lower values in urbanized landscapes compared to agricultural ones, despite the smaller patch sizes in more anthropized settings. This negative trend was consistent across pollinators with varying traits, though the magnitude of the effect differed among pollinator groups. Ground-nesting and exposed-nesting pollinators were most influenced by patch size, while lepidopterans and wasps, as well as species with either very small or large body sizes, solitary behavior, and nesting in exposed sites or cavities, were most affected by landscape anthropization. Conservation and management efforts should prioritize habitat provisioning for these most impacted groups to support mangrove ecosystem resilience.

RESUMEN

El impacto de los cambios en el uso del suelo sobre la diversidad de polinizadores puede variar según factores como el tamaño de los fragmentos remanentes de hábitat natural, el tipo e intensidad de las actividades antropogénicas y la composición funcional de las comunidades de polinizadores. Esta comprensión es particularmente crucial para los ecosistemas de manglar, que están críticamente amenazados por actividades humanas y son una prioridad en las estrategias globales de conservación. Este estudio investiga cómo la antropización afecta la diversidad de polinizadores en manglares, examinando cómo los polinizadores

con diferentes rasgos funcionales responden a las variaciones en el tamaño de los fragmentos de manglar y a los cambios antropogénicos en el paisaje circundante. Encontramos que la abundancia, riqueza y diversidad general de polinizadores aumentó en fragmentos de manglar más pequeños, lo que podría ayudar a mitigar efectos negativos como la endogamia y la deriva genética, comunes en poblaciones de manglar fragmentadas y aisladas. Sin embargo, estas métricas de los polinizadores disminuyeron con el aumento de la antropización del paisaje, con valores notablemente más bajos en paisajes urbanizados en comparación con los agrícolas, a pesar de que los fragmentos eran más pequeños en los entornos más antropizados. Esta tendencia negativa fue consistente entre polinizadores con diferentes rasgos, aunque la magnitud del efecto varió entre los distintos grupos. Los polinizadores que anidan en el suelo o en sitios expuestos fueron los más influenciados por el tamaño del fragmento, mientras que los lepidópteros y las avispas, así como las especies con tamaños corporales muy pequeños o grandes, comportamiento solitario y anidación en sitios expuestos o en cavidades, fueron los más afectados por la antropización del paisaje. Los esfuerzos de conservación y manejo deben priorizar la provisión de hábitat para estos grupos más impactados, a fin de apoyar la resiliencia del ecosistema de manglar.

1 | Introduction

Pollinator diversity has declined worldwide, with anthropization being one of the main causes (González-Varo et al. 2013; Sánchez-Bayo and Wyckhuys 2019; Millard et al. 2021). This process involves transforming landscapes that were once dominated by pristine natural ecosystems into human-dominated mosaics, comprising various land uses such as agriculture, livestock, mining, and urbanization, interspersed with patches of natural ecosystems. As human activities alter landscapes, natural ecosystems become fragmented, leading to the loss of their original composition, structure, and functionality. This fragmentation diminishes resource availability for pollinators, ultimately resulting in declines in pollinator diversity.

Pollinator diversity in fragmented natural ecosystems within anthropogenic landscapes often mirrors the patterns observed in island species diversity (MacArthur and Wilson 2001). Specifically, diversity tends to increase with greater habitat complexity in larger patches but decreases with increasing isolation due to reduced connectivity (Stewart et al. 2018; Lázaro et al. 2020; Grossmann et al. 2023). However, pollinator diversity may not always respond to patch size if habitat complexity does not increase proportionally (Lázaro et al. 2020), or if smaller patches, with their greater prevalence of edge areas, provide additional resources and habitats for pollinators (Ren et al. 2023). Furthermore, larger perimeter-to-area ratios in small habitat patches can facilitate pollinator arrival (Tscharntke et al. 2012; Griffin and Haddad 2021). The negative effects of low resource quantity and diversity in small patches may also be mitigated as the number of patches increases and their proximity allows for species movements (Tscharntke et al. 2012; Fahrig 2020).

Pollinator diversity also depends on the composition of the anthropogenic matrix, that is, the area surrounding natural ecosystem patches. In agriculture-dominated landscapes, pollinator diversity generally benefits from more heterogeneous matrices that include a greater variety of croplands, pastures, and semi-natural areas, which provide additional habitats and resources; conversely, in simplified agricultural landscapes, pollinators face reduced resource availability and suffer from the intensification of pesticide use and mechanization (Sánchez-Bayo and Wyckhuys 2019; Millard et al. 2021; Desaegher et al. 2023). In urban-dominated landscapes, pollinators are negatively affected by drivers like increased impervious surface area, the prevalence of exotic plant species, pollution, and the hotter temperatures caused by the urban heat island effect (Wenzel et al. 2020; Fenoglio et al. 2021; Millard et al. 2021). However, compared to highly intensified agricultural landscapes, urban areas may better support pollinator diversity by offering a wider variety of habitats and resources, even in densely populated settings (Wenzel et al. 2020; Prendergast et al. 2022).

Pollinator responses to anthropization vary among species due to several morphological, physiological, and behavioral traits that influence their adaptability to environmental changes (functional traits; Violle et al. 2007). Traits such as body size and sociality, which affect the foraging range and food amount requirements of pollinators, play a significant role in their ability to disperse between habitat patches and survive habitat loss (Zanette et al. 2005; Merckx et al. 2018). Additionally, the degree of resource specialization, crucial for exploiting new resources in anthropogenic areas when natural resources are lost, is also influenced by body size and sociability (with larger and solitary species generally being more specialized) (Wenzel et al. 2020; Raiol et al. 2021). Specialization also depends on the type of feeding resources used during larval stages, as evidenced by the greater specialization observed in lepidopteran phytophagous larvae compared to other pollinator larvae (Millard et al. 2021; Desaegher et al. 2023). Furthermore, the type of nesting resources used by pollinators can shape their responses to anthropization, as the availability of nesting sites varies with land use (Fenoglio et al. 2021; Prendergast et al. 2022). These responses may vary among pollinator guilds or taxonomic groups, such as bees, flies, and lepidopterans, due to the shared functional traits found among phylogenetically related species (Millard et al. 2021; Desaegher et al. 2023).

Understanding how pollinators respond to land anthropization in different environmental contexts is essential for making accurate generalizations and designing more effective ecosystem management strategies, especially as human land use is projected to increase in the coming decades (Tilman et al. 2001; Seto et al. 2012). This understanding is particularly crucial for mangrove ecosystems, which have been prioritized in global conservation strategies due to their vital role in ecosystem service provisioning and their critical endangerment from anthropogenic activity (Lee et al. 2014; Goldberg et al. 2020). Additionally, because mangrove ecosystems are isolated in patches at river mouths along coastal zones, their

pollinator diversity may be particularly vulnerable to changes in patch size and the surrounding landscape matrix, which affect their ability to inhabit and disperse between these patches. While previous research has explored mangrove pollinator diversity in various locations (e.g., Sánchez-Núñez and Mancera-Pineda 2012; Landry 2013a, 2013b; Landry and Rathcke 2012; Diniz et al. 2022), there has been limited focus on the effects of anthropization, despite evidence showing that mangrove genetic diversity decreases with habitat degradation (Salas-Leiva et al. 2009; Nettel-Hernanz et al. 2013; Millán-Aguilar et al. 2016).

This study investigates the effects of anthropization on mangrove pollinator diversity by assessing how pollinators with different functional traits respond to variations in mangrove patch size and land use changes in surrounding landscape matrices. We hypothesize that pollinator diversity will increase with larger mangrove patches but decline in landscapes dominated by human activities, with distinct patterns emerging among different pollinator groups.

2 | Methodology

2.1 | Study Area and Landscape Variables

The study was carried out in the Department of Magdalena, located in the Caribbean region of Colombia (Figure 1). The climate in the region is characterized as warm and dry, with the dry season typically spanning from December to April. The annual mean precipitation varies between 1000 and 1500 mm, while the mean temperature ranges from 26°C to 28°C (IDEAM 2020). The density of mangrove patches in this area is relatively low due to the dry climate, which reduces the availability of fresh water necessary for mangrove formation. Additionally, increasing anthropogenic development has been converting former mangrove and dry forest areas into urban and agricultural land.

We strategically selected seven mangrove patches based on their distribution along a gradient of patch size and surrounding landscape composition (Table 1). These patches consisted of community assemblages dominated by the mangrove species *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, and *Rhizophora mangle*, along with a few sparsely dispersed non-mangrove plant species (Rodríguez-Rodríguez et al. 2016). While the exact coverage of each mangrove species varied with patch size, we did not quantify this. However, we observed a qualitative increase in population sizes of all mangrove species as patch size increased, while the number of mangrove species remained constant. As a result, in our analysis we used patch size as a surrogate measure for the abundance, but not for the richness, of mangrove species.

The size of the mangrove patches and the surrounding land-use areas was calculated using Landsat images (scale 1:10,000) from Google (2021) and QGIS 3.22 (2022). We shaped polygons around the mangrove patches and the land uses within 1000-m radius buffers centered on each mangrove patch, taking into account the mean foraging distances of many central place foraging insects (Greenleaf et al. 2007). The landscape within each buffer was then classified according to the dominant land use into four types: conserved, agricultural, suburban, and urban (Table 1).

2.2 | Pollinator Data

Pollinator data were gathered through flower-based focal sampling on the mangrove species *Avicennia germinans*, *Conocarpus erectus*, and *Laguncularia racemosa* in each patch. We chose these species for sampling pollinators due to their common occurrence in the mangrove patches and their shared traits as generalist, entomophilous-pollinated species (e.g., Sánchez-Núñez and Mancera-Pineda 2012; Landry 2013a, 2013b; Landry and Rathcke 2012; Diniz et al. 2022). Monthly visits were conducted in each patch between September 2020 and March 2021, with each visit corresponding to a sampling session. The number of sampling sessions per mangrove species ranged from zero to five due to flowering phenological variation among patches and the absence of *C. erectus* at the Manzanares site (see Table 1).

In each mangrove patch, we selected two blooming trees per species for pollinator sampling, prioritizing individuals with high flower abundance and visitation frequency. This number was chosen because two individuals per species was the minimum available in several patches, and we aimed to standardize sample size across patches to avoid sampling bias. Sampling was conducted on the accessible flowers of each tree for two 10-min periods separated by at least 1 h (total sampling effort per sampling session was 10 min × 2 sampling periods × 2 trees = 40 min). During each sampling session, we also recorded the number of flowers on the blooming tree and made qualitative observations on climate (sunny, cloudy, light rain) and wind speed (calm, medium, strong). Sampling took place between 08:00 and 14:00, corresponding to the period of highest pollinator activity (Sánchez-Núñez and Mancera-Pineda 2012).

All flying flower visitors that contacted the stigma and anthers of flowers were collected and regarded as pollinators. We excluded ants and the exotic bee species *Apis mellifera*, as our focus was on native flying pollinators that may contribute to pollen transfer among mangrove patches. The collected specimens were preserved in 70% alcohol and later mounted in the laboratory for identification. Identification was carried out to the lowest possible taxonomic level, and the voucher specimens were deposited in the entomological collection of the Marine Natural History Museum Makuriwa—INVEMAR.

2.3 | Functional Traits

The classification of pollinator species involved five qualitative functional traits known to respond to habitat degradation (Williams et al. 2010; Merckx et al. 2018; Fenoglio et al. 2021; Török et al. 2022): pollinator guild, body size, feeding preference, sociality, and nesting site. Pollinator guilds were categorized as bee, beetle, fly, lepidoptera, and wasp. Body size was determined by measuring the body area (intertegular distance × body length) and subsequently classified as small-sized ($< 20\,mm^2$), medium-sized ($20–40\,mm^2$), or large-sized ($> 40\,mm^2$) based on the frequency peaks observed in the distribution of sizes among pollinators. We chose to use body area instead of intertegular

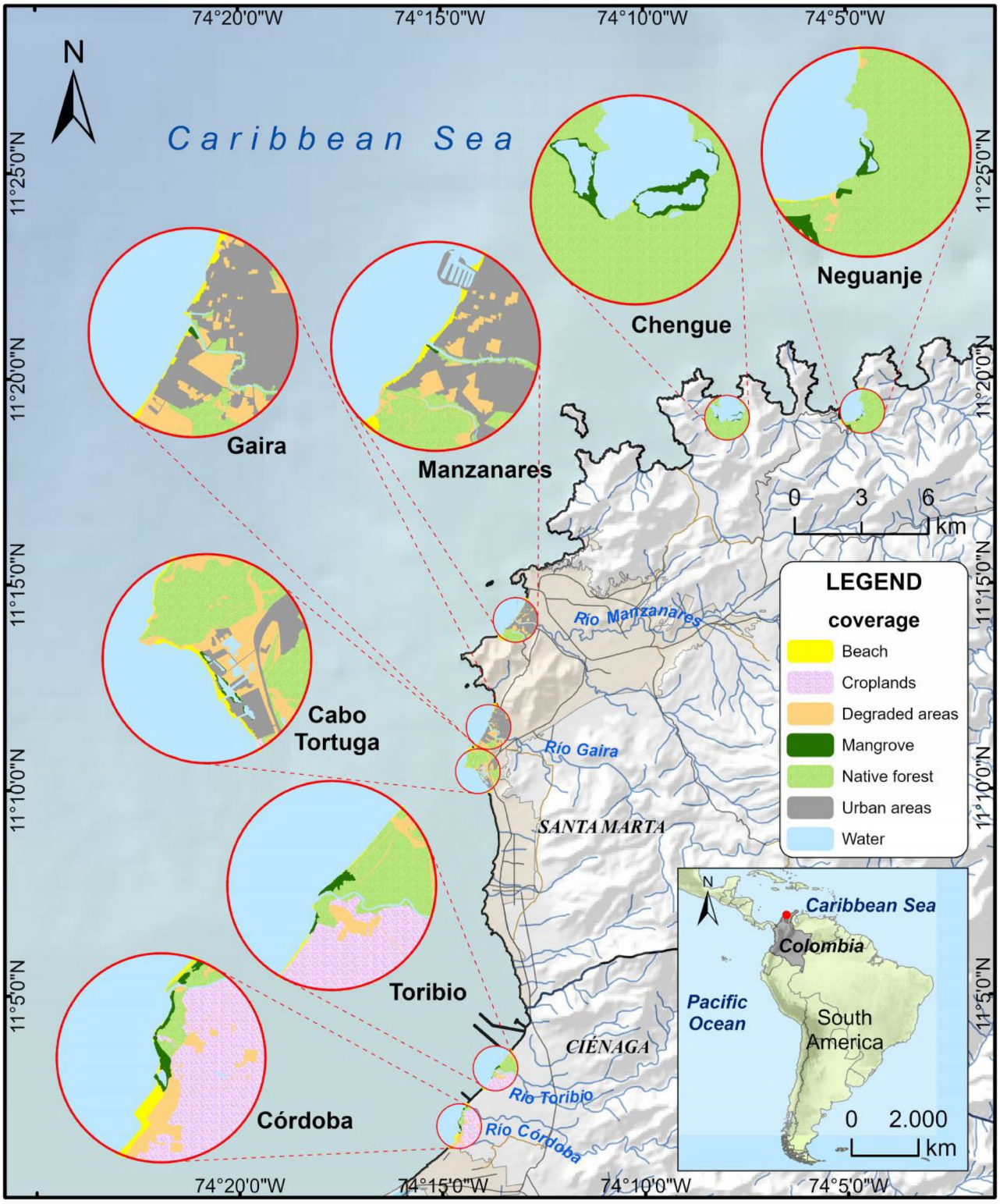

FIGURE 1 | Map illustrating the study area, delineating the positions of sampled mangrove patches along the Caribbean coast of Colombia. The figure depicts the distribution of land uses within 1000-m radius landscapes surrounding the mangrove patches.

distance alone, as body length varied widely among pollinator guilds and was not consistently correlated with intertegular distance. Feeding preference was classified by considering the feeding habits during larval stages, encompassing florivorous, phytophagous, predator (including parasites), or saprophagous behaviors. Sociality was categorized as nonsocial (solitaries and a few semi-social) or social. Nesting location was classified as cavities, exposed, no nest, and ground.

Information on feeding preference, sociality, and nesting location was compiled by the authors based on their expertise and supplemented with additional information from the literature when

TABLE 1 | List of mangrove patches used as sampling locations on the Caribbean coast of Colombia, including patch size, landscape descriptions and types, and sampling effort.

Site	Patch size (ha)	Landscape description	Landscape type	Number of sampling sessions		
				Avicennia germinans	*Laguncularia racemosa*	*Conocarpus erectus*
Chengue	16.03	Mangrove patches within Tayrona National Park, predominantly surrounded (over 90%) by preserved dry forest	Conserved	5	1	4
Neguanje	8.05			3	1	3
Cordoba	5.96	Mangrove patches predominantly surrounded (over 50%) by extensive banana and mango plantations	Agricultural	2	4	5
Toribio	2.89			3	3	4
Cabo Tortuga	1.77	Mangrove patch surrounded (over 50%) by a mixture of disturbed vegetation and urban areas	Suburban	5	4	4
Gaira	0.53	Mangrove patches predominantly surrounded (over 50%) by urban areas	Urban	3	2	5
Manzanares	0.38			5	5	0
Total sampling sessions per mangrove species				26	20	25

necessary. For species lacking complete trait information, data were inferred based on the traits of taxonomically related species, ensuring consideration of trait variability within the specific clade (same subgenus, genus, or tribe). Species with incomplete information were dropped from the analysis (< 5% of specimens).

2.4 | Statistical Analysis

Before data analysis, we checked for sampling completeness using Chao's estimate, spatial autocorrelation with the Mantel test, and autocorrelation among functional traits using Cramer's V tests (see Table S1). Data analysis was conducted using Bayesian multi-level models implemented with the "brms" package (Bürkner 2017) in R version 4.2.2 (R Core Team 2022). To assess the effects of patch size and landscape anthropization on mangrove pollinator diversity, we developed three separate models, each using a different response variable: pollinator abundance, species richness, and Shannon's H' diversity index. These metrics were calculated per sampling session for each mangrove species and recorded as zero if no pollinators were observed during a session, even when the mangrove plants were in bloom. Pollinator abundance and richness were modeled using negative binomial distributions, while diversity was modeled using a Gaussian distribution.

These models incorporated the additive population-level effects (fixed effects) of landscape type (with conserved landscapes as the reference group), patch size, and flower abundance (see Tables S2–S4). Patch size and flower abundance were centered and scaled prior to analysis. Additionally, group-level effects (random effects) of mangrove species, climate, and wind speed on the intercepts were included. These group-level effects, along with the effect of flower abundance, were included for control purposes; their effects were not further discussed, as they were not the primary variables of interest.

To explore the effects of patch size and landscape anthropization on the likelihood of encountering pollinator species with specific functional attributes, we developed four additional models. Each model focused on one functional trait as a population-level effect: guild, body size, nest location, and sociality (see Tables S5–S8). We did not model feeding preference due to a high autocorrelation with guild (Cramer's $V = 0.84$; see Table S1). The response variable in these models was the number of species exhibiting each attribute (e.g., large, medium, or small for body size) per sampling session for each mangrove species. This response was modeled using a negative binomial distribution. If no species with the respective attribute were observed during a particular session, the richness for that attribute was recorded as zero. Additional population-level effects included landscape type, patch size, flower abundance, and the two-way interactions between "functional trait × landscape type" and "functional trait × patch size." We also incorporated group-level effects from mangrove species, climate, and wind speed on the intercepts. Flower abundance and patch size were centered and scaled prior to analysis.

Weakly informative prior distributions were applied to slope and intercept parameters (Normal (0,2)), while default priors

were used for parameters of other classes in all models. The Bayesian approach utilized Markov chain Monte Carlo to derive the posterior distribution of the parameters of interest. We ran three chains of length 3000 each and discarded the first 1000 as burn-in, with a thinning rate of three. Chain convergence was assessed through visual inspection of trace plots, density plots, and autocorrelation plots, as well as employing the Gelman and Rubin diagnostic (R-hat), with convergence indicated by a value approaching one (Gelman and Rubin 1992).

Inferences were drawn from the magnitude of the effect coefficients and the 95% Bayesian credible intervals (95% CI). The strength of the effects was classified as "weak" when the 95% CI overlapped zero by more than 15%, "moderate" when the 95% CI overlapped zero by less than 15%, and "strong" when the 95% CI did not overlap zero. Model validation encompassed posterior predictive checking and residual analysis using the "brms" package and the "DHARMa" package (Harting 2022) in R version 4.2.2 software.

3 | Results

The studied mangrove pollinator communities included a total of 720 specimens distributed among 151 species. The observed pollinator richness was 57% of the expected richness (Chao's estimate = 265, SE = 35.1). Pollinator abundance per sampling session and mangrove species varied between 0 and 45 (mean = 11.2; SD = 8.6); pollinator richness ranged from 0 to 16 (mean = 5.7; SD = 3.8), and Shannon's diversity index varied between 0 and 2.6 (mean = 1.3; SD = 0.8). Pollinator dissimilarity among mangrove species ranged from 0.66 to 0.90 (mean = 0.79; SD = 0.07), with no significant spatial autocorrelation among sites (Mantel statistic $R = 0.136$, $p = 0.053$). The list of identified species is accessible from the Zenodo Repository; please refer to Data Availability.

Most pollinator species were represented by flies (40%) and wasps (34%), followed by bees (16%), beetles (6%), and lepidopterans (4%). In terms of body size, the majority were small (64%), followed by medium-sized (25%) and large (15%). Most species did not construct nests (64%), which included all fly, beetle, and lepidopteran pollinators. Among the nesting species, the majority built their nests in the ground (17%) or in cavities (14%), with 5% having exposed nests (all represented by wasps). Additionally, 15% of the species exhibited social behavior (all wasp and bee species), while 85% were nonsocial, including nonsocial wasps and bees, as well as all fly, beetle, and lepidopteran species.

The richness of pollinators with varying feeding preferences was correlated with the richness among guild groups. Specifically, all florivorous species were bees, all phytophagous species were lepidopterans, and 90% of predators were wasps, with the remaining predators being flies (9%) and beetles (1%). Among saprophagous species, 72% were flies and 28% were beetles. Due to these associations, the effect of feeding preference was discussed in conjunction with the effect of pollinator guild.

Mangrove pollinators decreased in abundance, richness, and diversity with patch size. The patch size effect was moderate on pollinator abundance while strong on richness and diversity (Table 2, Figure 2, Tables S2–S4). Pollinators were also negatively affected by landscape anthropization, as evidenced by decreases in abundance, richness, and diversity in agricultural, suburban, and urban landscapes compared to conserved landscapes. Landscape anthropization effects on pollinator abundance were smaller in agricultural and urban landscapes than in suburban landscapes, with weak negative effects in all landscape types. The magnitude of the landscape anthropization effects increased from agricultural to urban landscapes on richness and diversity, demonstrating weak negative effects of agricultural landscapes and moderate negative effects of suburban and urban landscapes (Table 2, Figure 2, Tables S2–S4).

The impacts of patch size and landscape anthropization on the richness of pollinators categorized by various functional attributes exhibited negative trends similar to those previously documented for overall pollinator richness. However, the extent and strength of these effects varied across different pollinator groups. While the negative effects of patch size showed minor variations among pollinator guilds, with only small and weak divergences, lepidopteran and wasp species were significantly more adversely affected by landscape anthropization compared to bees, beetles, and flies. This was particularly evident in the pronounced reduction in richness for lepidopterans and wasps in suburban and urban landscapes. Conversely, beetle richness increased in agricultural landscapes (Table 3, Figure 3, Tables S5–S8).

In terms of body size, the impact of patch size was consistently negative and moderate, with no significant differences among size groups. Conversely, landscape anthropization had a stronger

TABLE 2 | Estimates and 95% CI (within parentheses) of patch size and landscape anthropization effects on mangrove pollinator abundance, richness, and diversity (Shannon H') on the Caribbean coast of Colombia.

Response variable	Patch size	Landscape type				R^2
		Conserved (intercept)	Agricultural	Suburban	Urban	
Abundance	-0.4 $(-0.9, 0.1)^{m}$	2.8 $(1.0, 4.5)^{s}$	-0.4 $(-1.3, 0.5)^{w}$	-0.6 $(-1.8, 0.5)^{w}$	-0.4 $(-1.7, 0.8)^{w}$	0.33 (0.13, 0.49)
Richness	-0.4 $(-0.9, <0.0)^{s}$	2.1 $(0.3, 3.7)^{s}$	-0.3 $(-1.2, 0.5)^{w}$	-0.7 $(-1.7, 0.2)^{m}$	-0.8 $(-1.9, 0.3)^{m}$	0.30 (0.13, 0.46)
Diversity	-0.5 $(-0.9, <0.0)^{s}$	1.7 $(0.1, 3.3)^{s}$	-0.3 $(-1.1, 0.6)^{w}$	-0.7 $(-1.8, 0.3)^{m}$	-1.0 $(-2.1, 0.1)^{m}$	0.24 (0.12, 0.37)

Note: Superscript letters on estimates indicate the strength of the effects: "w" for weak (95% CI overlapping zero by more than 15%), "m" for moderate (95% CI overlapping zero by less than 15%) and "s" for strong (95% CI not overlapping zero). Estimates for abundance and richness are presented in log-link scale. Results from the full models are presented in Tables S2–S4.

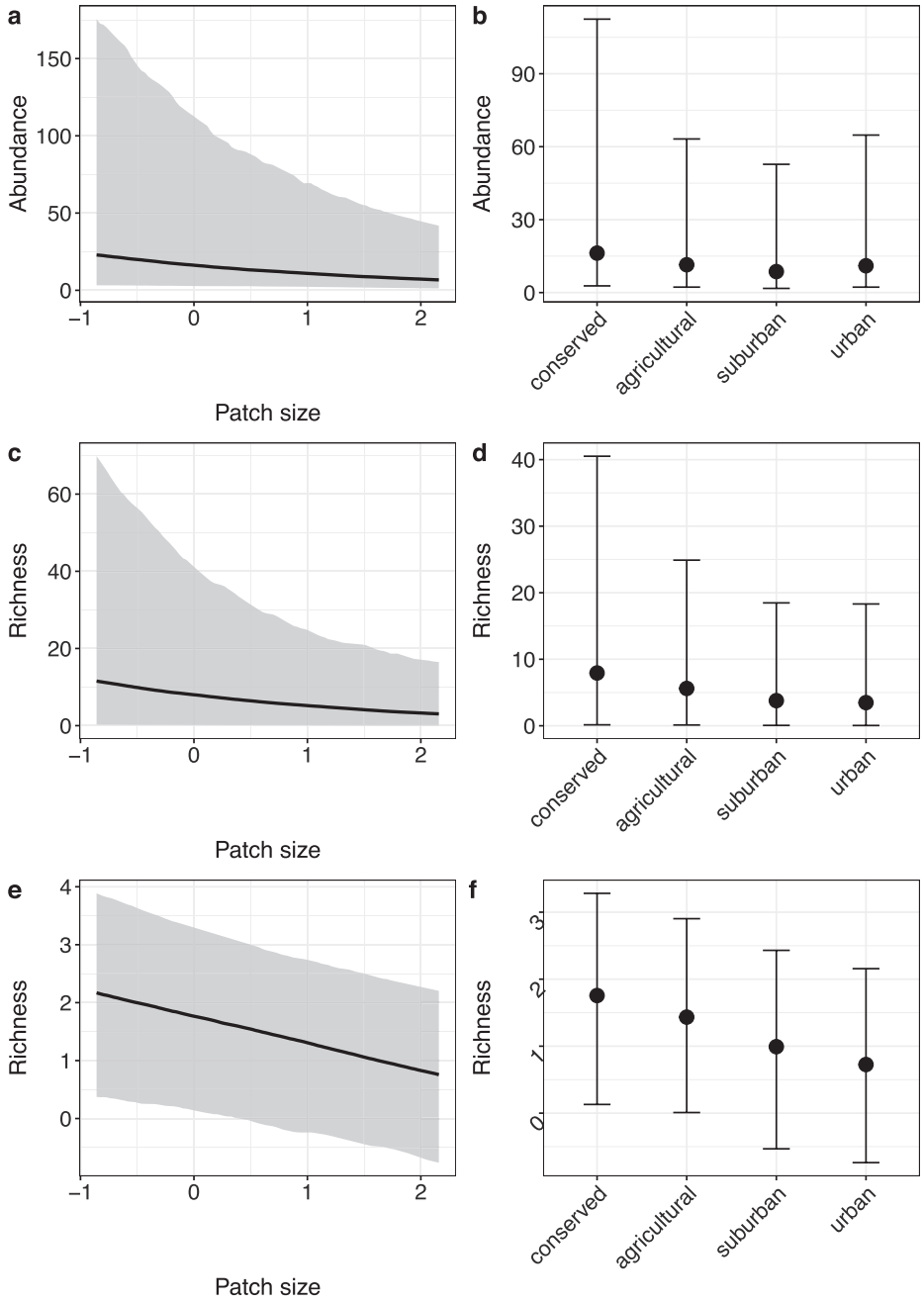

FIGURE 2 | Plots illustrating the conditional effects of patch size and landscape anthropization on abundance, richness, and diversity (Shannon H') of mangrove pollinators on the Caribbean coast of Colombia. Predicted means and standard deviations are indicated by solid lines and shaded areas, respectively, in patch size plots (a, c, e), and dots and error bars, respectively, in landscape type plots (b, d, f).

effect on both small-sized and large-sized species, resulting in more pronounced decreases in richness for these groups in suburban and urban landscapes. Agricultural landscapes had only small and weak negative effects across all size groups (Table 3, Figure 3, Tables S5–S8).

The effects of patch size and landscape anthropization varied among pollinators based on their nest locations. The negative effect of patch size was more pronounced and moderate for pollinators with exposed nests and ground nests. In agricultural landscapes, the effects on all nest groups were classified as weak. In suburban landscapes, pollinators nesting in cavities exhibited a moderate decrease in richness, whereas ground-nesting pollinators showed a moderately large increase. In urban landscapes, the most significant and moderate decrease in richness was observed for pollinators with exposed nests (Table 3, Figure 3, Tables S5–S8).

Regarding sociality, nonsocial species were more impacted than social species, experiencing larger and moderate declines in response to patch size, as well as in suburban and urban landscapes. In agricultural landscapes, both groups showed small and weak declines (Table 3, Figure 3, Tables S5–S8).

4 | Discussion

This study aimed to examine whether mangrove pollinator diversity shows the following trends: (a) an increase with larger

TABLE 3 | Estimates and 95% CI (within parentheses) of the effects of functional traits, patch size and landscape anthropization on the richness of mangrove pollinators on the Caribbean coast of Colombia.

		Landscape type				
Functional trait	**Patch size**	**Conserved (intercept)**	**Agricultural**	**Suburban**	**Urban**	R^2
Guild						
Bee (intercept)	−0.4 (−1.0, 0.1)[m]	−0.3 (−1.9, 1.4)	−0.2 (−1.2, 0.7)	−0.2 (−1.4, 0.9)	−0.4 (−1.6, 0.9)	0.38 (0.29, 0.46)
Beetle	0.3 (−0.6, 1.2)	−1.1 (−2.4, 0.2)	1.0 (−0.4, 2.6)	−0.3 (−2.3 1.6)	0.3 (−1.7, 2.4)	
Fly	−0.0 (−0.7, 0.7)	1.3 (0.3, 2.3)	−0.1 (−1.2, 1.1)	−0.4 (−1.8, 1.1)	−0.4 (−2.0, 1.1)	
Lepidopteran	−0.0 (−1.1, 1.0)	−0.9 (−2.3, 0.4)	−0.9 (−2.6, 0.9)	−1.6 (−3.9, 0.7)	−1.9 (−4.3, 0.4)	
Wasp	−0.2 (−0.9, 0.5)	1.6 (0.6, 2.6)	−0.5 (−1.7, 0.6)	−1.0 (−2.5, 0.4)	−1.1 (−2.7, 0.4)	
Body size						
Small (intercept)	−0.5 (−1.0, −0.1)	1.4 (−0.2, 3.0)	−0.4 (−1.1, 0.4)	−0.8 (−1.8, 0.1)	−0.8 (−1.8, 0.2)	0.45 (0.35, 0.54)
Medium	0.0 (−0.7, 0.7)	−1.3 (−2.3, −0.3)	−0.0 (−1.2, 1.1)	0.5 (−0.9, 1.9)	−0.2 (−1.8, 1.2)	
Large	0.2 (−0.4, 0.9)	−1.1 (−2.1, −0.2)	−0.1 (−1.1, 1.1)	−1.0 (−2.6, 0.5)	−1.3 (−3.0, 0.3)	
Nest location						
Cavities (intercept)	−0.1 (−0.7, 0.3)	−0.3 (−1.9, 1.2)	0.4 (−1.2, 0.6)	−1.4 (−2.7, −0.2)	−0.2 (−1.4, 1.0)	0.39 (0.29, 0.49)
Exposed	−0.5 (−1.2, 0.2)	0.8 (−0.2, 1.9)	−0.8 (−2.0, 0.5)	−0.4 (−2.2, 1.4)	−1.4 (−3.0, 0.2)	
Ground	−0.6 (−1.4, 0.1)	0.3 (−0.8, 1.4)	0.3 (−0.9, 1.6)	1.2 (−0.4, 2.8)	−0.8 (−2.5, 0.9)	
No nest	−0.3 (−0.9, 0.3)	1.5 (0.6, 2.4)	0.1 (−1.0, 1.2)	0.6 (−0.8, 2.1)	−0.6 (−2.0, 0.8)	
Sociality						
Nonsocial (intercept)	−0.5 (−0.9, −0.1)	1.6 (−0.1, 3.0)	−0.3 (−1.1, 0.4)	−0.8 (−1.7, 0.1)	−1.0 (−2.0, −0.0)	0.39 (0.26, 0.50)
Social	0.1 (−0.6, 0.7)	−1.1 (−2.0, −0.1)	−0.1 (−1.3, 0.9)	0.0 (−1.4, 1.4)	0.3 (−1.2, 1.8)	

Note: Superscript letters on estimates indicate the strength of the effects: "w" for weak (95% CI overlapping zero by more than 15%), "m" for moderate (95% CI overlapping zero by less than 15%) and "s" for strong (95% CI not overlapping zero). Estimates are presented in log-link scale. Results from the full models are presented in Tables S5–S8.

mangrove patch sizes, (b) a decline in response to landscape anthropization, and (c) varying responses based on pollinator functional attributes. Contrary to our first expectation, we found that pollinator abundance, richness, and diversity actually decreased with larger patch sizes. However, our second expectation was supported; we observed declines in these metrics in anthropized landscapes. Consistent with our third expectation, we noted a general negative trend in the responses of different pollinator trait groups, though the magnitude of these responses varied among the groups. In the following paragraphs, we discuss several hypotheses that may help explain these findings.

4.1 | Patch Size Effects

The unexpected decline in mangrove pollinators with increasing patch size contradicts previous research, which has generally found that pollinator diversity increases in larger forest patches within anthropogenic landscapes (Medeiros et al. 2019; Stewart et al. 2018; Lázaro et al. 2020; Grossmann et al. 2023). A plausible explanation for the lower diversity of pollinators in larger mangrove patches is their reduced plant diversity, which does not increase with patch size. This is particularly relevant in our study region, where mangrove patches are dominated by only four species (FAO 2007; Rodríguez-Rodríguez et al. 2016). Such low plant diversity may result in reduced floral resource availability and structural habitat complexity compared to more heterogeneous natural or anthropogenic ecosystems in the surrounding landscape matrix. Additionally, in larger mangrove patches, pollinator visits may be diluted among the more abundant flowers of extensive mangrove populations (Tscharntke et al. 2012). In contrast, smaller patches may benefit from larger perimeter-to-area ratios, potentially enhancing pollinator influx from the surrounding landscape (Griffin and Haddad 2021). Opposite patterns might be observed in highly diverse mangrove ecosystems, such as those in Asia with up to 40 plant species (FAO 2007), where plant richness and structural complexity are more likely to increase with patch size. Observations from these species-rich mangrove systems could help determine whether the negative relationship between pollinator diversity and patch size found in this study is primarily driven by the low plant diversity characteristic of Neotropical mangroves.

The responses to patch size were consistent across different pollinator groups. However, ground-nesting pollinators exhibited a more pronounced decline, likely due to the scarcity of bare

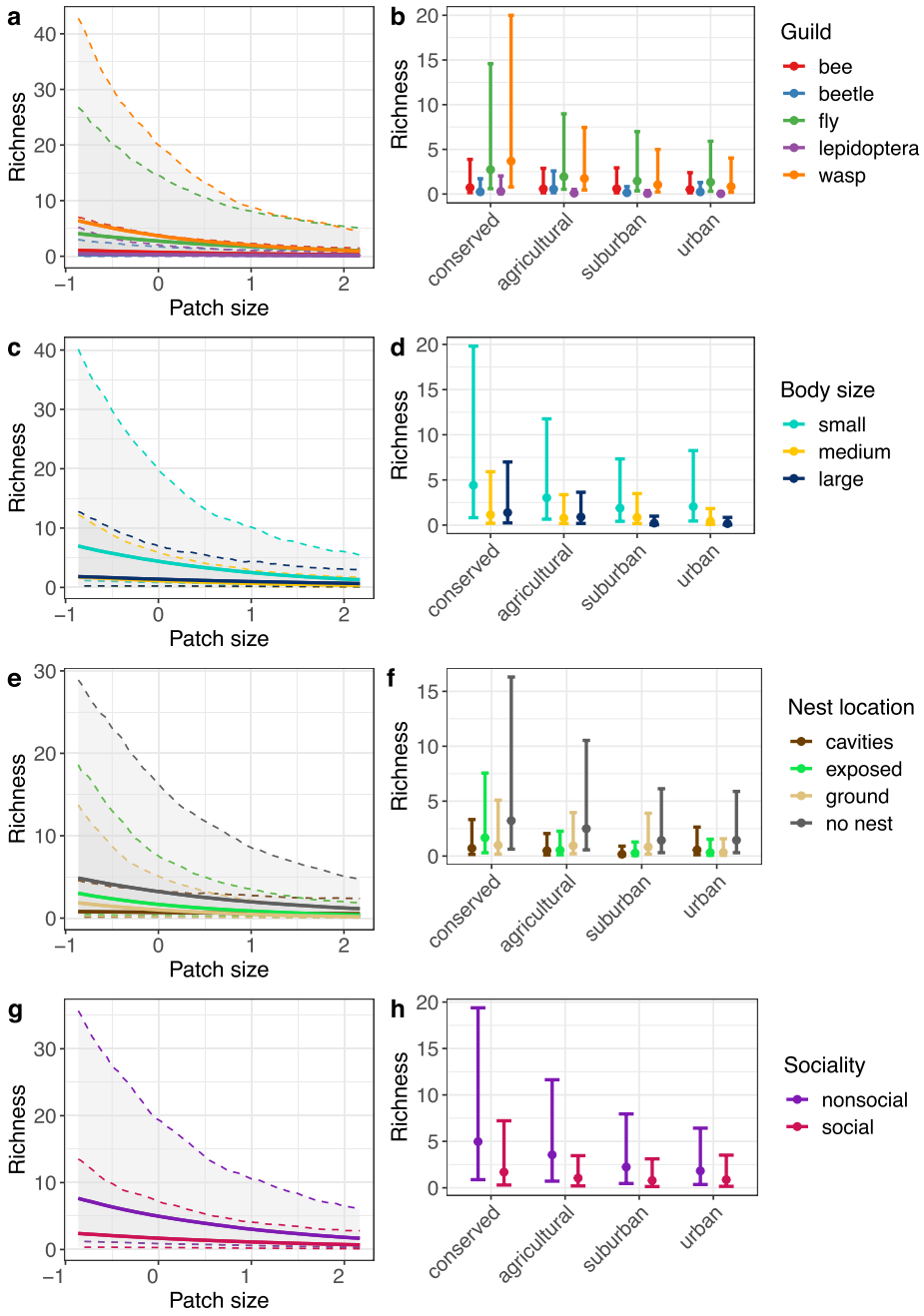

FIGURE 3 | Plots illustrating the conditional effects of patch size and landscape anthropization on the richness of species characterized by diverse functional attributes on the Caribbean coast of Colombia. Predicted means and standard deviations are indicated by solid lines and dashed lines, respectively, in patch size plots (a, c, e, g), and dots and error bars, respectively, in landscape anthropization plots (b, d, f, h).

ground in mangrove patches, which are regularly subjected to tidal flooding. Exposed-nesting pollinators, represented entirely by social vespid wasps, also showed a significant decrease with increasing patch size. This may be because larger patches do not offer a sufficient variety of nesting materials required by these wasps, as mangrove plant diversity does not increase with patch size (Santos et al. 2007). In contrast, smaller mangrove patches may enable wasps to access a more diverse array of plant fibers from the surrounding, more plant-diverse landscape. Furthermore, exposed-nesting species may avoid nesting in harsh environments like mangroves, which are characterized by fluctuating temperatures, high salinity, and strong winds. These conditions can increase nest vulnerability to environmental stressors, especially when compared to nests built in cavities or underground (Santos et al. 2007). Future research, including the assessment of nesting resources for these pollinator functional groups, is needed to confirm the potential drivers of their declining diversity with increasing mangrove patch size.

4.2 | Landscape Anthropization Effects

The abundance, richness, and diversity of mangrove pollinators declined with increasing landscape anthropization. However, our models provided only moderate support for this trend, suggesting variability in pollinator responses across sites. This

variation may be attributed to factors such as climatic fluctuations during surveys, differences in plant diversity, and the degree of landscape connectivity, as well as the effect of a small sample size. Additionally, the autocorrelation between patch size and landscape anthropization (i.e., smaller patches occurring in more anthropized areas) could have influenced the results, as smaller patches were found to host greater pollinator diversity. Nevertheless, the negative trend in pollinator responses was consistent across all anthropized landscape types, with the magnitude of the decline increasing from agricultural to urban landscapes. This suggests that while the reduction in mangrove patch size caused by landscape anthropization might benefit pollinators, it is overshadowed by other negative effects likely associated with changes in anthropized landscape matrices.

Our findings are consistent with global reviews on the effects of landscape anthropization on pollinator diversity, which generally agree that abundance and richness decrease in anthropized landscapes compared to natural or semi-natural ones (Sánchez-Bayo and Wyckhuys 2019; Wenzel et al. 2020; Fenoglio et al. 2021). However, pollinator responses vary notably in comparisons between urban and agricultural landscapes, often responding better to urban landscapes due to higher resource availability and habitat heterogeneity (Wenzel et al. 2020; Prendergast et al. 2022). In our study, we observed more negative pollinator responses in urban and suburban landscapes compared to agricultural ones. A possible explanation is that croplands in the study region are less intensified and subject to fewer agrochemical inputs. This contrasts with croplands in temperate areas, where many studies have been conducted (Sánchez-Bayo and Wyckhuys 2019; Wenzel et al. 2020). Therefore, croplands in our study area may still provide more resources for pollinators compared to urban areas.

The responses of different pollinator groups to landscape anthropization were less consistent than their responses to patch size. While several groups were notably more adversely affected, others demonstrated weak decreases, and a few were even benefited from landscape anthropization. Among pollinator guilds, lepidopterans were the most negatively affected by landscape urbanization, presumably because of their high degree of host-plant specialization that seems to explain their typical decreases with urbanization across various ecosystems (Öckinger et al. 2009; Sánchez-Bayo and Wyckhuys 2019; Desaegher et al. 2023). Similarly, the richness of wasps decreased with urbanization, aligning with the expectation that predator insects could be more susceptible than insects from lower trophic levels due to their greater habitat specialization, lower population sizes, and reliance on more diverse food types (prey for larvae, floral resources for adults) (Burkman and Gardiner 2014; Corcos et al. 2019; Medeiros et al. 2019). Contrastingly, beetle pollinators showed richness increases in agricultural landscapes that were primarily attributed to the presence of saproxylic species from the family Oedemeridae. These beetles were likely attracted by the abundance of decaying wood resulting from logging activities (Rubene et al. 2017; Foster et al. 2019), which were particularly frequent in the mangrove patches in agricultural landscapes.

Fly pollinators were only weakly affected by landscape anthropization, likely due to the broad variability in their feeding requirements (including both predator and saprophagous species). This variability may have enabled them to maintain their diversity across different landscape types by replacing species with those possessing more adaptable traits for each specific environment (e.g., Parry et al. 2016; Bertucci et al. 2023). Bee pollinators also showed weak responses in anthropized landscapes, despite the global trend of decreasing bee diversity with anthropization (Prendergast et al. 2022). The weak responses of bee pollinators may also reflect differential responses among bee species with different traits, such as nest location, social level, or body size (Williams et al. 2010; Prendergast et al. 2022), which are described below.

Based on body size, both small and large species decreased in suburban and urban landscapes. Previous studies have presented similar contradictory insights regarding the relationship between pollinator body size and landscape urbanization (Wenzel et al. 2020). Some studies reporting greater decreases in small-bodied species than in large-bodied ones attribute their findings to the reduced dispersal capacity of small-bodied species, which may hinder their ability to move between isolated vegetation patches in urban landscapes (Merckx et al. 2018). Conversely, studies that observe greater decreases in large-bodied species hypothesize that these species are more vulnerable due to their greater habitat specialization, larger food requirements, and heightened sensitivity to hotter temperatures in urban areas (Merckx et al. 2018; Fenoglio et al. 2021; Raiol et al. 2021). Our results align with both sets of findings, as both large-bodied and small-bodied species were similarly and more affected by urban landscapes than medium-sized species. Medium-sized species in our study probably were less affected as they were large enough to disperse between isolated patches and small enough to require less specialization, find sufficient resources, and withstand the higher temperatures in urban landscapes.

The responses of pollinators to landscape anthropization varied significantly depending on their nesting location. In urban landscapes, the richness of exposed-nesting vespid wasps declined, which likely contributed to the overall decrease in wasp richness. This decline aligns with previous research, which links such responses to reductions in nesting materials (e.g., plant fibers) and prey availability, especially for species with specialized needs (Santos et al. 2007; Medeiros et al. 2019). Additionally, the removal of wasp nests by city residents concerned about potential stings has been identified as a major factor (Zanette et al. 2005; López et al. 2012).

The richness of cavity-nesting species showed greater decreases in suburban landscapes than in agricultural and urban landscapes. This result is inconsistent with previous findings indicating that urban landscapes usually benefit cavity nesters due to the increased availability of cavities from urban constructions (Zanette et al. 2005; Wenzel et al. 2020; Fenoglio et al. 2021; Prendergast et al. 2022). It is possible that in this suburban landscape, where urbanization has started more recently, cavity-nesting pollinators have not yet fully colonized the new cavities created by buildings and constructions.

Conversely, the richness of ground-nesting pollinators increased in the suburban landscape, possibly in response to the

increased availability of bare ground in the larger areas of disturbed vegetation (Zanette et al. 2005; Williams et al. 2010). In more urbanized landscapes, ground-nesting pollinators did not decrease despite the general trend of decreasing ground-nesting insect diversity with urbanization (Wenzel et al. 2020; Fenoglio et al. 2021; Prendergast et al. 2022). This could be because the urban landscapes in this study still possess small patches of degraded vegetation and beaches where these pollinators can nest. Nonnesting pollinators did not show any specific response to any landscape type, suggesting a probable advantage of not having nesting requirements, making them less sensitive to environmental changes. This result may also explain the weak responses observed in fly pollinators, as 73% of the nonnesting species were flies.

Nonsocial species were more negatively affected by urbanization compared to social species, as has usually been found in similar studies (Zanette et al. 2005; Wenzel et al. 2020), although with several exceptions (Prendergast et al. 2022). Social species are typically less affected by urbanization, likely due to their cooperative behavior, which enables them to better navigate the challenges posed by urban landscapes. Their collective efforts enhance efficiency in various activities such as foraging, defense against predators, and thermal regulation. In contrast, solitary species do not store food and must undertake all these tasks individually, rendering them more vulnerable to urban conditions.

In conclusion, our study provides evidence of a negative effect of mangrove patch size on pollinator diversity, with consistent responses observed among different pollinator groups. This contradicts general findings of positive patch size effects in other ecosystems. These results are likely due to the specific characteristics of mangrove patches, such as low plant diversity, structural homogeneity, and harsh environmental conditions. The increased diversity of pollinators in smaller patches may help mitigate negative consequences like inbreeding and genetic drift, which are common in naturally patchy and isolated mangrove populations. Despite the potential benefits of reduced patch size in mangroves resulting from landscape anthropization, our findings indicate that this anthropization decreases pollinator diversity, overshadowing the effects of patch size, with increasing severity observed along the gradient from agricultural to urban landscapes. We also observed differential responses among various pollinator trait groups, highlighting the importance of tailoring management practices for pollinator conservation by prioritizing habitat provisioning for the most affected groups. Nevertheless, further research is needed to elucidate the specific mechanisms through which landscape anthropization impacts different pollinator groups.

Author Contributions

Paula María Montoya-Pfeiffer conceived the ideas, designed the methodology, collected and analyzed the data, and led the writing of the manuscript. Jenny Alexandra Rodríguez-Rodríguez conceived the ideas, designed the methodology, contributed critically to drafts of the manuscript, and gave final approval for publication. Carlos E. Sarmiento, Augusto Montoya, and Eliana Buenaventura collected the data, conducted the taxonomic identification of the species, and contributed critically to drafts of the manuscript, and gave final approval for publication.

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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 openly available in the Zenodo Repository, https://doi.org/10.5281/zenodo.7106170.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Autocorrelations between mangrove pollinator traits using Cramer's *V* test. **Table S2:** Results from the Bayesian multi-level model assessing the impacts of mangrove patch size and landscape anthropization on pollinator abundance. This model incorporates the control effect of flower abundance and accounts for group effects of wind speed (calm, medium, strong), climate conditions (sunny, cloudy, light rain), and mangrove species (*Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*). **Table S3:** Results from the Bayesian multi-level model assessing the impacts of mangrove patch size and landscape anthropization on pollinator richness. This model incorporates the control effect of flower abundance and accounts for group effects of wind speed (calm, medium, strong), climate conditions (sunny, cloudy, light rain), and mangrove species (*Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*). **Table S4:** Results from the Bayesian multi-level model assessing the impacts of mangrove patch size and landscape anthropization on pollinator diversity (Shannon's *H′*). This model incorporates the control effect of flower abundance and accounts for group effects of wind speed (calm, medium, strong), climate conditions (sunny, cloudy, light rain), and mangrove species (*Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*). **Table S5:** Results from the Bayesian multi-level model assessing the impacts of pollinator guild, mangrove patch size and landscape anthropization on pollinator richness. This model incorporates the two-way interactions between "guild * landscape type" and "guild * patch size," the control effect of flower abundance and accounts for group effects of wind speed (calm, medium, strong), climate conditions (sunny, cloudy, light rain), and mangrove species (*Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*). **Table S6:** Results from the Bayesian multi-level model assessing the impacts of body size, mangrove patch size and landscape anthropization on pollinator richness. This model incorporates the two-way interactions between "body size * landscape type" and "body size * patch size," the control effect of flower abundance and accounts for group effects of wind speed (calm, medium, strong), climate conditions (sunny, cloudy, light rain), and mangrove species (*Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*). **Table S7:** Results from the Bayesian multi-level model assessing the impacts of nest location, mangrove patch size and landscape anthropization on pollinator richness. This model incorporates the two-way interactions between "nest location * landscape type" and "nest location * patch size," the control effect of flower abundance and accounts for group effects of wind speed (calm, medium, strong), climate conditions (sunny, cloudy, light rain), and mangrove species (*Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*). **Table S8:** Results from the Bayesian multi-level model assessing the impacts of level of sociality, mangrove patch size and landscape anthropization on pollinator richness. This model incorporates the two-way interactions between "sociality * landscape type" and "sociality * patch size," the control effect of flower abundance and accounts for group effects of wind speed (calm, medium, strong), climate conditions (sunny, cloudy, light rain), and mangrove species (*Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*).