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Vertical stratification in orchid bees (Apidae: Euglossini)?: a meta-analysis

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Abstract – Vertical stratification of animal assemblages has been observed in several arthropod taxa. However, for some groups there is conflicting evidence, such as for the neotropical orchid bees. Here, we used a meta-analysis to evaluate trends in abundance and diversity of euglossine bees across strata. We found no evidence of stratification in terms of diversity, but abundance was higher in the understory. Our results highlight the effect of sampling technique as a source of heterogeneity. For instance, studies that used McPhail traps reported higher diversity, higher similarity between strata, and were more accurate for quantifying abundance, as compared to improvised traps. Studies that used higher number of bait types sampled higher diversity in general. The higher abundance in the understory tended to decrease with the number of bait types used. Variables like elevation and latitude of the study influenced bees' distribution. We also discuss other influential variables, ecological implications, and recommend areas for future research.

Canopy / Neotropics / Orchid bees / Understory / Vertical stratification

1. INTRODUCTION

Vertical stratification of the vegetation in tropical forests generates marked differences in physical and biological characteristics between the canopy and the understory (Shuttleworth et al. 1984; Valladares et al. 2016). This vertical heterogeneity may be related to factors such as microclimate variation in temperature, humidity,

light, or biotic interactions such as competition, predation, or niche differentiation (Basset et al. 2003; Ulyshen et al. 2011). Consequently, this can generate vertical stratification in the distribution of organisms associated with each stratum (Dowdy 1951). Evidence of stratification in animals has been widely reported in arthropods, showing that communities can vary between vertical strata in ants (Brühl et al. 1998), butterflies (Devries and Walla 2001), collembolans (Rodgers and Kitching 1998), beetles (Charles and Basset 2005), flies (Maguire et al. 2014), parasitoid wasps and flies (Giovanni et al. 2017;

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Šigut et al. 2018), among other orders of insects (Basset et al. 2001; Neves et al. 2014).

However, it is unclear whether such stratified distribution exists for other insect assemblages, as in the case of euglossine bees (Apidae: Euglossini), commonly known as orchid bees, a tribe with around 230 recognized species (Nemésio and Rasmussen 2011), which are important pollinators in the neotropics (Ackerman 1986). Orchid bee males collect natural scents (e.g., from flowers) that they use to attract females (Eltz et al. 1999) and one consequence of this behavior is that males can be sampled by means of chemical baits to estimate diversity and abundance (e.g., Powell and Powell 1987; Roubik and Ackerman 1987; Roubik 2001; Nemésio 2013; Nemésio et al. 2015; Ramírez et al. 2015). However, the use of chemical baits for evaluating whether abundance and diversity vary across vertical forest strata has not produced conclusive results. While some studies reported apparent abundance and diversity stratification, particularly reporting higher values in the understory (Martins and Souza 2005; Otero and Sallénave 2003; Reyes Ledezma et al. 2020; Roubik 1993; Santos-Murgas et al. 2012; Vilhena et al. 2017), others suggested higher values in the canopy (Ferreira et al. 2011; Oliveira and Campos 1996; Santos-Murgas 2014; Santos-Murgas et al. 2011) or even parity between strata for some or all of the estimates (Ferreira et al. 2011; Vega-Hidalgo et al. 2020; Vélez and Pulido-Barrios 2005).

Evidence of vertical stratification in flying insects comes from different taxa (Brehm and Axmacher 2006; Fermon et al. 2005; Sutton et al. 1983); however, as euglossine males can fly relatively long distances (from 2 to 50 km, Pokorný et al. 2015), it might be expected that they would not be solely restricted to one stratum. Alternatively, some orchid bees could be associated with the distribution of their floral resources within a particular stratum, as is seen in other neotropical bees (Ramalho 2004). Moreover, variation in results across studies may be in part due to the different sampling designs (e.g., type of trap, sampling effort) together with

the abiotic and biotic conditions inherent to each study site, such as latitude and elevation. We expected improvised traps with variable designs made from plastic bottles to generate more variation in results across studies when comparing bee community composition between the understory and canopy than factory-made McPhail traps with an invariable design. Here, we used a systematic review to carry out a meta-analysis of the current literature to evaluate whether abundance and diversity of orchid bee communities vary across forest strata and we also evaluated potentially influential variables. This work contributes to understanding patterns of insect community composition in the canopy, which has been historically less studied than the understory. Understanding stratum variation in euglossine communities may shed light on the importance of these bees for plant diversity patterns in the neotropics, given their importance as pollinators (Ackerman 1983).

2. MATERIALS AND METHODS

2.1. Systematic review

We were aware of all the studies about “stratification” in orchid bees, with a total of 13 articles published between 1993 and 2020. However, we corroborated this by performing searches in Web of Science (WOS), Google Scholar, Dimensions, and the journal portals of the University of Panama (Table S1). We performed the searches during January of 2021 and kept articles that compared the canopy and understory in terms of diversity and abundance. For instance, in Web of Science, we searched for the topic “orchid bee” or “orchidbee” and refined the search afterward with the terms “canopy” or “understory” or “dosel” or “sotobosque.” In Google Scholar, we used the terms “abejas de las orquídeas” or “orchid bee” and “estratificación vertical” or “vertical stratification.” Overall, we did not find additional studies from any of these search engines. To give an example, the WOS search yielded 19 studies, but after excluding the

ones that corresponded to other types of studies, only five were appropriate to our parameters, and those were already included in our original dataset. Details on the search results for all engines are provided in the supplementary material (Table S1), and we also used the list of references cited by each study as a method to find all the studies on vertical stratification of orchid bees (Table S2).

2.2. Overview of selected studies

These studies were carried out in locations ranging from 0 to 1000 m above sea level in Panama (7), Brazil (4), Colombia (1), and Peru (1). Regarding the sampling time, five studies sampled one or two times in one particular year (cross-sectional studies). The other eight studies carried out long-term samplings in both the dry and rainy seasons (longitudinal studies).

Sampling methods included McPhail traps (inverted funnel and factory made, Figure S1A) and manually modified plastic bottles (hereafter bottle, Figure S1B), using bait types such as eucalyptol, methyl salicylate, eugenol, skatole, 1.8-cineole, vanillin, benzyl acetate, methyl cinnamate, β -ionone, benzyl benzoate, β -myrcene, thyl butyrate, linalool, methyl benzoate, and 2-phenyletanol. Traps were placed in the understory (0.5–1.8 m) and canopy (11–38 m) but two studies included a stratum between the canopy and understory (Santos-Murgas et al. 2011; Vélez and Pulido-Barrios 2005). The sampling effort was variable in each study with a range of 6 to 2880 trap days.

2.3. Data analysis

2.3.1. Species richness and diversity

To standardize results across studies using different types of analysis, we extracted the species richness data for the canopy and understory from each study. The alpha diversity indices were calculated for each stratum (canopy and understory): Simpson's diversity index (1-D), species

equitability index (J), Shannon index (H), and dominance (D). Additionally, we calculated Bray–Curtis dissimilarity (Sb) indexes, which is a measure of beta diversity (dissimilarities) between the two strata (Magurran 2004).

We performed comparisons of the Simpson index (dominance, D) and Shannon index (H) between the strata by using a Simpson t -test (Brower et al. 1998) and a Shannon t -test (Hutcheson 1970), using PAST 3.26 (Hammer et al. 2001). In addition, a paired t -test was applied to both indices using the function *t.test* in R (R Core Team 2021). We used a linear model (LM, function *lm*) to explore potential variables influencing Shannon indices. We included “type of trap” (Mcphail vs. bottle) and “type of study” (cross-sectional vs. longitudinal) as categorical variables and as covariates we included “latitude of the study site,” “elevation of the study site,” “number of trap days” (number of sampling days multiplied by number of traps used), “trap height,” and “number of bait types.” We simplified the full model in terms of the second-order Akaike Information Criteria (AICc). We also evaluated the effect of the same variables on the Bray–Curtis distances by using a linear model, after square root transformations, and we simplified it in terms of AICc.

2.3.2. Abundance

Abundance of each species per stratum was used as replicates and mean differences were calculated to represent the effect size of each study. This method is not applicable for the analysis of diversity or species richness since these indexes consisted of one value per stratum per study (without replications). Most studies provided the raw data from which we calculated the mean, standard deviation, and sample size for each stratum. Besides, part of this information was obtained from the text. For Roubik (1993) and Vélez and Pulido-Barrios (2005), we extracted information from the figures by using the software ImageJ (Schneider et al. 2012). In order to assess whether abundances varied between strata, we calculated the standardized mean difference (Hedge's g), which is the difference

between the means of canopy and understory, as described by Borenstein et al. (2009), which incorporates a correction term for small sample bias. This correction term uses sample sizes for the estimation and since the number of bees collected per study depends on both the number of sampling days and number of traps used, we used the sampling effort (sampling days multiplied by number of traps) as the correction term. Therefore, studies with larger sampling effort were given more weight in the meta-analysis. A positive effect size value indicated higher abundance in the canopy and a negative value indicated higher abundance in the understory.

We performed the meta-analysis of abundances with the function *rma.mv* (package *metafor*) in R. We first calculated a weighted average effect size for a fixed effect model with maximum likelihood, followed by a heterogeneity test (*Q*). A significant *Q* value indicated that effect sizes were heterogeneous across studies, and therefore we used a random effects model that included the same moderator variables used for the linear and linear mixed models previously described. We included country as a random factor in all analyses and considered an effect size value significant if the 95% confidence interval did not include zero.

2.4. Results

2.4.1. Species richness and diversity

A total of 97 species were reported in the 13 studies. For the understory, 84 species were reported, and 85 species were reported for the canopy. Out of this total, 12 species were found only in the canopy and 13 species were found only in the understory (Table 1S). The number of species collected varied between studies, ranging from 4 to 33 species collected in the understory and 3 to 35 species in the canopy.

Dominance was equally low in both the understory (*D*, mean \pm sd = 0.28 ± 0.16) and in the canopy (*D*, mean \pm sd = 0.28 ± 0.16 , df = 12, *p* = 0.96). Species equitability was relatively high in both the understory (*J*,

mean \pm sd = 0.67 ± 0.13) and canopy (*J*, mean \pm sd = 0.74 ± 0.15). Overall, species diversity did not vary between the two strata as measured with Shannon indices (understory: mean \pm sd = 1.75 ± 0.54 ; canopy: 1.76 ± 0.72 ; *t* = 0.08, df = 12, *p* = 0.94) or Simpson's diversity indices (1-*D*; understory: mean \pm sd = 0.27 ± 0.15 ; canopy: 0.27 ± 0.16 , *t* = 0.05, see LM below). However, seven studies showed differences in the two strata in terms of dominance (*D*) of species and diversity (*H*, Fig. 1). Out of the seven studies, three found a higher diversity in the canopy (Fig. 1) and four found higher diversity in the understory (highlighted red in Fig. 1). Finally, Bray–Curtis beta diversity distances (Sb) ranged between 0.11 and 0.42 (mean \pm sd: 0.29 ± 0.20).

Shannon diversity indexes were not influenced by the stratum (*t* = -0.05 , *p* = 0.96), absolute latitude (*t* = -0.62 , *p* = 0.54), or the sampling effort (*t* = -0.95 , *p* = 0.35). However, Shannon indexes tended to increase with elevation (*t* = 4.09, *p* = 0.0005, Figure S2a), the number of bait types (*t* = 4.6, *p* = 0.0002, Figure S2b), and studies that used McPhail traps reported higher indexes (*t* = 2.9, *p* = 0.008; McPhail: 2.00 ± 0.5 ; bottle: 1.54 ± 0.65 , Figure S2c).

Bray–Curtis dissimilarity values were not influenced by the absolute latitude (*t* = -1.56 , *p* = 0.17), elevation (*t* = -0.48 , *p* = 0.64), the number of baits (*t* = -1.63 , *p* = 0.15), or the sampling effort (*t* = 0.76, *p* = 0.48). Studies that used McPhail traps tended to report higher similarity between strata, but the trend was not significant (*t* = -2.2 , *p* = 0.06; McPhail: 0.21 ± 0.12 ; bottle: 0.36 ± 0.25).

2.4.2. Abundance

A total of 13,759 individuals were collected by the 13 studies with approximately 60% of the individuals being collected in the understory. Nine studies found a trend of higher abundance in the understory (Fig. 2). Only one study showed significantly higher abundance in the canopy, while another two studies showed non-significant trends in favor of the canopy (Fig. 2).

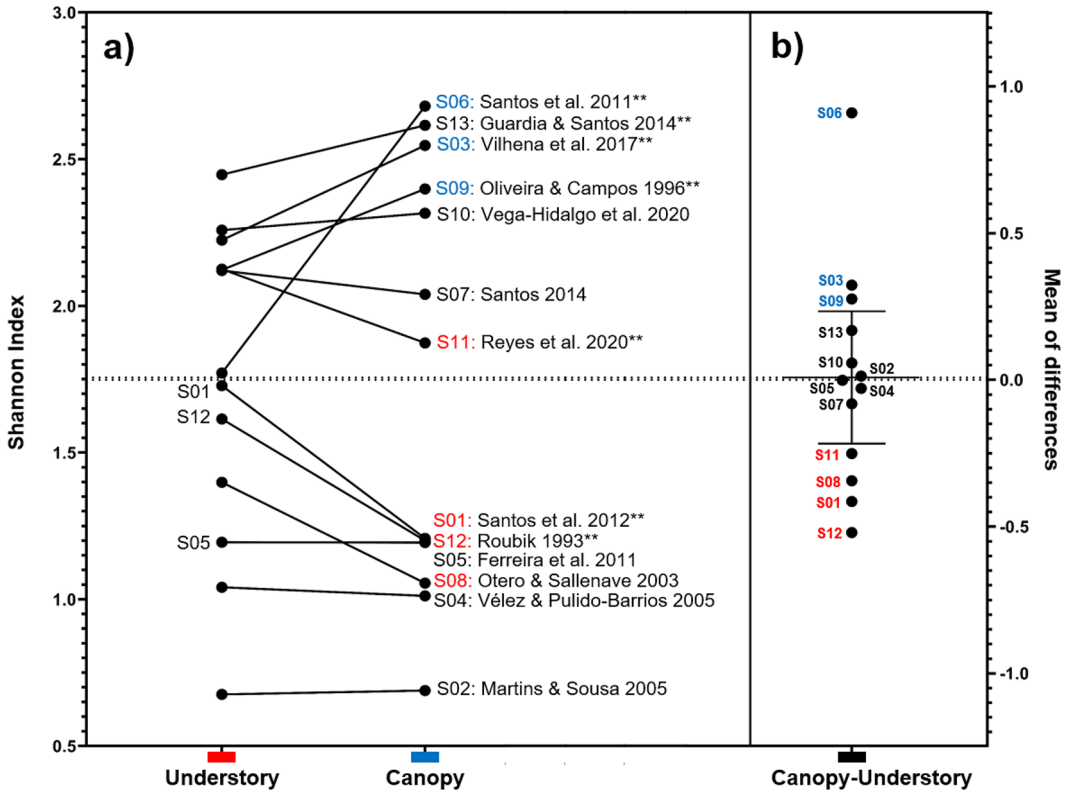


Fig. 1 Comparison of alpha diversity (Shannon index) between understory and canopy strata. **a** Per study (S). Values with ** indicate significant differences between strata according to Shannon's t test. **b** Mean differences per study; studies highlighted in blue indicate that the difference in means favors the canopy, the red one indicate that the difference favors the understory, while values in black show nonsignificant differences

One study did not show a trend in a particular direction (Guardia and Santos 2014, Fig. 2).

The average weighted effect size for abundance indicated a higher abundance in the understory than in the canopy ($g = -0.30$, CI95: $-0.53, -0.07$, $n = 13$, Fig. 2). However, this effect size showed significant heterogeneity across studies ($Q = 502.8$, $df = 12$, $p < 0.0001$). To explore this heterogeneity, the reduced model with the moderator variables significantly accounted (Wald-type test = 388.6, $df = 7$, $p < 0.0001$) and significantly reduced the heterogeneity (see Q above) ($Q = 8.5$, $df = 4$, $p = 0.08$). Although most of the effect sizes reported indicate higher abundance in the understory, these effect sizes tended to increase with absolute latitude, indicating that the larger abundance

in the understory decreases with the latitude ($z = 7.2$, $p = 0.0001$, Figure S3a). Another trend indicates that the higher abundance in the understory decreases with the elevation of the study site ($z = 8.1$, $p < 0.0001$, Figure S3b). The higher abundance in the understory tended to be stronger with increases in the height in which the traps were placed in the canopy ($z = -6.6$, $p < 0.0001$, Figure S3c). The higher abundance in the understory tended to decrease with the number of bait types used ($z = 4.2$, $p < 0.001$, Fig. 3a).

Although both types of studies reported higher abundance in the understory (cross-sectional: $n = 8$, $g = -0.47$, CI95: $-0.53, -0.41$; longitudinal: $n = 5$, $g = -0.20$, CI95: $-0.37, -0.03$), the effect was stronger for cross-sectional studies ($z = -2.2$,

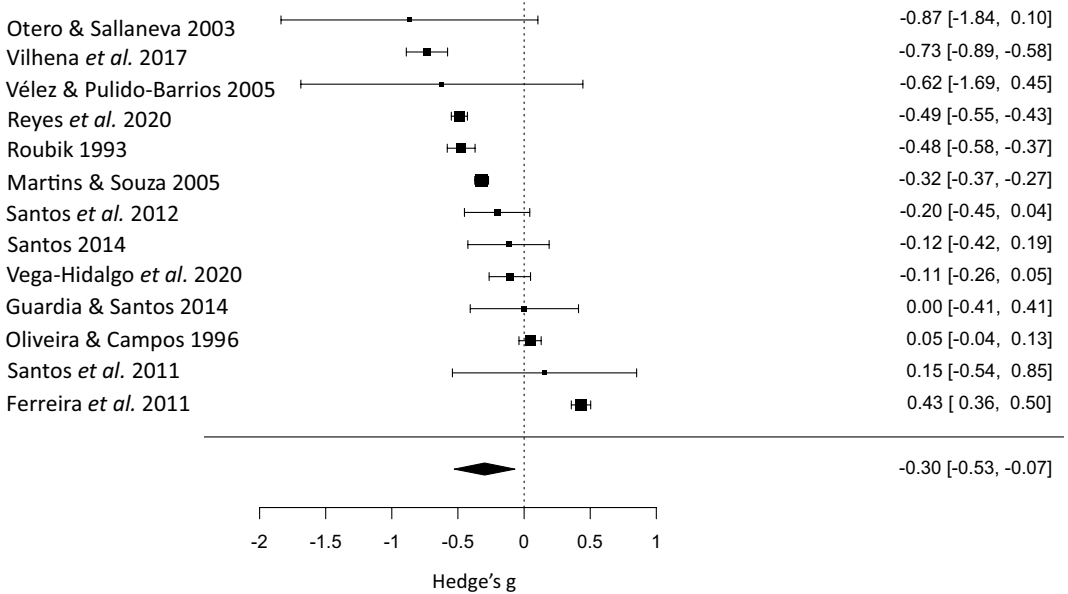


Fig. 2 Effect sizes (Hedge's *d*) of differences in abundance of orchid bees between understory and canopy levels per study. Positive effect sizes indicate higher abundance in the canopy, while negative effect sizes indicate higher abundance in the understory. Each square represents the effect size per study and horizontal lines represent 95% confidence intervals. Studies are ordered by the observed effect size and the precision of the estimate is represented by the size of the square. Effect sizes are significant if the 95% interval does not include zero. The diamond show the average weighted effect size with its 95% confidence intervals

$p=0.03$; Fig. 3b). Both types of trap showed negative effect sizes, but studies that used McPhail traps reported higher effect size ($z=3.5, p=0.0005$) and

bottle traps tended to show larger variance (McPhail: $n=6, g=-0.31, CI95: -0.23, -0.39$; bottle: $n=7, g=-0.34, CI95: -0.61, -0.07$, Fig. 3c).

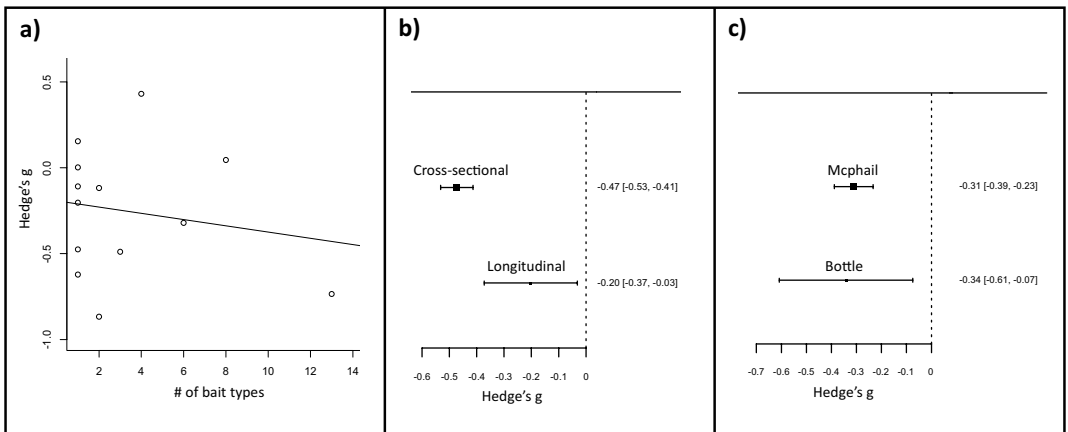


Fig. 3 Effect sizes (Hedge's *g*) of mean differences in abundance of orchid bees between understory and canopy levels in relation to the number of bait types used in the study **a**, type of study **b**, and type of trap **c**. Hedges' *g* with a positive value indicates higher abundance in the canopy and negative values indicate higher abundance in the understory. Effect sizes are significant if the 95% interval does not include zero

3. DISCUSSION

We found no evidence that the diversity of euglossine bees varies with forest strata, differing from individual studies on other neotropical bees (trap-nesting bees, Stangler et al. 2016) or temperate bees (Ulyshen et al. 2010) which found higher diversity in the canopy. Our results match the trends indicating that elevation influences composition of orchid bee communities at large geographical scale (Opedal et al. 2020). It should be noted that the increase in overall diversity with elevation that we detected goes against observed trends for orchid bee communities (Pinto et al. 2019), other neotropical bees (Perillo et al. 2017), and temperate alpine bees (Lefebvre et al. 2018), but increases in bee diversity with elevation have been reported (Perillo et al. 2021; Widhiono et al. 2017). However, the effect of elevation in most of these studies was evaluated within a relatively narrow latitude range, which makes it difficult to disentangle the effects of elevation and latitude (but see Perillo et al. 2021). Future studies that combine elevation and latitude for the whole neotropical region can provide deeper insights into the dynamics of euglossine communities in the region.

We found that the higher abundance of bees in the understory decreases with increases in both latitude and elevation. Although both factors may influence overall abundance, diversity, and phylogenetic diversity (Abrahamczyk et al. 2014; Opedal et al. 2020), it is unclear how they could induce differences in abundance between both strata. A possibility is that abiotic factors related to the detection of baits change with latitude and elevation (e.g., evaporation rates, Gates et al. 1999; Bailey et al. 2018). Another possibility is that the body sizes of some euglossine increase within the tropics with latitude (e.g., Anderson 2017; Gérard et al. 2018) or elevation (e.g., Classen et al. 2017; Brehm et al. 2019), and therefore larger bees may be more likely to be caught in canopy traps (Baw, 1990; Martins and Batalha 2007; Roubik 1993). Alternately, changes in bees' communities along altitudinal or latitudinal gradients favor a higher proportion

of species that tend to fly higher in the forest (e.g., our results, Perillo et al. 2017).

The influence of trap height in reducing the effect sizes (favors higher abundance in the understory) matches the fact that the only study (Ferreira et al. 2011) showing a significant effect size of higher abundance in the canopy placed traps at lower heights as compared to studies reporting higher abundance in the understory. In summary, the higher the placement of a trap in the canopy, the less likely that euglossine bees will be trapped. Perhaps, under low trap heights or forests with short canopies (e.g., 10–12 m), orchid bees are as likely or more to visit traps due to similarities in bait propagation associated with wind dynamics in each stratum. For instance in Costa Rica, Mccay (2003) reported roughly similar maximum wind speeds in the afternoon between heights at 2.5, 5.0, and 10 m above the forest floor. Perhaps within that height range, similar dissipation rates may cause similar trapping rates between strata. However, unknown variable(s) may have caused an increase in canopy abundance in Ferreira et al. (2011) or the other two studies with non-significant trends (Oliveira and Campos 1996; Santos-Murgas et al. 2011). Wind dynamics and other abiotic factors should be evaluated to understand under which conditions an experimental design may induce or detect higher abundance in the canopy.

Perhaps the lower abundance of orchid bees in the canopy contributes to explain the lower abundance and diversity of euglossine-dependent plants in the canopy like orchids (Hernández-Pérez et al. 2018). Also, given the effect of trap height on abundance, we expect plants' gene flow (via pollen) driven by euglossine (Opedal et al. 2017) to be dynamic and change with shifts in canopy height. For instance, shorter canopies in young or regenerating forests may have a higher proportion of euglossine bees in the canopy, which may decrease as the forest ages and the canopy height increases. Altogether, these predictions follow the suggestion that many euglossine bees may not be relevant pollinators in the neotropics in forests with high canopy (> 25 m) since they may avoid it (Roubik 1993).

Following the same line of thought, plants that are pollinated by euglossines in the understory may depend on other pollinators in the canopy, like other plant—pollinator systems (Sanfiorenzo et al. 2018). However, if pollination by euglossine is an obligate dependence, like in orchids (Ramírez et al. 2014) which can grow at different heights (de la Rosa-Manzano et al. 2014), then we would expect a difference in pollination rates among vertical strata. For instance, in the pollination system of *Chilogottis* orchids, *Neozeleboria* wasps, *N. cryptoides*, and *N. monticola* can both be lured to the flower by the same attractant. However, when the effect of floral height is introduced into the system, males of *N. cryptoides* preferred dummy flowers few centimeters above the ground and males of *N. monticola* preferred dummies on the soil (Schiestl and Peakall 2005), suggesting that pollinator behavior imposes selection on floral height in orchids. Future work addressing pollination rates or diet specializations on species at different forest strata may provide a higher resolution perspective on differential resource use of euglossine bees in neotropical forests.

Our results highlight some methodological details that may have increased the heterogeneity across studies. Firstly, cross-sectional studies tended to report a stronger difference in abundance in the understory as compared to longitudinal studies. However, this could mean that bees may use forest strata differently throughout the year and short-term studies only give a snapshot view. Therefore, changes in abundance in the canopy might be the result of shifts in local resources (Hietz et al. 2006). Secondly, our results suggest that sampling with McPhail traps generate more consistent results in terms of abundance and species composition, which is in line with the evidence that trap design can influence the estimates of abundance and richness in orchid bee communities (Sydney and Gonçalves 2015). Thirdly, our results align with the idea that the number of bait types used plays a major role in the differences across studies in terms of overall diversity and abundance (Nemésio 2012; Opedal et al. 2020). However, it is unclear how the number of bait types could drive differences

between strata in abundance. One possibility is that some species show specific bait attraction (e.g., Nemésio 2008) and may be true canopy dwellers, then we may expect that the probability of sampling those bees in the canopy increases with the number of bait types, as suggested by the trend for effect sizes of abundance. Whether the detection of certain species relies on specific baits, stratum combinations could be investigated with a bifactorial experimental design. Moreover, species compositions of sampled euglossines vary depending on the mix of baits used, which is an issue often ignored by researchers (Nemésio 2012). Again, deploying certain bait mixes could increase the probability that a larger proportion of larger bees reach canopy traps (Bawa 1990; Martins and Batalha 2007; Roubik 1993). Future studies require standardized protocols considering type of baits, sampling effort, and trap design, particularly if the aim is to study stratification at a regional scale or for comparison of populations.

A potentially important factor that may be influencing our results is forest fragmentation, a variable difficult to retrieve from our metadata. Stangler et al. (2016) found that proximity to the forest edge reduces the diversity of trap-nesting bees but orchids bees may not always be affected by fragmentation and disturbance (Botsch et al. 2017). Besides, bees' abundance can be affected by agricultural cover and larger bees are more affected at the landscape scale (Benjamin et al. 2014). Since agricultural cover can affect larger bees at the landscape scale and they are more likely to reach the canopy, therefore this may result in a lower proportion of bees flying to the canopy near agricultural areas as compared to canopies in undisturbed habitats. Moreover, other factors that may influence richness and abundance must be considered when comparing understory and canopy communities such as bee and plant phenologies, ambient temperature, precipitation, water vapor pressure, wind speed, forest fragmentation, among others (Kammerer et al. 2021; Margatto et al. 2019; Nemésio and Silveira 2010; Perillo et al. 2021, 2017). Overall, higher resolution studies that evaluate these factors and potential interactions with elevation and

latitude are needed to appraise whether changes in orchid bee communities could result in some cases in differences between forest strata.

On the other hand, rather than trying to identify differences between strata, perhaps we can put more effort on trying to identify species that are true stratum specialists, as seen in other insects (Ozanne 2005). For instance, Roubik (1993) captured *Euglossa heterosticta* only in the canopy and another four species only in the understory during a 1-year monitoring in Panama. In that sense, researchers first need to develop a standardized definition for the vertical strata that is applicable across forested systems, particularly strata in between the understory and canopy. Finally, we should be cautious when making strata comparisons since any potential difference may be an artifact related to current sampling methods. Nemésio (2012) highlights that the use of pure synthetic baits does not represent a natural scenario for the bees and questions whether the bees would be observed in a particular habitat in the absence of the baits, as he exemplifies the case with the orchid bee *Eufriesea nigrohirta*. Less invasive methods (e.g., camera monitoring, telemetry, use of naturally occurring fragrances) can certainly improve our knowledge about euglossine bee distributions and movements. In conclusion, our meta-analysis suggests that euglossine bees are predominantly more abundant in the understory but diversity, dominance, and composition are similar between strata. More importantly in the study of orchid bees is the fact that baited-based methods only reveal information on movement patterns of males. It is urgent to develop new tools and methods to better understand the biology and spatial distribution of females.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-022-00939-0>.

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AUTHOR CONTRIBUTION

The idea for the study came from YA. All authors participated in the literature search and extraction of data from the selected studies. Data analyses were performed by YA and DG. Drafting of the manuscript was done by all three authors. Revision and correction of the manuscript was done by DG. All authors read and approved the final version of the manuscript.

AVAILABILITY OF DATA AND MATERIAL

All data supporting this study is available as supplementary material.

CODE AVAILABILITY

Codes supporting the analysis of this study are available as supplementary material.

DECLARATIONS

Ethics approval This study did not require sampling or handling of animals.

Consent to participate This study did not involve human subjects.

Consent for publication All authors agreed to publish the data obtained from this study.

Conflict of interest The authors declare no competing interests.

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