




# Effect of climate seasonality and vegetation cover on floral resource selection by two stingless bee species

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Received 14 August 2020 – Revised 14 June 2021 – Accepted 28 June 2021

**Abstract** – The response of two stingless bees (*Tetragonisca angustula* and *Melipona eburnea*) to changes in vegetation cover was evaluated on seasonal and spatial scales. Seasonal variation was analysed for 15 months, with monthly melitopalynological assessments of hives located in three different vegetation covers: forests, fallows, and grasslands, in the Colombian Central Cordillera. Fallows, with an intermediate disturbance degree, presented the highest pollen taxa richness for both bee species (33 and 40 taxa for *M. eburnea* and *T. angustula*, respectively). Both bee species presented a high preference for plant families Melastomataceae, Sapindaceae, and Peraceae. *Miconia minutiflora* and *Mi. prasina* (Melastomataceae) were the most selected species, with an alternation in their use between dry and wet seasons. *Clethra* spp., *Pera arborea*, and *Ilex laureola* were also highly selected by both bee species. *M. eburnea* showed higher pollen richness values during the dry season, when the largest number of plant species flowered. Despite both bee species being polylectic, *T. angustula* presented higher pollen richness values during wet periods, which was reflected in a greater amplitude of trophic niche compared to *M. eburnea*. Both bee species showed a higher preference for typical plants in forest environments, enhancing meliponiculture as an economically sustainable practice that can promote forest conservation and the maintenance of stingless forest interactions.

**meliponiculture / plant–bee interaction / meliponini / foraging niche / fragmentation**

## 1. INTRODUCTION

Bee pollination is a key ecosystem service for native and cultivated species (Rosso and Nates-Parra 2005). Together with vertebrates, bees are responsible for pollen dispersal and the pollination of 88% of flowering plants (Angiosperms), both native plants and crop species (Nates-Parra et al. 2008; Ollerton et al. 2011; Reyes-González et al. 2016; Klein et al. 2018). Bee pollination has a key role in crop species, due to their influence on the quantity and quality of food production, and is necessary for approximately 75% of crop species,

which means that the volume of crop production is potentially vulnerable to declines in wild pollinators (Potts et al. 2010; Powney et al. 2019).

Stingless bees of the Meliponini tribe stand out for their great diversity and abundance in the Neotropics and for their fundamental role in plant pollination (Nates-Parra et al. 2008). They are regarded as bioindicators of ecosystem conservation due to their strong mutualistic plant-insect interactions and their high sensitivity to environmental disturbances (Brown and Albrecht 2001). For this type of bee, their response to changes in the floristic composition and vegetation structure of their habitat is highlighted. Additionally, stingless bees respond favourably to the increase in forest masses and the availability of arboreal resources and are sensitive to changes in vegetation

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Handling editor: James Nieh

structure, such as the implementation of agroecological systems (Fisher et al. 2017; Landaverde-González et al. 2017). Colombia embraces a great diversity of stingless bees with nearly 120 species grouped into 14 genera (Nates-Parra and Rosso-Londoño 2015). Some bee species play a fundamental role in the local economy, since farmers commercialize hives by their products, such as honey, pollen, wax, and geopropolis (Reyes-González et al. 2016; Gemim and De Melo Silva 2017).

The constant biodiversity loss associated with high deforestation rates and land use changes is a worldwide problem, with a loss of more than 40% of the natural habitats for bees around the world (Bailey et al. 2010; Fahrig 2010; Xiao et al. 2016; Collado et al. 2019). Furthermore, the reduction in bee populations in recent years has been attributed to anthropogenic disturbances of natural ecosystems, having strong social, economic, and environmental consequences (Brosi 2009; Brown and Paxton 2009; Powney et al. 2019; Potts et al. 2010). Forest fragmentation and land use changes have a strong impact on species richness and abundance (Winfree 2010; Xiao et al. 2016; Theodorou et al. 2020), which deteriorates not only ecosystem structure and function but also species interactions (Valladares et al. 2012; Xiao et al. 2016; Escobedo-Kenefic et al. 2020), and increases the extinction of pollinators as a result of the 50–60% habitat loss, as recorded by Keitt (2009) and Hadley and Betts (2012).

The influence of habitat loss on plant density and pollinators has been recorded in various studies (Potts et al. 2010; Hadley and Betts, 2012; Souza et al. 2018; Escobedo-Kenefic et al. 2020; Stein et al. 2021). Moreover, there is literature showing the effect of forest fragmentation or changes in the floristic composition of vegetation that alter the behaviour of pollinators due to processes of isolation and restrictions in habitat size (Hadley and Betts, 2012). However, individual species' responses and their plant interactions are not fully understood on different spatial and time scales (Blaauw and Isaacs 2014; Teixeira et al. 2016; Gutiérrez-Chacón et al. 2018).

The decrease in forest extensions impacts bee populations by restricting their movement,

increasing isolation (Beismejer and Slaa 2007; Hadley and Betts 2012), and compromising floral resource availability (Volpe et al. 2016). Previous studies have used spatial approaches focused on the diversity variation of stingless bees in response to habitat disturbances (Brown and Albrecht 2001; Zanette et al. 2005; Nates-Parra et al. 2008; Brosi 2009; Meléndez et al. 2012; Xiao et al. 2016; Fisher et al. 2016; Poveda-Coronel et al. 2018; Escobedo-Kenefic et al. 2020). Nevertheless, other factors such as the effects of fragmentation, climatic seasonality, and its influence on the availability of flowering resources have been less understood. These factors are important determinants of stingless bees' behaviour, affecting not only their resource selection but also the species diversity of this group (Poveda-Coronel et al. 2018; Souza et al. 2018; Stein et al. 2021).

In the Andes, forest fragmentation studies have targeted landscape spatial structure analysis, characterized by forest patches and crop fields, such as coffee plantations immersed in grasslands, and agroforestry systems of coffee and natural forests (Nates-Parra and Rosso-Londoño 2015; Fisher et al. 2017; Gutiérrez-Chacón et al. 2018; Armas-Quiñonez et al. 2020). This research aimed to assess changes in the selection of floral resources by two stingless bees (*Tetragonisca angustula* and *Melipona eburnea*) in anthropogenically disturbed natural forests, both at spatial and seasonal scales. This study aimed to answer the following research questions: 1) How do seasonal floral preferences of *T. angustula* and *M. eburnea* vary given a gradient of anthropogenic disturbances on vegetation? 2) Do these floral preferences differ between the two bee species, and are they competing for the same resources?

To answer these questions and identify changes in floral selection and availability in different spatially distributed vegetation coverages and climate seasonality, melissopalynological analyses of artificial hives of both bee species were performed throughout one year. The spatial composition of three vegetation types was also analysed with contrasting anthropogenic intervention levels: secondary forests, fallows, and grasslands located in a premontane forest.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study was carried out in wet and pluvial premontane forests in the municipality of San Carlos, in the Antioquia Department located in the Colombian Andean Central Cordillera (between 6.10 and 6.13°N and 74.58 and 75.2°W). This site has a mean annual temperature of 23°C (IDEAM 2017). The mean annual precipitation varies between 4200 and 4500 mm and is bimodally distributed, with an initial maximum peak of precipitation between April and May and a second between August and October. The vegetation area was constituted by a mix of dense and open secondary forests and fallow vegetation, intertwined with agricultural crops, mainly sugar cane, banana, and grasslands for livestock.

Three different vegetation types with contrasting degrees of anthropic intervention were selected for the study: (1) secondary forests (low intervention degree); (2) fallows, areas covered by early successional vegetation recovered from previous human interventions (medium anthropic intervention); and (3) grasslands, areas with a few trees, associated with livestock activities or human dwellings, in addition to subsistence crops (high anthropic intervention) (Fig. 1).

### 2.2. Bee selection

The selection of these stingless bee species was based on two criteria: (1) body size differences, represented by the intertegular distance: 0.9 mm for *T. angustula* and 3.1 mm for *M. eburnea* (Lopes 2017); and (2) the differences in foraging activities, reflected in their flight ranges and the specificity of resource selection. Although both species are considered generalists regarding the selection of floral resources, *T. angustula* is more plastic in nesting habits and has a broader trophic niche (Morgado et al. 2011; Obregon, 2011; Vaner et al. 2015; Teixeira et al. 2016).

### 2.3. Bee monitoring and sample processing

Thirty-six hives were monitored monthly, corresponding to six hives per bee species (2) and six

hives per vegetation cover (3), for 15 months (February 2018–April 2019). Ten millilitres of honey was collected monthly from each hive. Honey was collected from operculated pots, located in the upper part of the hive to avoid sampling honey stored in previous months.

The samples were prepared using standard protocols for the extraction of pollen (Erdtman 1986; Faegri and Iversen, 1975), with slight modifications due to the destruction of pollen grains by the standard acetolysis method. Therefore, honey samples were diluted with water in a 1:3 ratio (1 honey: 3 water). Samples were placed in a water bath and mixed with 10 ml 10% KOH by vortexing. Pollen grains were counted in an 8 µl sample with a transmitted light microscope until reaching a total of 500 to 550 pollen grains.

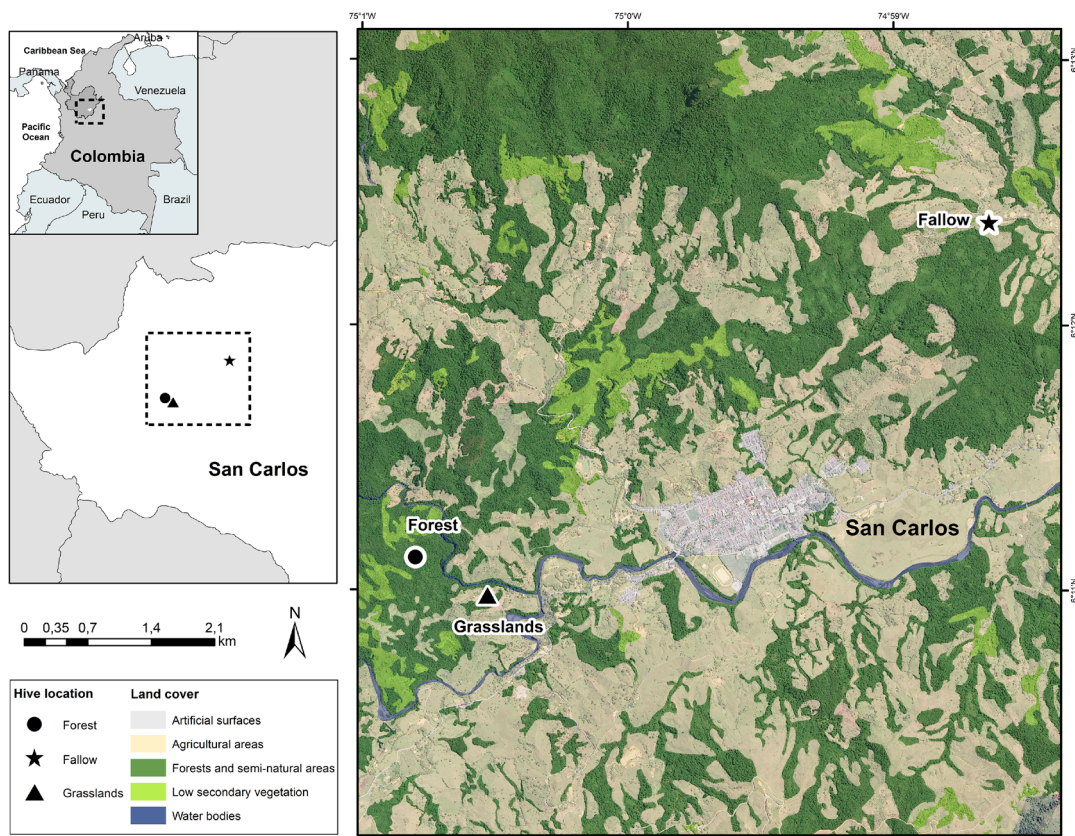
### 2.4. Seasonality of floral resource availability

To analyse the floral resources selected for each bee species, the monthly variation in taxa richness, Shannon-Wiener evenness, and Simpson dominance index were calculated with pollen taxa percentages and represented on a diagram constructed using the C2 1.7.7 software package (Juggins 2007). This diagram presents the percent pollen per bee species counted in each sample for each month and is separated by the three types of vegetation cover. Differences in the pollen taxa among vegetation coverage were identified using Student's *t* test, with a significance level of 0.05 (R package STAT 0.1.0; Bolar 2019).

A redundancy analysis (RDA; CANOCO 4.5 software; ter Braak and Smilauer 2002) was conducted to detect the relationship between pollen taxa (selected by each bee species) and precipitation (49 to 790 mm/month), extreme temperatures (16 to 32°C), and relative humidity (63 to 86%). This analysis was coupled with the phenological status of the plant species (Fournier 1974) as an indicator of floral diversity.

### 2.5. Foraging niche

To analyse the differences in pollen taxa composition used by each bee species across the three vegetation covers throughout the study, cluster



**Figure 1.** Location of the hives monitored for 15 months in three vegetation covers: forest, fallow, and grasslands.

analysis was performed using the Jaccard similarity index (R package *Vegan* 2.5–5; Oksanen et al. 2019). This index was chosen to compare the sites based on the presence-absence of species and its insensitivity to double zeros or absences in two land covers. An analysis of similarities (ANOSIM) was made to check the dissimilarities between the set of samples and the possible significant differences of the cluster (R package *Vegan* 2.5–5; Oksanen et al. 2019).

In addition to these tests, multiscale bootstrap resampling for hierarchical cluster analysis was carried out using the package *Pvclust* (Suzuki et al. 2019). This test provides an ‘SI’ (selective inference)  $p$  value, ‘AU’ (approximately unbiased)  $p$  value, and ‘BP’ (bootstrap probability) value for each cluster in a dendrogram. An alpha of 0.1 for significance and Euclidean distances were used.

Degrees of interaction specialization were assessed by measuring two properties of the interaction network: (1) the bee specialization index ( $d'$ ), which reflects how specialized a bee species is with respect to the available floral resources, ranging from 0 (little specialization) to 1 (high specialization) (Blüthgen et al. 2006); and (2) the resource range index, which expresses the variability in the floral selected resources (Alarcon et al. 2008), and presents values of 0 when all species are used, and 1 when only one species is used.

To avoid the influence of the dynamic interaction between species at two levels, for the network metrics (Dormann 2019), Patefield’s algorithm was used to simulate 1000 random interaction networks for each bee species in each land cover (forest, fallow, and grassland). Then,  $\Delta$ -transform was computed for each network, which reflects

the degree to which a network metric deviates from a random expectation (Dalsgaard et al. 2017; Escobedo-Kenefic et al. 2020; Stein et al. 2021). In addition, the Kruskal–Wallis test was used to compare these group-level indices between land covers and bee species. All analyses were processed with the R Bipartite 2.13 package (Dormann et al. 2009, 2019) and represented in a bipartite graph constructed with the R D3 0.2.0 Bipartite package (Terry 2019).

### 3. RESULTS

#### 3.1. Temporal responses of bee species to contrasting degrees of intervention

The greatest accumulated pollen-taxa richness throughout the studied period was recorded in the fallow cover by both bee species, with 33 and 40 pollen taxa for *M. eburnea* and *T. angustula*, respectively.

*M. eburnea* did not present significant differences in richness, evenness, or dominance of the visited plant taxa among vegetation coverages. In the case of *T. angustula*, pollen-taxa richness was significantly different between hives located in grasslands and fallows ( $p = 0.0118$ , Table I). *T. angustula* had significantly higher pollen-taxa richness than *M. eburnea* for hives located in both forests and fallows ( $p < 0.05$ ). In contrast, no differences were found between the two bee species (data not presented) in the evenness and dominance of pollen taxa between the vegetation coverages.

#### 3.2. Seasonal availability of flower resources

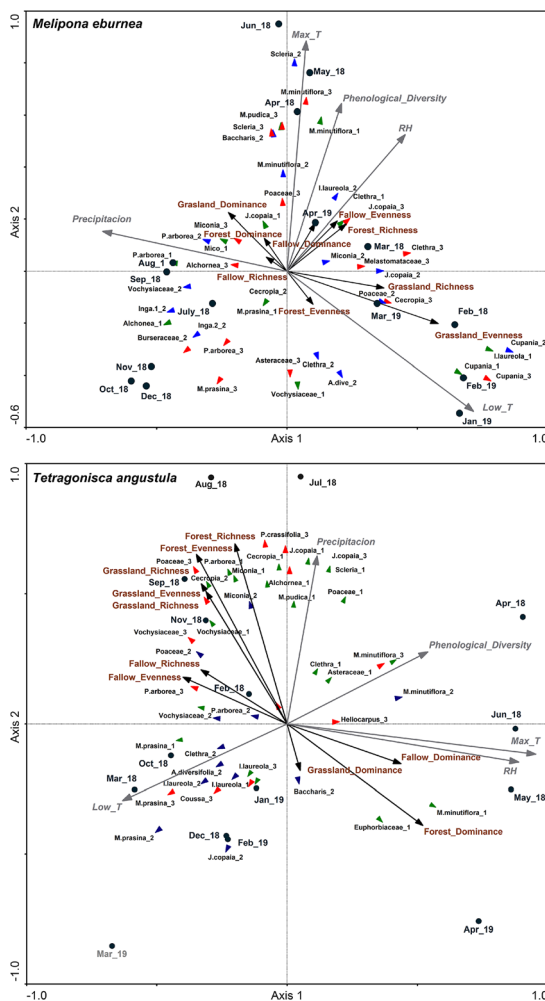
The pollen of genus *Miconia* (mainly *Miconia minutiflora*) had the highest dominance levels (Simpson index between 0.7 and 0.9) among all plant species selected by *M. eburnea* throughout the analysed period.

For *M. eburnean*, a clear variation was observed in the floral resources selected during the 15 months, driven mainly by precipitation seasonality and flower availability in the standing vegetation. There was an inverse relationship between precipitation seasonality and flower availability. The first two axes of the RDA explained 72% of the pollen percentage variance in the floral species selected by *M. eburnea*, with eigenvalues of 0.18 and 0.12 on the first and second axes, respectively (Fig. 2, Top; Table S1). The first axis was related to the amount of precipitation, with the highest intersect correlation value of  $-0.6$  (Table S1). On the left side of the plot, the rainiest months of the year were grouped when a reduction in the pollen taxa selected by *M. eburnea* was detected, due to the strong diminution of floral available resources. A few taxa registered a relevant selection (more than 50% of total pollen count; Fig. S1), such as *P. arborea*, *Miconia prasina*, and species of the family Vochysiaceae, which flowered from August to September. On the right side, in contrast, the plot presented the driest months related to the honey samples with the highest values of pollen-taxa richness related to the increase in flowering species during this season. In general,

**Table I.** Significance levels ( $t$ -test;  $p < 0.05$ ) of the comparison of pollen richness in both bee species (*Tetragonisca angustula* and *Melipona eburnea*) at each vegetation coverage (forest, fallows, and grasslands).

	<i>M. eburnea</i> Forests	<i>M. eburnea</i> Fallows	<i>M. eburnea</i> Grasslands
<i>T. angustula</i> Forests	0.0041*	0.1384	0.046*
<i>T. angustula</i> Fallows	3.26E-02*	0.0059*	0.0009*
<i>T. angustula</i> Grasslands	0.0619	0.8431	0.4562

\*Significant differences at the 95% confidence level



**Figure 2.** Biplot of the RDA results performed with the percentages of pollen per month recorded in the honey of *Melipona eburnea* (Top) and *Tetragonisca angustula* (Bottom). The samples are represented by the collection dates of each sample (●). The dotted arrows represent each recorded pollen taxon. The colours of the arrows show the vegetation coverage where each taxon was recorded: forest (green arrow →), fallow (blue arrow →), and grasslands (red arrow →). The number that accompanies each taxon indicates the coverage in which it was recorded, as follows: Taxa name\_1 (Forest), Taxa name\_2 (Fallow), and Taxa name\_3 (Grasslands). The solid black arrows (→) correspond to the diversity registered in each vegetation coverage: Equi = Shannon evenness index, Dom = dominance of Simpson index, Rich = richness of pollen taxa in honey samples. The solid grey arrows (→) correspond to the environmental variables that affect the diversity of the floral availability in the standing vegetation, T\_min = minimum temperature (recorded every 30 min), T\_max = maximum temperature (recorded every 30 min).

the fallow cover offered the greatest diversity of plant species among the studied land covers during the months sampled.

Despite that, during the minor second dry season of the year (May–June; Fig. 2, Table II), the three vegetation coverages registered the highest

plant diversity and the highest temperature. *M. eburnea* in this season had the highest dominance value of selected plant species, related to the massive flowering of *Mi. minutiflora*, which increased the pollen resources more than 90% during this period (Table II, Fig. S1). During the

wet season (August–November, Fig. 2), the reduction in diversity of the plant taxa selected by this bee species was reflected by the change in dominance of the selected pollen taxa, which changed from *Mi. minutiflora* to *Mi. prasina* in response to massive flowering (Table S3, Fig. S4).

*T. angustula* also showed temporal variation in the selection of floral resources. The first two axes of the RDA (Fig. 2; Table S1) explained 66% of the variance in pollen percentages of selected plant taxa, with eigenvalues of 0.49 and 0.17 for the first and second axes, respectively. Along the first axis, the extreme temperatures decreased from right to left, and they were strongly related to the selection of the floral resources, with an intersect correlation value for the highest temperature of 0.58. When the maximum phenological diversity was recorded, maximum values of dominance were recorded in the three coverages. This pattern was reflected for *T. angustula* in the second dry season (May and June, Fig. 2), when it presented a greater preference for pollen taxa from Melastomataceae. The dominance of *Mi. minutiflora* (Simpson index between 0.8 and 0.9, Table II) on the three vegetation coverages had a relative abundance above 70% (Fig. S2)

in response to the flowering peak (Table S3, Fig. S4).

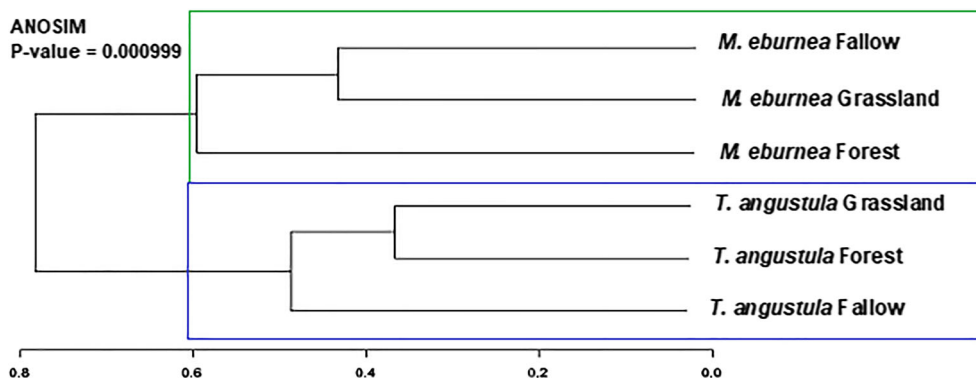
Precipitation was the variable with the highest correlation value (0.604) for the second axis, and it was related to the wettest months (August–September) when *T. angustula* recorded the highest diversity in pollen taxa selected in the three vegetation coverages. This diversity in the selected pollen taxa by *T. angustula*, contrasted with the lower availability of flowers compared to the dry season, presenting a pattern of diversification in selected resources, with a high pollen percentage in species such as *P. arborea*, *J. copaia*, and *Cecropia* spp. This pattern was in contrast to that of *M. eburnea*, which showed the highest diversity during the dry season.

### 3.3. Foraging niche overlap

Cluster analysis with the pollen taxa recorded in sampled honey throughout the 15 months divided the samples into two groups according to bee species, and within each group, three subgroups were found, corresponding to the floristic composition of the three vegetation coverages (Fig. 3), evidencing clear differences in pollen taxa composition, with a *p* value of 0.000999

**Table II.** Summary of the pollen record variation between seasons for both bee species (*Tetragonisca angustula* and *Melipona eburnea*) at each vegetation coverage (forest, fallows, and grasslands).

Season	POLLEN RECORD	
	<i>Melipona eburnea</i>	<i>Tetragonisca angustula</i>
<b>Dry season</b>	Forest <i>I. laureola</i> (60–80%) <i>Clethra</i> sp. (50%) <i>Jacaranda copaia</i> (10%) Fallow and Grassland <i>M. minutiflora</i> and <i>Cupania</i> (40–60%) <i>Alchornea</i> (20%) Asteraceae (20%)	Forest, Fallow, and Grassland Dominance was high in response to the high preference for Melastomataceae taxa During the transition between dry and wet periods, <i>M. prasina</i> (> 80%) was preferred, followed by <i>I. laureola</i> , <i>Clethra</i> spp., and <i>Cupania</i> spp.
<b>Rainy season</b>	Forest, Fallow, and Grassland Lower richness and greater pollen taxa dominance <i>Clethra</i> sp. (40%) <i>P. arborea</i> (50%). Vochysiaceae (40%) Burseraceae (60%)	Forest, Fallow, and Grassland Greater taxa richness in floral resources <i>P. arborea</i> (higher than 50%) Others included Vochysiaceae, Burseraceae, Cyperaceae, Poaceae, and Asteraceae.



**Figure 3.** Diagram of cluster analysis of the pollen taxa registered in the hives throughout the sampled period (February 2018–April 2019), separated by vegetation coverage and bee species. (Jaccard similarity index and ‘complete’ method)

according to the ANOSIM. Additionally, this aggrupation of bee species can be detected at first, and then between three types of cover vegetation, with an *AU* (approximately unbiased) *p* value > 90% (Fig. S3).

The interaction network of each bee–plant species recorded in honey with respect to vegetation cover is presented in an interactive graph available for download at: (<https://drive.google.com/open?id=1IiO8QETC8IFCABe6KTBnqlwzdnVwF7fT>). *Mi. minutiflora* is not only a preferred resource used by both bee species, but it also comprised 33.29% of the total pollen proportions recorded in honey of the two species of bees throughout the sampling period. Other taxa, such as *M. prasina* (19.61%), *Pera arborea* (8.38%), *Clethra* spp. (7.73%), and *Ilex laureola* (6.51%), also were highly preferred by both bee species throughout the study period, mainly by *M. eburnea*.

*M. eburnea* recorded higher values on the *d'* index than its counterpart (Table S2), with values ranging between 0.20 and 0.28, while *T. angustula* presented lower values on this index (between 0.06 and 0.18). The same trend was recorded by the resource range index, where *T. angustula* presented the lowest values (between 0.03 and 0.13; Table S2). Significant differences (*p* value < 2.2e−16) were found between land cover and bee species for this specialization index (Fig. 4), suggesting a wider trophic niche or higher generalism in the selected floral resources for *T. angustula* compared to *M. eburnea*.

## 4. DISCUSSION

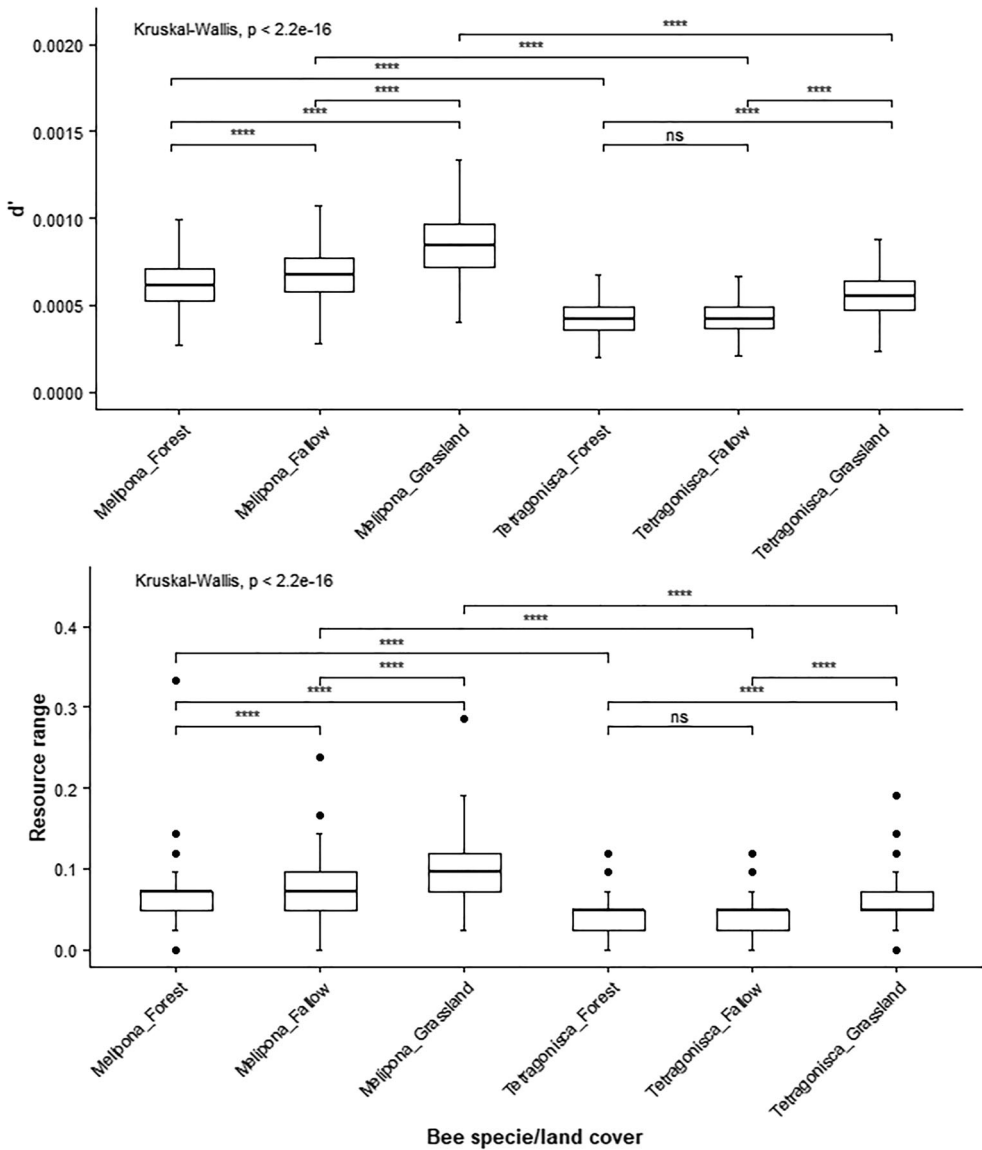
### 4.1. Relationship between vegetation coverage and floral preferences

Despite being considered generalist stingless bee genera, *Melipona* and *Tetragonisca* have shown a predilection for certain taxa that can be interchanged according to their seasonal availability (Flores and Sanchez, 2010; Rogel and Roubik 2016). *T. angustula* and *M. eburnea* presented floral preferences for tree species typical of native forests in the study area throughout the year. However, some changes in flower selection were observed due to floral resource availability related to monthly precipitation and extreme temperature fluctuations.

In contrast to our expectations, *M. eburnea* and *T. angustula* did not show differences in the selection of floral resources among the three different land cover types (forest, fallow, and grasslands), as demonstrated by Student’s *t* test. This pattern was related to the high preference in the diets of both bee species for typical species of the native forests, despite being considered generalist species and presenting different flight ranges.

Although there were no differences in resources between the land cover types, the highest pollen richness was recorded for the two bee species in the fallow areas. This may be related not only to the high plant species richness, typical of intermediate successional stages, but also to the diversity of plant growth forms found there





**Figure 4.** Network metrics. Bee specialization ( $d'$ ) and resource range index from the interaction network between bee species and vegetation coverage.

(Roberts et al. 2017; Fahrig et al. 2019). This pattern was also detected in studies where intermediate disturbances and edge effects, in some cases, benefited the supply of floral resources and increased the diversity of bee species (Hadley and Betts, 2012; Fisher et al. 2017; Landaverde-González et al. 2017; Armas-Quíñonez et al. 2020). These results highlighted the importance of forest conservation for the provision of nesting

resources for these stingless bee species and encourage the advancement of the succession of secondary forests, which are fundamental in the provision of floral resources for bees. Such land cover combinations would also have benefits for alloyed agriculture systems by increasing the diversity and abundance of pollinators in the areas (Samnegård et al. 2015; Landaverde-González et al. 2017; Armas-Quíñonez et al. 2020).

Conversely, neither species showed a predilection for garden plants grown near houses (observed in grassland cover), indicating possible negative effects due to the conversion of natural covers to grasslands and agricultural areas, which would not provide the quantity and quality of the required flowering resources. This was also detected in a meta-analysis carried out by De Palma et al. (2016), where negative effects of agricultural expansion on the composition of bees were found, mainly in ecosystems of South America.

Accordingly, both studied bee species preferred floral resources from tree and shrub species of Melastomataceae, Peraceae, and Vochysiaceae families and herbs of Asteraceae, as recorded in other studies on stingless bees (Flores and Sanchez 2010; Morgado et al. 2011; Obregon 2011; Braga et al. 2014; Nazareno et al. 2014; Fisher et al. 2017; Morgado et al. 2018; Souza et al. 2018; Vossler 2019).

Both bee species showed a seasonal variation in the selection of floral resources in response to floral availability related to precipitation and extreme temperature changes. *M. eburnea* recorded the lowest accumulated richness of pollen taxa during the rainy season, when honey samples were dominated by pollen of *Cupania* spp., *Ilex laureola*, *Pera arborea*, and *Vochysia* spp. The effects of climatic conditions on floral phenology and honey production have been reported previously (van Schaik et al. 1993; Aleixo et al. 2016). In particular, in the Colombian Andean region (Obregon, 2011), the distribution of floral resources and their selection by *M. eburnea* were influenced by precipitation, and the dry season occurred during the El Niño-Southern Oscillation phenomenon.

For *T. angustula*, unlike *M. eburnea*, the highest taxa richness of the year occurred during the most intense rainy season or during the transition from dry to wet seasons. As a generalist species, *T. angustula* collects a wider variety of floral resources (Aleixo et al. 2016), including herbaceous and shrubby anemophilous plants of the families Poaceae, Piperaceae, Urticaceae, Asteraceae, and Cyperaceae, which could offset the reduction in tree flowering during the wettest periods (Roulston and Cane 2000; Obregon 2011), as these taxa have flowers throughout the year (Oliveira 2009).

Several studies have also recorded the use of anemophilous plants by stingless bees (Barth 2004; Sierra and Smith 2008; Oliveira 2009; Lopes 2012; Freitas and de Novais 2014; de Novais and Absy 2015; Ferreira and Absy 2017; Absy et al. 2018; Radaeski et al. 2019; Rezende et al. 2019) in other tropical forest ecosystems, such as humid forests in Colombia (Obregon, 2011) and the Atlantic Forest in Brazil (Morgado et al. 2011, 2018; Braga et al. 2014). In the field, *T. angustula* was often observed foraging these anemophilous plants and adding their pollen loads to honey pots in the hives, highlighting the variety of plant resources involved in the diet of Meliponini bees (Lorenzon and Matrangolo 2005; Aleixo et al. 2016; Vijayakumar and Jeyaraj 2016; Villanueva-Gutiérrez and Roubik 2016; Bobadoye 2017; Absy et al. 2018).

Notably, the high preference for plant species of the Melastomataceae family was recorded in both bee species. For the case of *Melipona* bees, this is related to their poricidal anthers and the vibration capacity of the flight muscles of these bees (buzz pollination) to extract pollen (Roulston and Cane 2000; Obregon, 2011), which makes this an even more specialized relationship (Barth 2004; Nazareno et al. 2014). *Mi. minutiflora* and *Mi. prasina* were the most important plant species for the studied bee species due to their mass flowering near the hives, which decreases energy costs by exploiting more abundant resources, as previously recorded (Nazareno et al. 2014; Valverde, 2016). These two *Miconia* spp. bloom year-round but are asynchronous, alternating flowering peak events in response to rain distribution. The mass flowering of *Mi. prasina*, which occurs during the rainy season, becomes a key resource for this period due to the reduced availability of floral resources in all vegetation coverage, with a consequent decrease in honey production, especially for *M. eburnea*.

In contrast, the preference for species of Melastomataceae by *T. angustula*, which lacks the ability to vibrate, is also related to its high abundance and mass flowering registered in the study zones. However, *T. angustula* is an opportunistic generalist and a small bee (Morgado et al. 2011; Lopes 2017), which allows greater mobility and plasticity in the selection of resources

(Morgado et al. 2011; Obregon, 2011), as well as access to floral nectaries and pollen released by the vibration performed by other bees. Although *T. angustula* also showed seasonality in the selection of floral resources throughout the year, both due to flower availability and climatic conditions, its hives displayed a higher richness of pollen taxa compared to *M. eburnea* in the three study zones related to such opportunistic behaviour.

This climatic variation, observed in changes in rainfall regime and temperatures, affected stingless bees mainly by modifying the structure of the bee community and causing their diversity to fluctuate between wet and dry seasons due to the availability of floral resources, which contributes to the increase or decrease in bee species (Samnegård et al. 2015; Dalsgaard et al. 2017; Landaverde-González et al. 2017; Poveda-Coronel et al. 2018; Souza et al. 2018; Escobedo-Kenefic et al. 2020). Similarly, other studies have identified a seasonal pattern with greater availability of floral resources in times of lower precipitation and a greater selection of resources, mainly for *M. eburnea*.

Moreover, the effects of changes in seasons linked to the availability of resources have been evidenced in several investigations (Do Nascimento and Nascimento 2012; Samnegård et al. 2015; Armas-Quíñonez et al. 2020; Theodorou et al. 2020), where bottom-up effects (from flowering plants to bees) were highlighted. The behaviour, diversity, and foraging activity of bees are addressed by the flowering seasons, availability, and quality of floral resources. Do Nascimento and Nascimento (2012) presented a pattern of variation in *M. asilvai* hive activity directed by the season and flowering. The authors recorded higher activity for this type of bee in drier periods and with greater available resources, which is similar to the pattern detected for the case of *M. eburnea* during the months of lower precipitation.

#### 4.2. Interspecific competition for foraging niches

The differences between the floristic composition of pollen taxa found in honey samples of *T. angustula* and *M. eburnea* were mainly related to the narrower and more selective trophic range

of *M. eburnea* ( $d2'$  index  $< 0.18$ , Fig. 4), reflected in their lower pollen taxa richness in the honey samples. *T. angustula* showed a wider trophic niche (Fig. 4) and is considered a more generalist and plastic species (Morgado et al. 2011; Obregon, 2011) that is better adapted to changes in climatic conditions and resource availability (Morgado et al. 2011; Obregon, 2011). (see Fig. 4).

These differences in the floral resources selected by each bee species were also related to intrinsic factors, such as the effective flight distances (Araújo et al. 2004; Obregon, 2011; Figueiredo-Mecca et al. 2013; Aleixo et al. 2016). Despite the greater flight radius, *M. eburnea* has lower recorded pollen taxa diversity, due to the fact that their resources were concentrated throughout the year in a smaller plant taxa group. *T. angustula* has a narrower flight range, which would be thought to restrict accessibility to a wider range of floral resources. However, *T. angustula* showed higher pollen taxa richness, probably due to its generalist behaviour and use of resources not only from trees, but also from shrubby and herbaceous plants (Roubik and Moreno, 2009). Thus, *T. angustula* was less selective of floral resources, as found in the variety of resources selected in fallow coverage. External factors, such as climatic variations and changes in floral availability, also play a key role in patterns of bee visitation to flowers, as previously explained in our and other research (Do Nascimento and Nascimento, 2012; da Silva et al. 2013).

The overlap of the trophic niche, evidenced by the simultaneous use of *Ilex laureola*, *Pera arborea*, and *Miconia* spp. by both bee species detected in the bee–plant interaction network, reveals an interspecific competition (Braga et al. 2014; Nazareno et al. 2014; Maia et al. 2015; Morgado et al. 2018; Souza et al. 2018). Niche overlap was evident during massive and abundant plant flowering during the dry season, as reflected by the Fournier index values and the RDA of both bee species, which allowed trophic niche partitioning, as observed in other studies (Obregon, 2011; Roulston and Cane 2000; Valverde, 2016).

Although the network metrics indicated that *T. angustula* is more of a generalist than

*M. eburnea*, both species had a higher specificity and lower range of resources in the most anthropised coverage (grasslands), in response to the limited floral resources available, as reflected in a smaller selection of pollen taxa. This effect of environment with lower floral availability, due to seasonal changes or human transformation, has been identified in other studies (Souza et al. 2018; Escobedo-Kenefic et al. 2020), where the networks were more compact with a greater degree of specialization in response to limited resources, as well as a reduction in bee diversity and number of interactions (bee–plant), as a consequence of the land use intensity and land-cover transformation (Stein et al. 2021).

Despite differences in the width of the trophic niches, both bee species preferred floral resources from tree species across the sampling period, indicating the importance of nearby forests in ecological plant–bee interactions. This pattern likely responds to a trade-off between foraging and the quality of floral resources (Eltz et al. 2001). In this study, it was evident that tree species represent an important resource for both bee species. This resource provided by trees is so important that it compensates for the long dispersal of bees found in areas dominated by pasture to remnant forest patches in search of food, as evidenced by *M. eburnea* and *T. angustula* located in the most transformed cover (grasslands). This selection of resources used by the studied stingless bees was driven by phenological diversity, weather conditions, and mass flowering peaks, in addition to the food quality offered by tree species, as observed in other studies (Obregon, 2011; Aleixo et al. 2016).

Our results highlight the importance of conserved environments with larger interconnected forest patches to provide a greater diversity and richness of floral resources and to maintain a constant flow of the pollinator–plant interactions, or more specifically, bee–forest interactions, especially for these types of bees, which have been recognized as sensitive to fragmentation processes (Escobedo-Kenefic et al. 2020). The importance of preserving these ecological interactions is noteworthy, not only as a conservation strategy for native bees, but also to

implement meliponiculture as an economically sustainable practice, reducing deforestation rates and promoting forest conservation that guarantees ecosystem services.

## ACKNOWLEDGMENTS

We are grateful to the farm owners for their support and goodwill during the field phase; and to the forest engineers María Cristina Vargas and Carolina Álvarez, for their collaboration monitoring the hives.

## AUTHORS' CONTRIBUTIONS

All authors contributed to the study conception and design of the project.

## FUNDING

This research was carried out under the project “Identification of relationships established by *M. eburnea* and *T. angustula* bees, with local flora and microorganisms associated with honey; the physico-chemical quality and temporal variation of honeys associated with climatic variables of San Carlos and San Rafael municipalities”, sponsored by the Regional Autonomous Corporation (CORNARE), ISAGEN, Empresas Públicas de Medellín (EPM) and the National University of Colombia, in Medellín, Colombia.

## AVAILABILITY OF DATA AND MATERIAL

The data sets generated during the current study will be available from the corresponding author on reasonable request.

## CODE AVAILABILITY

The code made in the research was presented as a supplementary data.

## DECLARATIONS

**Conflicts of interest/competing interests** This paper has not been published before and it is not under consideration for publication anywhere else. If accepted, it will not be

published elsewhere in the same form, in English or in any other language, including electronically without the written consent of the copyright holder.

**Ethics approval** Not applicable.

**Consent to participate and publication** This manuscript has been approved by all co-authors, and by our University. Declarations of interest: none. The publisher will not be held legally responsible for any claims for compensation.

**Influence de la fragmentation des forêts et de la saisonnalité sur le choix des ressources florales de deux espèces d'abeille sans dard.**

**méliponiculture / interactions plante-abeille / Meliponini / niche alimentaire / fragmentation.**

**Einfluss von Waldfragmentierung und Saisonalität auf die Blütenressourcen-Wahl zweier Stachelloser Bienenarten.**

**Meliponikultur / Pflanze-Bienen Interaktionen / Meliponini / Nahrungsnische / Fragmentierung.**

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