ORIGINAL PAPER

The attractive role of floral elements in heterantherous species without pronounced stamen differences

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Abstract

Floral resources can be recognized by visitors through attractants that signal their presence. However, besides petals, it is still unclear how floral elements in heterantherous species are perceived by visiting bees. In this study, we aim to understand the role of stamens and petals of *Pleroma granulosum* and *P. raddianum* in attracting pollination bees, mainly by evaluating whether pollinator behaviour differs in response to different sized stamens between which there is no apparent colour contrast. Using colour visual models, we estimated bee colour discrimination between stamen sets and corolla in both species and carried out preference experiments among floral elements, using the bees *Bombus morio* and *Xylocopa frontalis* as models in the field. Pollination and feeding stamens are not discriminable by bees in both plant species. Bees only preferred flowers with petals, indicating that they are essential to long-distance attraction. During preferential tests, bees seemed to better respond to visual stimuli on the right side, suggesting lateralization. We also demonstrate that tactile stimulation by the anthers is necessary to trigger bee buzzing behaviour. Thus, since bees were not specifically attracted to any stamen set, heteranthery without colour differences between stamens is not enough to determine bee choice behaviour.

Keywords Bee behaviour · Bee preference · *Bombus morio* · Pollen flower · *Pleroma granulosum* · *Pleroma raddianum* · *Xylocopa frontalis*

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Introduction

Bees visit flowers in search of resources, like nectar and pollen. These resources are usually associated with floral signals such as shape, size, colour and odour that condition the visitation and behavioural responses of bees (Carr et al. 2015; Nicholls and Hempel de Ibarra 2017). Among angiosperms, more than 20,000 species offer only pollen as a floral resource to motivate bee visits (Vogel 1978). Despite the huge phylogenetic diversity of such pollen flowers (sensu Vogel 1978), they have common characteristics such as the absence of floral nectaries and the presence of poricidal anthers (Vallejo-Marín et al. 2010; Barrett 2010). Usually, the poricidal anthers are differentiated into one or more sets of stamens, varying not only in their sizes and positions, but also in colour and odour, which is known as staminal heteromorphism or heteranthery (Vallejo-Marín et al. 2009).

The occurrence of morphological as well as colour and odour differentiation between stamen sets in pollen flowers has been justified through the intrafloral division of labour hypothesis (Müller 1883; Solís-Montero and Vallejo-Marín

2017; Velloso et al. 2018). In these flowers, large stamens are usually inconspicuous to bees, with colour similar to petals and pollen grains intended for pollination (hereafter pollination stamens). On the other hand, pollen present in small stamens (hereinafter feeding stamens), which conversely often have colours contrasting with petals, is mostly available as a resource for bees (Luo et al. 2009; Velloso et al. 2018). In this system, the morphological coupling between flowers and pollinators, as well as the subsequent grooming behaviour of bees, is critical to the pollination process (Solís-Montero and Vallejo-Marín 2017). In general, small stamens deposit pollen mainly on the easily groomed abdomen of bees, while large stamens deposit pollen grains in areas that are hard for bees to clean, the so-called safe sites (Koch et al. 2017; Tong and Huang 2018). This functional distinction between stamens prevents total pollen load consumption by bees, promoting an intrafloral division of labour (Luo et al. 2008).

Given the differential allocation of pollen as a food and reproductive resource associated with morphological adjustment during the visit, bees are expected to respond differently to the presence of different stamen sets in pollen flowers. In fact, the bee's decision to visit a pollen flower is strongly influenced by the presence of yellow feeding stamens contrasting with the corolla (Luo et al. 2008; Vallejo-Marín et al. 2009; Telles et al. 2020). However, although variations in size and colour of stamens are relatively common in pollen flowers, some species do not present any apparent contrasting morphological differences, even though they present pollen load partitioning (Brito and Sazima 2012; Maia et al. 2018). Thus, the function of such stamens in attraction, bee behaviour during the visit and consequently in the intrafloral division of labour is unclear.

To investigate the role of less pronounced stamen morphological differences in bee preference and pollination behaviour, we selected two pollen flower species: *Pleroma granulosum* (Desr.) Cogn. and *P. raddianum* (DC.) Gardner (Melastomataceae). Both species present anthers with colours apparently similar to petals, but different degrees of stamen dimorphism, as well as differences in the amount of pollen between anthers of feeding and pollination stamens (Brito et al. in prep.). Specifically, we evaluate (i) whether the colour of stamens from different sets is distinguishable from each other and from the petals, according to the bee visual system; (ii) the preference and (iii) the behaviour (approximation, landing and vibration) of pollinators in relation to the presence/absence of petals and one or both sets of stamens. In large Melastomataceae flowers, pollen from feeding stamens are often more accessible to bees than pollen from pollination stamens because of their arrangement within flower as well as bee positioning during vibration (Luo et al. 2008). Therefore, if bees are capable of perceiving the existence of such intrafloral division of pollen load

regardless the morphological and colour differences between stamen sets, they should prefer flowers with small stamens (i.e. feeding stamens) even if these stamens have the same colour as large ones.

Material and methods

Study area and species

We conducted the study during January and February 2013 and 2014, in the Serra do Mar State Park, located in the municipality of Ubatuba (23º22′ S and 44º48′ W), São Paulo, Brazil. The vegetation of the study area is considered dense ombrophilous lowland forest (Veloso et al. 1991). The climate of the region is tropical rainy, with average rainfall exceeding 200 mm per month, and average annual temperature of about 22 ℃ (Morellato et al. 2000; Bencke and Morellato 2002).

Two species from the genus *Pleroma* (Melastomataceae) were studied. This family consists of about 5500 species, mainly concentrated in tropical and subtropical regions (Renner 1993; Bacci et al. 2019). In addition, many species have flowers with pronounced herkogamy, different sized stamens, and depend on bees capable of performing buzz pollination to reproduce (Renner 1989; Buchmann 1983). *P. granulosum* and *P. raddianum* are trees that present hermaphroditic flowers with dimorphic stamens and poricidal anthers arranged in two whorls; however, this stamen dimorphism is expressed more in *P. raddianum* (Fig. 1e, j). The flowers of both species open around 05:00 and are visited only during the first day (Brito and Sazima 2012; Leite 2016). The only resource available to visitors is pollen. The main pollinator of *P. granulosum* is the bee *Xylocopa frontalis*, but other bees like *Bombus morio*, *X. brasilianorum*, *Eulaema* sp. and *Epicharis flava* also visited this plant species (Leite F., unpublished data). The main pollinator of *P. raddianum* is *B. morio*, followed by *X. brasilianorum*, *X. frontalis*, *E. flava* and *Eufriesea* sp. (Brito and Sazima 2012; Leite 2016).

Colour of floral elements and bee perception

We modelled the colour of flowers according to the bee visual system using newly opened flowers from three different individuals ($n = 9$ flowers per species). For each flower, we measured the spectral reflectance of petals (tip and base) and anthers of pollination and feeding stamens relative to a calibrated white DH 2000-CAL (Ocean Optics) and black (light absence) standards using a spectrophotometer (Ocean Optics S2000, Ocean Optics, Dunedin, FL; Fig. 1). We assumed a standard green background (Chittka and Kevan 2005), a daylight illumination (D65; Wyszecki and Stiles 1982) and
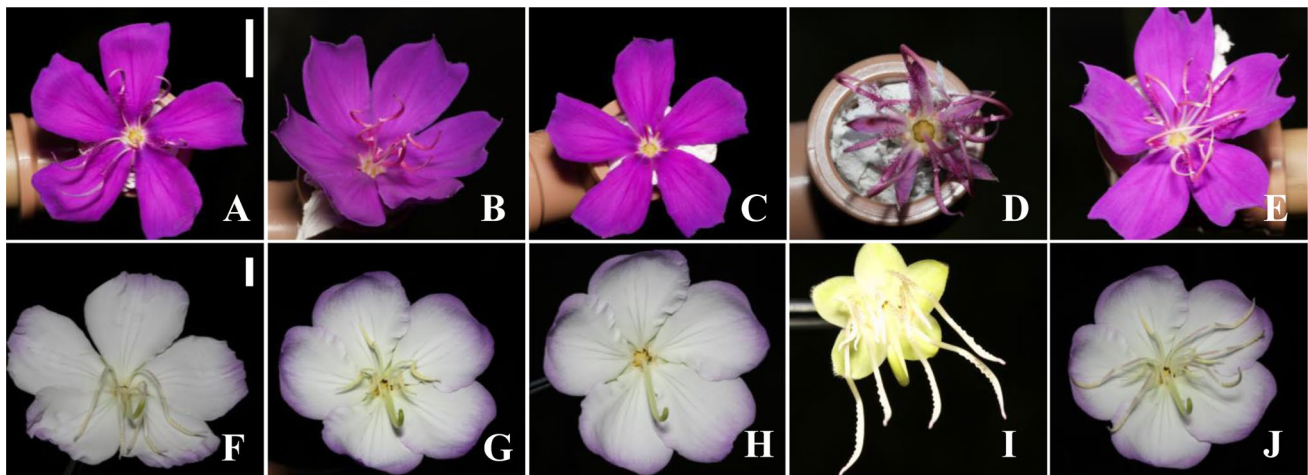
Fig. 1 Flower treatments used to test the role of floral elements on bee attraction and behaviour in (**a**–**e**) *Pleroma granulosum* and (**f**–**j**) *Pleroma raddianum*. Flowers were manipulated by removing different floral elements (adapted from Luo et al., 2008): **a** and **f**—flowers with pollination stamens only (POLLINATION); **b** and **g**—flowers with feeding stamens only (FEEDING); **c** and **h**—flowers with no stamens (STAMENLESS); **d** and **i**—flowers with no petals (PETALLESS). We also had control flowers: **e** and **j**—complete flowers (WHOLE). The flowers were presented to bees in a paired system, considering all possible combinations between treatments. White bars = 10 mm

the spectral sensitivity of *B. terrestris* as surrogate, since both plant species are often visited by the sister species *B. morio*. We used the colour hexagon model (Chittka 1992) to predict the colour discrimination capacity of bees among floral elements. We established the discrimination threshold of 0.09 hexagon units based on the previous behavioural experiments (Dyer et al. 2008).

Bee attraction and behaviour on treated flowers

To test the role of floral elements on visitor attraction and behaviour, we carried out preference experiments in the field with the main pollinators of both plant species (*X. frontalis* and *B. morio*). We manipulated flowers by removing different floral elements (Fig. 1), namely: A—flower with pollination stamens only (POLLINATION); B—flower with feeding stamens only (FEEDING); C—flower with no stamens (STAMENLESS) and D—flower with no petals (PETALLESS). We also had control flowers: E—complete flower (WHOLE). Flowers were presented to bees in a paired system, using a 1-m stick with a U-shaped end (hereinafter pollination stick), considering all possible combinations between treatments. We repeated each combination ≥ 26 times for *P. granulosum* and ≥ 21 times for *P. raddianum*, alternating sides with each new trial. We positioned flowers at the end of the pollination stick, separated 35 cm from each other (Fig. S1; adapted from Thomson 1988). After 10 presentations, we replaced flowers for new ones (previously bagged to avoid visitation). Whenever we observed a pollinator visiting natural flowers, we carefully positioned the stick such that the bee occupied the centre. The presentations were carried out between 05:30 and 10:00, the period

corresponding to the highest activity of bees for both plant species (Brito and Sazima 2012; Leite 2016).

For each treatment and plant species, we recorded the flower chosen by bees and consequently the side choice on the stick. Once we noticed bees moving towards a test flower, we characterized their behaviour in three consecutive steps: "Approach"—the bee approached the flower, but did not land; "Landing"—the bee approached and landed on the flower, but did not vibrate stamens and "Vibration"—the bee approached, landed and vibrated stamens (adapted from Schmitt & Bertsch 1990).

Data analysis

For each plant species, we tested if bees could discriminate pollination from feeding stamens as well as whether they could perceive differences among these stamens and the tip and the base of petals performing a one-tailed t-test. To that end, we compared the colour distances between floral elements applying the 0.09 hexagon units as threshold under a 95% confidence interval.

To test the attraction of bees to flowers with different sets of floral organs, we built separate models for each pair of treatment considering both plant species, since combinations were tested independently. We used generalized linear models (GLM) with a binomial response and a logit link function considering the flower the bee chose, regardless of the subsequent behaviour. For each treatment pair, we used the frequency of side choice (attraction) to each treatment as the response variable, and bee and plant species as explanatory factors. For each pair of treatment, we applied model selection to test for differences in attraction, and whether

the proportion of choices were different between plant and flower visitor species. Our null model included no factors, forcing the intercept to be 0 and representing no attraction towards any treatment. Additionally, we had a model only with an intercept to represent attraction towards one of the treatments, regardless of plant or pollinator species. We also included models with either plant or pollinator species separately, and both together. We compared and selected models using the corrected Akaike Information Criterion (AICc). Values of ΔAIC within 0–2 are considered to have support, within 4–7 considerably less support and greater than 10 have no support (Burnham and Anderson 2002). When more than one model fell within the first category, we chose the simplest model as the best one. Since bees seemed to present laterality, by choosing one side more often independently of the flower treatment presented, we additionally tested for a side preference, regardless of the treatment. For that, we used a GLM with the side chosen by bees as response variable, and the treatment, bee species and plant species as predictors.

We also tested for differences in bee behaviour once they chose a flower applying a three-way contingency chi-squared analysis. For that, we grouped the information of experiments and tested if the proportion of "Approaches", "Landings" and "Vibrations" differed between flowers, considering different sets of organs and plant species. Bee species were not considered in this analysis because they showed no clear difference in the attraction test and to maximize the power of the test by not increasing the number of degrees of freedom. All statistical analyses were performed in the R software (R Development Core Team 2020).

Results

### Colour of floral elements and bee perception

Stamens and petals of *P. granulosum* reflect mostly in blue and red waveband of the visual spectrum, while these structures reflect mostly in blue, green and red wavebands in *P. raddianum* (Figs. S2 and S3). Petals and stamens of *P. granulosum* occupy different regions of the colour hexagon (Fig. S4A). In this species, petals are UV-blue and stamens are mostly blue when considering the hexagon colour vision model. In *P. raddianum*, colour loci of petals and stamens are all localized in the blue-green region of the hexagon colour model (Fig. S4B). Feeding and pollination stamens in *P. granulosum* and *P. raddianum* presented similar colours and, assuming the surrogate visual system of *B. terrestris*, they are not perceived as different by bees (Fig. 2; Table S1). However, both stamens sets could be discriminated against the tip and base of petals in *P. granulosum* (Fig. 2; Table S1). On the other hand, for *P. raddianum*, stamens sets were camouflaged against the petals (Fig. 2; Table S1).

### Bee attraction and preference on treated flowers

Overall, the attraction for treatments in most of the tests was independent of bee and plant species, except for the comparison between POLLINATION and PETALLESS, where bee attraction to flowers with petals was higher for *P. granulosum* than for *P. raddianum* (Fig. 3; Table 1; Table S2). Bees were similarly attracted to the combinations between WHOLE, POLLINATION, FEEDING and STAMENLESS treatments (Fig. 4; Table 1; Table S2). Contrary, bees were clearly more attracted to these treatments when they were paired with PETALLESS flowers (Fig. 4; Table 1; Table S2).

The analysis of side preference revealed that bees chose the right side of the pollination stick more often (right = 283;

Fig. 2 Colour contrast between floral elements in (**a**) *Pleroma granulosum* and (**b**) *P. raddianum* according to the hexagon colour model (*n* = 9 flowers/species). Dots = mean hexagon values of colour distance; error bars = 95% confidence interval; dashed line = discrimination threshold (set as 0.09 hexagon units). *PS* pollination stamen; *FS* feeding stamen; *PT* petal tip; *PB* petal base
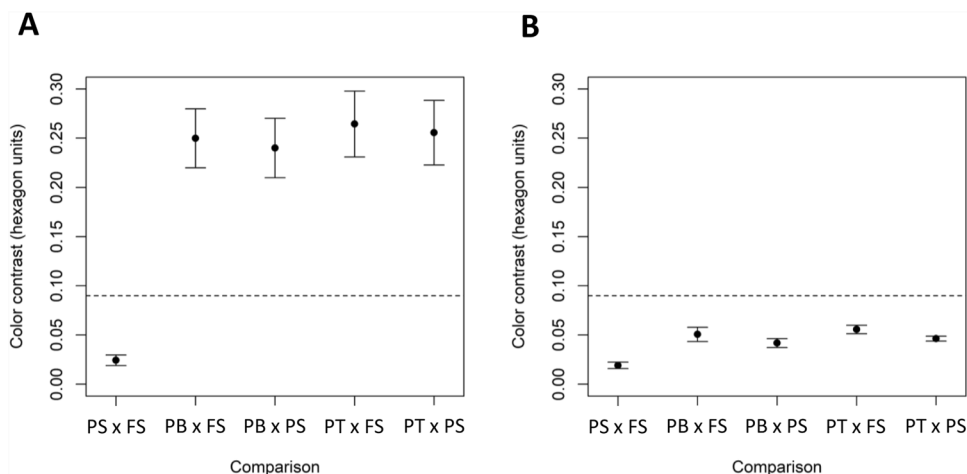
Fig. 3 Number of bees attracted to POLLINATION and PETALLESS floral treatments in *Pleroma granulosum* and *Pleroma raddianum*. POLLINATION treatment corresponds to manipulated flowers with only pollination stamens, while PETALLESS refers to flowers with no petals
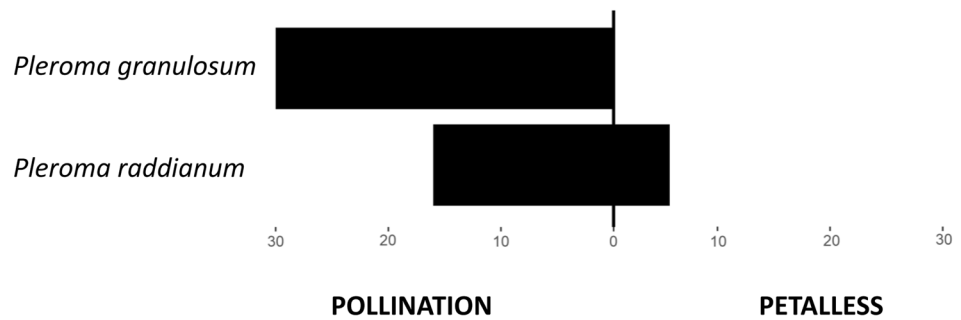
Bee behaviour

Bee behaviour varied among flower treatments for the two plant species (*P. granulosum*: Chisq = 70.92; df = 8; $p < 0.01$; *P. raddianum*: Chisq = 120.8; df = 8; $p < 0.01$; Fig. 5a, b). In *P. granulosum*, bees vibrated WHOLE treatment flowers more often than performing "Approach" and "Landing" behaviours. In the POLLINATION and FEEDING treatments, the proportion of visits with "Vibration" was similar, and in both treatments, there were few "Landings". In the STAMENLESS treatment, most visits were only "Approaches", while the PETALLESS treatment only received "Vibration" visits (Fig. 5a). In *P. raddianum*, most of the visits to the WHOLE treatment were also "Vibration" type. The POLLINATION treatment showed similar proportions of "Approach", "Landing" and "Vibration" visits, and FEEDING presented slightly more "Vibration" visits. In *P. raddianum* the STAMENLESS treatment, as in *P. granulosum*, received most visits with only "Approach", and the PETALLESS treatment received most visits with "Vibration" (Fig. 5b).

Discussion

Although the stamens of *P. granulosum* contrast with petals, bees visiting the flowers of both *P. granulosum* and *P. raddianum* did not differentiate the colours of pollination and feeding stamens. Most bees are generalists and visit several types of pollen flowers (Russell et al. 2017). However, when they forage for pollen, visits occur more frequently in flowers with yellow UV-absorbing feeding stamens contrasting against the corolla (Muth et al. 2015; Velloso et al. 2018). In such pattern, the feeding stamens are innately attractive to bees and signal that pollen is available (Gumbert 2000). Moreover, bees can be better oriented within flowers with

yellow UV-absorbing patches since it allows easy identification of where the pollen could be (Lunau et al. 1996; Orbán and Plowright 2013). However, although bees visiting flowers whose only resource is pollen present innate preferences, they can modify this preference due to experience, long-term information retention and associative learning (Russell et al. 2016). Petals and stamens are involved in the learned preference of bees, but some studies suggest that the stamens response is stronger (Muth et al. 2015; Russell et al. 2016). Even in the absence of the common UV-absorbing yellow pattern of feeding anthers, bees that pollinate *P. granulosum* may have learned that there is a satisfactory quality and quantity of resources in the anthers using the stamen–petal contrast between blue and UV-blue, respectively, as a cue. Such learning process can also be effective even in *P. raddianum* in which both stamen sets are cryptic in relation to the corolla.

In our experiment, bees were attracted to the WHOLE, POLLINATION, FEEDING and STAMENLESS combinations of treatments with similar frequencies. All those treatments had one common floral element: the petal. Bees use petals as long-distance floral cues and once in front on the flowers, other floral elements, such as contrasting yellow anthers and floral guides might become more relevant (Brito et al. 2015; Lunau and Wester 2017; Lunau et al. 2017). Bees were also more attracted to the POLLINATION treatment in *P. granulosum* than in *P. raddianum* when it was paired with PETALLESS treatment. This suggests that, in *P. granulosum*, contrasting pollination stamens may reinforce the signalling of feeding stamens as it is common in other heterantherous species (Tang and Huang 2007; Ushimaru et al. 2007; Luo et al. 2008; Velloso et al. 2018; Telles et al. 2020). Combined with the same general attraction pattern found for *P. raddianum*, our result indicates that bees can generalize the search for floral colour patterns and be attracted by different colour combinations between petals and stamen in pollen flowers (Lunau et al. 1996). On the other hand, in PETALLESS treatments, the lack of petals drastically decreases bee attraction in both plant species, even when the resource was available. Altogether, these results indicate

Table 1 Model selection for generalized linear models testing for bee attraction to *Pleroma* spp. flowers with different floral elements removed

| Model	D.f	Whole × stamenless	Whole × petalless	Whole × pollination	Pollination × feeding	Pollination × stamenless	Pollination × petalless	Feeding × whole	Feeding × stamenless	Feeding × petalless	Stamenless × stamenless
Null	0	**0**	**0**	**0**	2.1	**0**	43.4	**0**	**0**	39.2	52.2
Attraction	1	1.8	**0**	2.1	**0**	1.9	7.5	2	1.4	**0.9**	**0**
Plant	2	2	0.7	4.1	2.2	3.7	**0**	3.5	2.6	**0**	1.6
Bee	2	3.5	2	4.2	2.1	3.8	6.3	2.4	3.3	1.8	0.9
Plant + Bee	3	4	2.7	6.1	4.4	5.2	2.3	4	4.5	1.5	2.9

For each pair of treatments, a null model without any difference between treatments was compared with a model with attraction and no difference between plant or bee species, a model with differences between bee species, another with differences between plant species, and a complete model with differences between both bee and plant. Delta-AICc values are shown for each model. Values in bold represent the best model considering a threshold of ΔAIC < 2 and, within this threshold, the simplest model
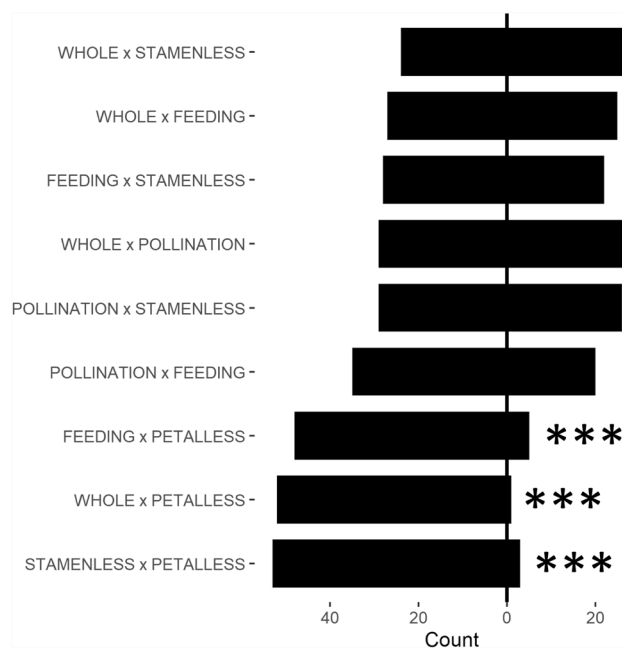
Fig. 4 Number of bees attracted to each pairwise floral treatment. Flowers were manipulated by removing different floral elements: POLLINATION—flowers with pollination stamens only; FEEDING—flowers with feeding stamens only; STAMENLESS—flowers with no stamens; PETALLESS—flowers with no petals. We also had control flowers: WHOLE—complete flowers

that bees are mostly guided by the presence of petals and that the slight morphological difference between stamens does not affect bee decision making when visiting heterantherous species without pronounced morphological differences between stamen sets.

On the other hand, the behaviour ("Approach", "Landing" or "Vibration") of pollinators (*B. morio* and *X. frontalis*) was different among treatments. Bees only triggered "Vibration" behaviour when in contact with stamens, even in flowers that had their petals removed. This behaviour was triggered in a similar proportion for the POLLINATION and FEEDING treatments, indicating that bees need a tactile stimulus to perform vibration in these flowers. Although petals are not bilaterally arranged in most Melastomataceae flowers, there is a stamen arrangement that creates the spatial separation between stamens sets and also favours the bee body to be aligned to the stamen bilateral axis during the visit (Luo et al. 2008; Ferreira and Araújo 2016). This positioning strategy can even be found in Melastomataceae species without stamen colour differences (Konzmann et al. 2020), and may occur with both species studied here. As bees performed the "Vibration" behaviour only when in contact with stamens in this typical positioning, it is possible that the spectrum of heterantherous stamen functions goes beyond the traditional division of labour to also include the positioning and further vibration triggering of buzzing bees in such
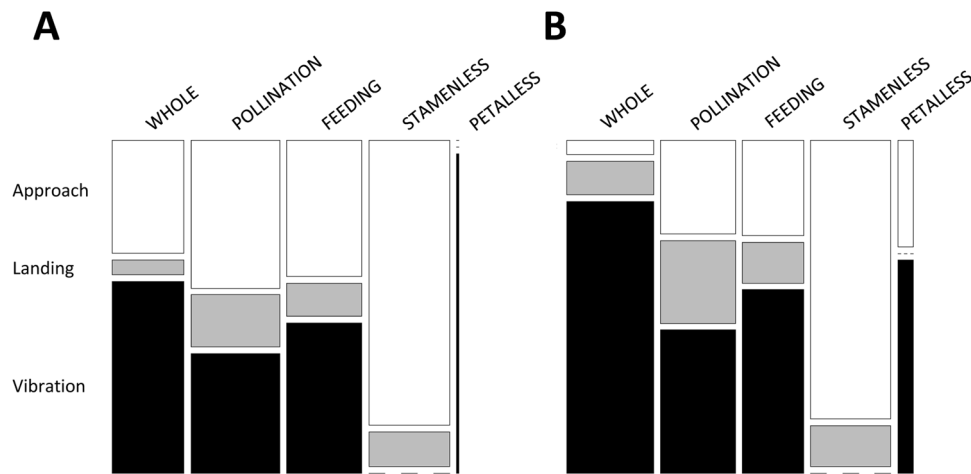
Fig. 5 Frequency of behaviours displayed in each flower treatment in (**a**) *Pleroma granulosum* and (**b**) *Pleroma raddianum*. Visits were categorized into three progressive behaviours: "Approach"—the bee approaches the flower but does not land; "Landing"—the bee approaches and lands on the flower but does not vibrate stamens; "Vibration"—the bee approaches, lands and vibrates stamens. Flow-ers were manipulated by removing different floral elements: POLLI-NATION—flowers with pollination stamens only; FEEDING—flow-ers with feeding stamens only; STAMENLESS—flowers with no stamens; PETALLESS—flowers with no petals. We also had control flowers: WHOLE—complete flowers. The width of bars indicates the relative number of overall visits received by each treatment.

flowers. Interestingly, bees that visited the POLLINATION treatment in these *Pleroma* species were very far from the centre of the flower, but they still vibrated the anthers at similar proportions as in the FEEDING treatment when in the right positioning. This also suggests that bees only perceive the presence or absence of feeding stamens or even pollen grains in these anthers after vibration. This discrimination must be more difficult when the difference between stamen sets is reduced, even when the division of labour occurs through differences in pollen load between anthers, as seen in *P. granulosum* (Leite 2016).

B. morio and *X. frontalis* visited treatments on the right side of the pollination stick more often, showing some degree of lateralization or side preference. Under natural conditions, asymmetries can occur at the population level when more than 50% of individuals are lateralized in the same direction (Rogers and Andrew 2002). Olfactory asymmetries were recorded in *Apis mellifera*, which demonstrated greater learning with their right antenna than with their left, possibly explained by the higher number of sensory cells on the right antenna (Letzkus et al. 2006). Further evidence of lateralization in the olfactory learning of *A. mellifera* was confirmed by several other studies (Rogers and Vallortigara 2008; Anfora et al. 2010; Frasnelli et al. 2010). *B. terrestris* has also been recorded with differential response between the right and left antenna, with right preferred over the left (Anfora et al. 2011). In addition to this olfactory differentiation, *A. mellifera* seems to rely more strongly on its right eye than on its left one to associate a visual stimulus with a floral resource. Thus, other bees than *A. mellifera* could predominantly use the right eye to detect objects and forage,

biasing the decision making during the attraction process (Letzkus et al. 2008).

The present study indicates that heteranthery, when not associated with pronounced colour and size differences between stamens, does not determine the behaviour of floral visitors, since bees were not specifically attracted to feeding stamens as expected. However, our study reinforces that petals play an important role in long-distance bee attraction. At short distances, bees can discern the resource through cognitive associations related to stamen and pollen, possibly using tactile stimulus in their positioning and to trigger the "Vibration" behaviour. Our results indicate that floral structures can influence the vibration behaviour of bees, a process that has been poorly studied and deserves further investigation.

Compliance with ethical standards

in this study. This study respected the welfare of animals, and excluded situations when animals were in pain.

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