




What structures diurnal visitation rates to flowering trees in an Afrotropical lowland rainforest understory?

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Abstract. 1. As environmental change and degradation accelerate, perturbing insect populations, we need to better understand the resource use dynamics of diverse wild pollinators. Most tropical trees are adapted for biotic pollination, yet we still know little about plant–pollinator interactions in African rainforests.

2. We addressed this gap from a community perspective, identifying what floral traits – colour, scent, reward accessibility and visibility – structure visitation patterns among insect functional groups to tree species flowering in the understory of Korup National Park, Cameroon. To understand how visitor groups share resources, we used joint modelling that explicitly considers zero-inflation in visitation rates and correlation among visitor groups.

3. Most tree species had exposed floral rewards, and all were visited by multiple insect groups among which ants, bees, beetles, and flies were most abundant. Visitation rates varied more among tree species than among individual trees. Floral scent differences were important for structuring visits, particularly for flies, bees, and ants. Ant and bee visitation rates decreased while fly visits increased marginally throughout the season, correlated with the dry to wet season transition.

4. Comparison with other lowland tropical understories suggests flies may be uniquely diverse and important to this system, and differences in seasonality and forest structure may be drivers of community differences. Floral scent is likely a key functional trait structuring flower–insect interactions in tropical forest environments and should be emphasised in future studies. Lastly, a joint modelling approach can elucidate community structure, particularly in communities with ecologically generalised interactions.

Key words. Diptera, floral scent, Guineo-Congolian, insect diversity, Korup, plant–pollinator interactions, tropical rainforest, understory.

Introduction

As environmental change and degradation accelerate, perturbing insect populations, we need to better understand the resource use dynamics of diverse wild pollinators (Wagner, 2000; van Klink *et al.*, 2020). Tropical rainforests represent some of the least-

studied undisturbed habitats yet harbour the highest insect diversity (Basset *et al.*, 2012). Most tropical trees are dependent on animal pollinators for reproduction and gene flow (Bawa & Webb, 1984; Bawa, 1990; Knight *et al.*, 2005) and many insect taxa depend entirely or in part on floral resources for their nutritional needs as adults, or throughout their life cycles (Rader *et al.*, 2020). Members of diverse flower-visiting groups such as flies, beetles, and bugs are less studied than bees; however, they are potential pollinators of many species and are also important in the context of pathogen transmission, as agricultural pests

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or as biocontrol agents (Orford *et al.*, 2015; Rader *et al.*, 2020; Raguso, 2020). These insect groups feature prominently in the tropical rainforest, but quantitative community-level studies are limited. Such studies would build upon earlier classic work (e.g. Bawa *et al.*, 1985; Kress & Beach, 1994; Momose *et al.*, 1998; Devy & Davidar, 2003) suggesting that there may be differences among tropical rainforests in terms of the composition and relative importance of different pollinators groups. Much less is known about flower-visiting communities in African rainforests, but a better understanding of how plant–pollinator interactions are structured in these systems is key for the management and conservation of both groups, with implications for biodiversity maintenance, agricultural productivity, and food security in forest zones (Klein *et al.*, 2007; Gemmill-Herren *et al.*, 2014).

Insects are attracted to or repelled from flowers via combinations of floral traits such as colour, scent, size and shape, that act as sensory (visual, chemical, and structural) cues to help them locate suitable resources (Leonard & Masek, 2014; Woodcock *et al.*, 2014). The ability of insects to detect and respond to floral cues depends on sensory system characteristics that are conserved to varying degrees within taxonomic groups and associated with innate preferences, to the extent that different insect groups have been associated with clusters of floral traits known as pollination syndromes (Briscoe & Chittka, 2001; Schiestl, 2010, 2017; Dyer *et al.*, 2011). However, such distinctions are rarely absolute, as many flowers show broad ecological generalisation, i.e., they are attractive to multiple groups of pollinators (Ollerton *et al.*, 2007; Armbruster, 2017). Likewise, many insects are able to respond to learned cues in order to take advantage of available resources (Riffell, 2011; Leonard & Masek, 2014). Additionally, environmental context will determine, which cues can be perceived most effectively (Arnold & Chittka, 2012; Koski, 2020). Understanding how floral cues partition resources in the community in space and time can give us insight into how numerous plant and pollinator species coexist in a given system (Junker *et al.*, 2010; Larue *et al.*, 2016).

Floral visitation patterns in natural systems may be influenced by various interacting factors beyond the attractiveness of trait-based cues, such as phenological matching, pollinator life history, and emergent ecological interactions such as competition, that result in differences in visitation rates in space and time (Valdovinos, 2019). Previous work in tropical forests suggests that many tree species are visited by ‘small diverse insects’ (Bawa *et al.*, 1985; House, 1989; Momose *et al.*, 1998). Quantifying visitor abundance in this case becomes particularly important, as differences in an insect group’s abundance at different flower types can reveal differences in trophic interaction strength despite broad ‘connectedness’ (Vázquez *et al.*, 2007). Expressing abundance in terms of visitation rate can also reveal behavioural differences or similarities within and among groups, helping us to understand to what extent insect groups (whether categorised as functional or taxonomic) are homogeneous, and thus predictable, in their visitation patterns (Herrera, 2020). Additionally, unless interactions between plants and pollinators are tightly specialised, visitors should overlap in their use of floral resources and have the potential to influence one another. Joint modelling of visitor groups is one way to broadly assess

at what level they partition resources (Ovaskainen *et al.*, 2017). For example, a positive correlation between groups that visit the same tree species suggests that they are attracted to the same suite of flowering species, while a negative correlation between the same groups to individual trees suggests that, despite strongly overlapping floral niche space, visits are nevertheless partitioned either in space and/or time by these groups. However, further studies are still necessary to deduce the ecological or evolutionary drivers of such patterns.

For mobile foragers, spatial variation in visitation patterns should be primarily the result of the push and pull of patchy floral resources within the community (Grab *et al.*, 2017). Within-season temporal variation in visitation rates may result from different life-history strategies (Kishimoto-Yamada & Itioka, 2015). In ecosystems with strong seasonal differences, insect groups may track climate factors such as rainfall and/or seasonal resources through the timing of adult emergence or by migrating (Janzen, 1987; Maicher *et al.*, 2018). Species of flies and beetles, for example, have populations that can increase rapidly once conditions are favourable (Kishimoto-Yamada & Itioka, 2008; Chatelain *et al.*, 2018; Kirmse & Chaboo, 2018). Others, such as resource-stocking eusocial Hymenopterans, may show less population variability throughout the year (Heithaus, 1979) and changes in visitation rate to particular tree species are more likely to reflect adaptive foraging on preferred resources. Therefore, modelling visitation rate as a function of time is important for understanding the variation in rates not explained by floral traits and tree species identities.

We know the least about plant–pollinator relationships in Afrotropical forests, both in terms of the number of interactions studied and the proportion of total interactions they represent (Rodger *et al.*, 2004; Vizenin-Bugoni *et al.*, 2018). Few community-level studies exist from across the entire Afrotropical lowland rainforest biome, most focused on particular taxa (e.g. bees: Gikungu *et al.*, 2011; plants: Annonaceae, Gottsberger *et al.*, 2011; Marantaceae, Ley & Claßen-Bockhoff, 2009). Consequently, our understanding of tropical-temperate differences in pollination ecology is limited and geographically biased, as is our ability to make comparisons among tropical forests. For example, flies are currently thought of as dominant generalists in alpine systems (Lázaro *et al.*, 2015; Lefebvre *et al.*, 2018) and isolated islands (Shrestha *et al.*, 2016), with less prominent or more specialised roles in other habitats (Manning & Goldblatt, 1996). Here, we describe a rainforest understory community in Cameroon where flies are main pollinators, in terms of both their abundance and diversity.

Using direct observations and a joint-modelling approach, we examined the structure of insect group visits to trees flowering in the rainforest understory. First, we used ordination to describe community-level associations among insect groups and floral traits. Then, we quantified how group visitation rates varied by floral scent type, a key floral trait, as well as among tree species and tree individuals. We asked the following questions: (i) which floral traits – colour, scent, nectar accessibility and nectar visibility – most strongly structure visitation among insect groups, and how consistent are responses to such traits across groups? (ii) Do different groups show within-season temporal trends in visitation rates? (iii) Do correlations in floral visitation by visitor

groups at the level of tree species or individual trees suggest further resource partitioning among insect groups? This study from a Guineo-Congolian rainforest helps to address both taxonomic and geographic gaps in pollination ecology research by investigating what structures a plant–pollinator community (Ssymank *et al.*, 2008; Blüthgen & Klein, 2011; Gemmill-Herren *et al.*, 2014).

Materials and methods

Study site

This study was performed in the 50 ha Korup Forest Dynamics Plot (KFDP) in Korup National Park, Cameroon. Established in 1996, the KFDPP is part of a collaborative global network of long-term forest monitoring plots affiliated with the Smithsonian Forest Global Earth Observatory (ForestGEO). All trees > 1 cm in diameter at breast height (dbh) have been mapped, measured and identified (Thomas *et al.*, 2003). This lowland tropical mixed forest is part of the Guineo-Congolian forest zone; the KFDPP itself contains ~494 woody species (Thomas *et al.*, 2003). Mean maximum daily temperature is 32.6 °C, with a daytime range of ~10 °C, and mean annual rainfall is ~5000 mm, but strongly seasonal: the 3-month dry season from December to February receives less than 100 mm a month, with rainfall increasing to peak in July and August at over 900 mm (Thomas *et al.*, 2003). This strong seasonality produces a distinct flowering period beginning towards the end of the dry season, making it well suited for studying plant–pollinator interactions in a biodiverse community (D.W. Thomas, personal communication). The plot is a mature closed-canopy forest with low disturbance (Egbe *et al.*, 2012).

Field methods

We evaluated diurnally active insect groups that visited a guild of trees flowering in the understory at peak flowering. During a period from 29 February to 5 April 2016, we extensively searched the southern 25 ha of the KFDPP plot to find tree species flowering in the understory that were among those 169 identified in the plot standbook (Thomas *et al.*, 2003). These included trees with individuals >1 cm dbh that flower at the base of along the trunk (cauliflorous) and treelets with flowers under 4 m from the ground, the maximum distance we could observe them directly with a portable ladder. Our focal species do not contain other understory groups, namely herbaceous species, lianas and small shrubs not included in the plot census. Additionally, despite this being the peak flowering period, many species either had few or no reproductive individuals: we recorded 90 species with at least one reproductive individual.

We observed flowering trees for 15-min bouts during which we recorded all visitors either consuming a reward or contacting a flower's reproductive structures. The only taxa that had limited contact with reproductive structures were ants (not contacting anthers of some tree species). Observations were diurnal and an effort was made to observe each tree species at varying times of day from the time light penetrated the understory and

pollinators became active at ~8 h to just before the light began to dim at ~17 h (Supporting Information Fig. S1). We halted observations if there was rainfall, and we never recorded any breeze in the plot understory during the field season. From among the tree species we observed, we selected those which had accumulated at least 20 visits (median = 56 visits) and at least 1 h of observation (median = 5.4 h), yielding a sample of 20 tree species (median = 11 trees per species, range = 1–17 trees). Flowers we observed remained open, or where the corolla was reduced, were otherwise available to visitors for more than 24 h, thus nocturnal pollination may be important for some species. However, all focal species either produced nectar diurnally (as assessed with microcapillary tubes) and/or were visited by at least 20 insects, allowing us to conclude that diurnal visits are likely important to all focal species. Focal tree species, their visitor groups and floral traits are summarised in Table 1; the full bipartite network of our observations is shown in the Supporting Information Fig. S4, and Table S4 lists the 90 reproductive tree species, including number of individuals, reproductive stage, and where possible, educated guesses about pollinator groups.

We recorded visitor observations to taxonomic order generally, and to family where possible. A subset of approximately a fourth of the visitors was captured and has been initially identified to family by taxonomists (see Acknowledgements); these specimens are representative of the diversity we observed at the community level but not necessarily at the tree species level. In this analysis, we used coarse taxonomic resolution, as our goal was to determine to what extent we found consistent patterns of visitation within and among insect groups, using the largest dataset we could. Six groups were observed frequently enough to model: ants, bees, beetles, bugs, delicate flies (nematoceran-like) and robust flies (Brachyceran-like). These groupings were used to capture taxonomic and functional differences (e.g., between Hymenopteran groups) at the broadest scale: neither the size of the dataset nor the taxonomic resolution of our observations permitted more detailed partitioning. It should be noted that such broad grouping may still include high levels of functional diversity (e.g., body size, tongue length, foraging behaviour) that influence floral visitation and subsequent pollination effectiveness. We split flies into their two traditional suborders—nematocera, now considered paraphyletic (e.g., gnats, mosquitos), and Brachycera (e.g. houseflies, fruit flies) – because of their diversity in this sample (preliminary estimate of at least 14 families) and because morphological differences between them may be related to differences in visitation patterns. We included ant visitors because they could be influencing visitation by other more important pollinators, indirectly via their high relative abundances leading to reduced nectar availability, or directly via antagonistic interactions (Ashman & King, 2005).

We scored four species-level traits for the flowers of each of the 20 focal tree species. Colour, nectar accessibility (floral morphology), nectar visibility and scent are floral traits that mediate flower recognition and attraction (Fornoff *et al.*, 2017). We assessed and discreetly classified both colour and scent in terms of human perception: as broad categories identified by consensus among three field researchers. Although no substitute for more quantitative trait measurements that detect light absorption spectra or the chemical composition of a scent, broadly grouping

Table 1. Tree species and their floral visitors observed during peak flowering, 2016 in the Korup Forest Dynamics Plot, Cameroon.

Tree species*	Number of trees studied	Total obs. time (h)	Total visits, all groups	Total visits per minute	Number of visitor groups	Total visits recorded by insect group									
						Formicidae	Bees Apidae, Halictidae	Beetles†	Bugs Miridae, Tingidae	Delicate flies‡ Nematocera	Robust flies‡ Brachycera	Other visitors			
<i>Angylocalyx oligophyllus</i>	12	5.5	146	0.44	3	136	2	0	0	0	0	0	8	0	
<i>Cola digitata</i>	12	7.5	28	0.06	3	8	0	16	0	0	0	0	4	0	
<i>Cola flavovelutina</i>	18	6.25	85	0.23	6	71	3	1	6	4	0	0	0	1-wasp	
<i>Cola lepidota</i>	9	7.5	162	0.36	7	12	4	8	3	45	90	0	0	1-cockroach	
<i>Cola mambuana</i>	17	7.75	102	0.22	6	32	6	27	5	6	26	0	0	1-butterfly	
<i>Cola micrantha</i>	12	8.75	126	0.24	5	26	0	12	13	30	45	0	0	0	
<i>Cola semecarpophylla</i>	14	6.25	30	0.08	4	3	0	0	1	14	12	0	0	0	
<i>Cola suboppositifolia</i>	10	7.75	96	0.21	6	9	3	1	0	4	79	0	0	1-wasp	
<i>Crotonogynopsis korupensis</i>	13	6.75	51	0.13	5	29	15	4	0	0	3	0	0	1-bird	
<i>Diospyros preussii</i>	11	5.25	51	0.16	6	24	17	1	1	1	7	0	0	0	
<i>Drypetes molunduanu</i>	4	2.75	119	0.72	7	73	10	3	1	9	23	0	0	1-butterfly	
<i>Jollydora duparquetiana</i>	9	3.5	54	0.26	7	9	13	9	1	18	4	0	0	5-thrip; 2-wasp	
<i>Maesobotrya dunsenii</i>	5	4.5	29	0.11	6	19	2	1	1	0	6	0	0	9-wasp	
<i>Maesobotrya barteri</i>	9	7.75	95	0.2	7	12	21	10	1	21	30	0	0	2-wasp	
<i>Phyllobotryon spathulatum</i>	12	4	23	0.1	4	3	16	4	0	0	0	0	0	0	
<i>Rinorea kamerunensis</i>	9	5	26	0.09	4	4	18	2	0	0	2	0	0	0	
<i>Rinorea leiophylla</i>	6	2.5	20	0.13	3	0	17	0	0	0	3	0	0	2-wasp	
<i>Tricoscypha acuminata</i>	1	1	58	0.97	5	0	52	0	0	0	6	0	0	2-butterfly;	
<i>Tricoscypha kelinei</i>	12	4.25	62	0.24	7	17	17	10	2	11	5	0	0	3-bird; 2-wasp	
<i>Uvariopsis bakeriana</i>	8	4.25	23	0.09	6	6	1	5	2	0	9	0	0	7-cockroach	
Totals	203	108.75	1386			493	217	114	37	163	362			2-grasshopper	

*For further taxonomic detail, see also tree-visitor network: Supporting Information Fig. S4.

†Beetle Families: Cantharidae, Chrysomelidae, Curculionidae, Elateridae, Mordellidae.

‡Fly Families: Calliphoridae, Chloropidae, Diopsidae, Drosophilidae, Dolichopodidae, Muscidae, Neriidae, Platystomatidae, Rhiniidae, Ulidiidae, Cecidomyiidae, Culicidae, Mycetophilidae, Tipulidae.

Table 2. Floral traits for the 20 focal tree species.

Tree species	Floral Traits				
	Scent	Colour	Restrictive?	Reward*	Nectar visible
<i>Angylocalyx oligophyllus</i>	No diurnal detected	Yellow, white	Yes	Nectar	No
<i>Cola digitata</i>	Fruity	Red	No	Tissues	No
<i>Cola flavovelutina</i>	Sweet	White	No	Nectar	yes
<i>Cola lepidota</i>	Fermented, fruity	Red, pink	No	Nectar	yes
<i>Cola mamboana</i>	Fermented	Yellow	No	Nectar	yes
<i>Cola micrantha</i>	Fermented	Orange	No	Nectar	yes
<i>Cola semecarpophylla</i>	Carrion	Maroon	No	Deceit	No
<i>Cola suboppositifolia</i>	Fermented	White, orange	No	Nectar	yes
<i>Crotonogynopsis korupensis</i>	Sweet	Green, white	No	Nectar (m)	yes (m)
<i>Diospyros preussii</i>	Sweet	White	Yes	Nectar	No
<i>Drypetes molunduana</i>	Fermented	Yellow	No	Nectar (m), tissues (f)	yes (m)
<i>Jollydora duparquetiana</i>	Sweet	White	Yes	Nectar	No
<i>Maesobotrya dunsenii</i>	No diurnal detected	Red, pink	No	Nectar	yes
<i>Maesobotrya barteri</i>	Sweet, fruity	Pink, white	No	Nectar	yes
<i>Phyllobotryon spathulatum</i>	Sweet	Pink, white	No	Pollen	No
<i>Rinorea kamerunensis</i>	Sweet	Yellow	Yes	Nectar	No
<i>Rinorea leiophylla</i>	Sweet	Yellow	Yes	Nectar	No
<i>Tricoscypha acuminata</i>	No diurnal detected	Red	No	Nectar	yes
<i>Tricoscypha kelineii</i>	No diurnal detected	White	No	Pollen(m), ?(f)	No
<i>Uvariopsis bakeriana</i>	Spicy	Red	No	Stigmatic sec.	Yes (ss; f)

*All species potentially provide pollen as a reward, but this is only listed where pollen foraging was observed.

f = female; m = male; ss = stigmatic secretions.

human-perceived colours and scents can be useful if the differences between insect and human sensory systems are acknowledged. Our classification resulted in seven colour categories: white, pink, yellow, maroon, orange, red, green, and six scent categories: fermented (rotting fruit scent), sweet, undetected, fruity, spicy, carrion scented (Table 2). We classed both nectar accessibility and nectar visibility as binary, according to the restrictiveness of the perianth, where restrictive indicates nectar was found at the base of closed or tubular perianths, and visibility indicates whether nectar was visible to the human eye on the surface of the flower. All four species with restrictive flowers had nectar but four of the species with open flowers did not; we included stigmatic secretions (*Uvariopsis bakeriana*) in the 'visible nectar' category (Table 2).

Analysis

To identify which floral traits were most important for structuring visitation in this community, thus avoiding the need to model less informative traits, we performed an NMDS ordination on the aggregated matrix of visitor group by tree species, choosing the dimensionality (between 1 and 3) with the lowest stress. We first transformed abundance values for each visitor group to percentages out of total visits to each tree species so that species-level results would not be biased by sample size differences (Herrera, 2020). (Note that for the statistical models, we subsequently build, we account for sample size differences directly both by weighting visits by length of observation and by including tree species random effects.) In this and all

subsequent analyses, we used R v.3.6.3 (R Core Team, 2019). Using the `envfit` function from the *vegan* package (Oksanen *et al.*, 2019), we then fit traits, each coded as binary (e.g. 'white colour' present = 'yes' or 'no', for each tree species) as vectors onto the ordination space and used 9999 permutations to assess the significance of the vectors on each of the ordination dimension pairs. We used these traits as predictor variables in our model, however, because scent traits were statistically significant, we decided to include the 'undetected' scent category with >20 observation bouts per visitor group. 'Undetected' scent is also a category represented by multiple tree species that segregates distinctly from other scent categories on the ordination plot (Fig. 1). The other three categories, 'fruity', 'spicy' and 'carrion', had insufficient observations to model independently and were also represented by unique tree species. Visitor responses to these trait categories will be explored via tree species visitation estimates. In two cases where tree species were scored for two scent traits each, we assigned them to the dominant scent for inclusion in the statistical model (*Maesobotrya barteri* = 'sweet', *Cola lepidota* = 'fermented').

To understand how floral visitation is structured among insect groups, we specified a zero-inflated Poisson mixed model (ZIP GLMM) where the response, visitation rate for each insect group, was fit with a joint random-effects structure that allowed covariance among groups with respect to clustering variables. To estimate how correlated (similar or dissimilar) different insect groups were in their visitation rates to individual trees and tree species, visitation was modelled as clustered across insect groups at the level of individual trees, and both across and within groups at the level of tree species. As is often the case for

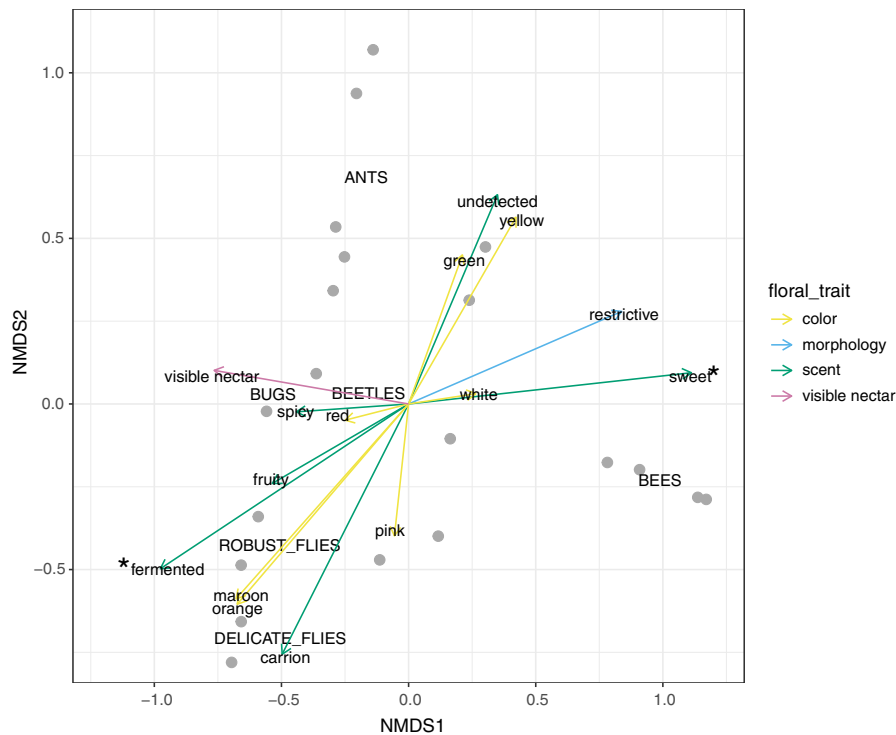


Fig 1. Non-metric multidimensional (NMDS) scaling of the aggregated visitation data as a matrix of proportion of visits by insect group (large black text) to tree species (grey points); first two axes out of three. The floral trait matrix has been fitted onto the ordination as vectors coloured by type of trait. Length of vectors indicate relative specificity of relationships between floral trait vector and particular insect groups, e.g. shorter vectors (such as ‘white’ or ‘red’) indicate little relationship with any particular group. Vectors with asterisk have significance level $P < 0.05$.

observations of floral visits, the data are zero-inflated, with many observation periods during which no visit occurs. Although rarely modelled in plant–pollinator studies, periods with no visits also need to be understood to better explain visitation patterns (Reitan & Neilsen, 2016). By explicitly modelling zeros as potentially either due to random error (such as not observing long enough or at the right time) or to a real lack of interaction between partners, we can gain insights into otherwise sparse-looking data (Blasco-Moreno *et al.*, 2019). In this model, the Poisson distribution estimates visitation rate given visits occur, while the zero-inflated part of the model estimates the probability of visits occurring at all (random zeros vs. structural zeros). Each set of Poisson and ZI parameters are estimated for each visitor group, which is necessary given our explicit interest in understanding differences in visitation rate as potentially stemming from group-level characteristics.

We specified and compared three different models, the full model (Model 1) that included scent categories and observation day (continuous) as fixed effects and tree species and tree individual as random intercepts, a model with scent categories only as fixed effects plus random intercepts as above (Model 2), and a model containing only random intercepts (Model 3). The rationale for three models was not to perform model selection but rather to produce estimates of observed rates, without introducing the distortion that would occur by estimating multiple fixed

effects together. In other words, whether or not there is a temporal trend in observed visits is irrelevant to estimating the median visitation rate to sweet scented species; however, including category ‘sweet’ is important when trying to identify temporal trends, as it is a potentially confounding variable. Therefore, the full model (Model 1) only tested for the effect of observation day, while accounting for the effects of traits. Observation day is strongly correlated with increasing rainfall – we do not have local rainfall data for the study period; however, our field notes show the expected increase in frequency of rainfall events as the flowering season progressed and the seasons shifted from dry to wet. The trait model (Model 2) provided visitation rate estimates for scent trait categories, and the third, random-effects-only model (Model 3) provided the direct tree species estimates of visitation rates. Zero-inflation estimates were taken from the full model but were nearly identical across models.

In syntax used by the brms statistical package, the models used were as follows:

- 1 Visitor count \sim ZIP mvm(offset(log (observation time) + scent category + observation day + 1|q|tree species + 1|p|tree individual))
- 2 Visitor count \sim ZIP mvm(offset(log (observation time) + scent category + 1|q|tree species + 1|p|tree individual))
- 3 Visitor count \sim ZIP mvm(offset(log (observation time) + 1|q|tree species + 1|p|tree individual))

Corresponding to the following GLMM full-model structure:

Likelihood:

$$y_{ij} \sim \text{Poisson}(\lambda_{ij} \times I_{ij})$$

$$I_{ij} \sim \text{Bernoulli}(Z)$$

$$\log(\lambda_{ij}) = \alpha_{ij} + \beta_1 \times \text{scent_ferment}_{ij} + \beta_2 \times \text{scent_sweet}_{ij} + \beta_3 \times \text{scent_undetected}_{ij} + \beta_4 \times \text{observation_day}_{ij} + u_i + v_j$$

Random-Effect Structure:

$$(u_i) \sim \text{Univariate}(\exp(1), L) \forall i \quad (v_j) \sim \text{Univariate}(\exp(1), L) \forall j$$

Priors:

$$L \sim \text{lkj_corr_cholesky}(1) \text{ (Correlation of Random Effects)}$$

$$u_i, v_j \sim \text{exponential}(1) \text{ (Standard Deviation of Random Effects)}$$

$$Z \sim \text{beta}(1, 1) \text{ (Zero-inflation)}$$

$$\beta \sim \text{Uniform over } \mathbb{R} \text{ (improper) (Fixed Effects)}$$

where i -subscripts denote individual trees and j -subscripts denote tree species

Finally, to determine whether visitation rates to different scent categories were affected by other, unmodelled traits potentially shared by closely related species among our focal trees, we also fit Model 2 (Model 2-phylo) using phylogenetically structured species-level random effects. We used the dated molecular phylogeny for the Korup plot developed by Parmentier *et al.* (2013), adding in two missing species at genus nodes (*Trichoscypha acuminata* and *Drypetes molunduanana*) using the packages *phytools* V.07-70 (Revell, 2012) and *MCMCglmm* V.2.32 (Hadfield, 2010) to prepare the phylogenetic correlation matrix.

Models were fit in a Bayesian framework using the *brms* package V.2.8.0 (Bürkner, 2016; Carpenter *et al.*, 2017). The default priors of the *brms* package were used for all parameters except the standard deviation of random effects; for this, we used an $\exp(1)$ prior rather than the half-cauchy prior to avoid biologically unrealistic parameter space. Gelman-Rubin-Brooks potential scale reduction factor ('R-hat') statistic was 1.00 for all parameters, the estimated effective sample size was over 2000 for all parameters, and no divergent transitions were encountered (Gelman *et al.*, 2014). To compare model performance, we used k -fold cross validation, a process in which the data are split randomly and re-fitted 10 times, each time leaving out a tenth of the data. K -fold cross-validation provides a point-wise estimation of out of sample prediction accuracy using within-sample fits (Vehtari *et al.*, 2017). We used expected log pointwise predictive density (elpd) estimates to compare models and understand the impact of adding fixed effects. To determine significant differences in visitation rate among scent categories, and among zero-inflation estimates, we assessed pairwise differences in posterior distributions at the 90% credible interval (CI) level; CIs that did not contain zero were considered statistically different.

Results

Insect visitors and floral traits: aggregate results

During a 5-week period, we observed the flowers of 203 trees from 20 species that flowered in the understory, for a total of ~109 h. We observed 1386 individual flower-visiting insects: flies (38%) and ants (36%) dominated, followed by bees (16%), beetles (8%) and bugs (3%) (Table 1). Other visitor groups too scarce to be modelled here included wasps (1.4%), cockroaches (0.6%), birds (0.3%) and butterflies (0.2%). Ants and robust flies were the most generalised groups, visiting all but two tree species, followed by bees (17/20) and beetles (16/20), while bugs and delicate flies both visited just over half the tree species. All tree species were visited by at least three insect groups (median = 5 groups). Among the subsample of specimens identified more narrowly, flies were the most diverse, followed by beetles, bees, bugs, and ants (Table 1).

To identify which floral traits were most important for structuring visitation, we performed an NMDS ordination analysis of the proportion of visits by each group, aggregated by tree species (Fig. 1). Three dimensions yielded the lowest stress level (0.052 in three dimensions, compared to 0.103 in three dimensions). We fit the tree species floral trait vectors to each of the three pairs of axes of the tree-visitor ordination and found that among the traits, only two scent traits, fermented and sweet, were significantly associated with the visitor ordination groupings, indicating that trait categories associated with flies ('fermented') and bees ('sweet') were most important for structuring this sample (Fig. 1; Supporting Information Table S1b).

Temporal trends in visitation rates

All visitor groups were observed throughout most of the sampling period (points, Fig. 2). Models 1 and 2 were nearly interchangeable in terms of model fit, both improved fits over the random-intercepts only model, Model 3 (Supporting Information Table S2). Model 2 with unstructured species random effects was also a much better fit than Model 2-phylo with phylogenetically structured species level random effects, suggesting that the type of scent traits and when they were available were important for predicting insect group visitation rates, particularly for ants, bees and flies (line, Fig. 2), as opposed to results being driven by other unmeasured traits which related species might share. Fermented-scented flowers did not bloom until mid-season, leaving the early flowering period to be dominated by species with sweet or undetected scents; later in the season, such species flowered also but were no longer the dominant resources (Fig. 2). As the flowering season progressed, ant and bee floral visitation decreased marginally while fly visitation increased marginally.

Floral scent as a predictor of visitation rate

Floral scent categories were associated with important differences in visitation rate among some but not all visitor groups: all groups visited the three floral scent categories, but rates

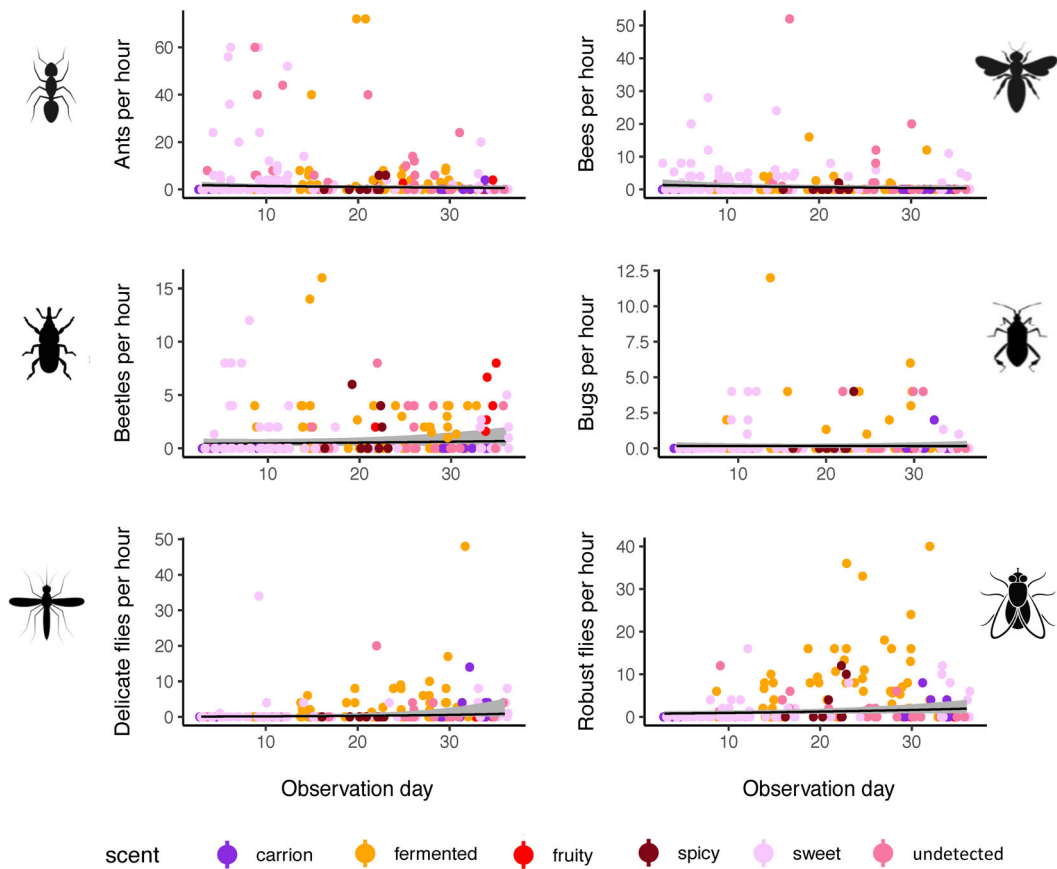


Fig 2. Observed visitation rates (y-axis) for visitor groups plotted by sample date and coloured by scent categories. Marginal effect estimates of sample day are shown as black lines with 95% CIs in grey, from Model 1: full scent category + observation day + random intercepts. No strong temporal trends: marginally important trends decreasing for ants; increasing for delicate flies, robust flies.

(Poisson probabilities) differed among categories and among groups (Fig. 3). Fermented or rotting-fruit scented flowers were attractive to all groups, though significantly more attractive to

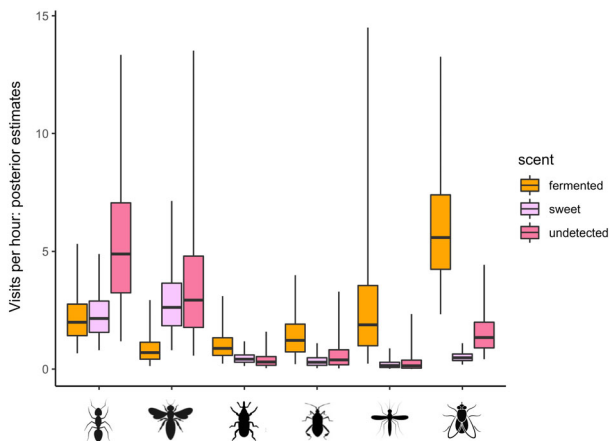


Fig 3. Posterior median estimates of visitation rate by visitor group to flowers in three different scent categories with 50% quantile intervals (boxes) and 95% quantile intervals (lines), based on Model 2: scent category + random intercepts.

robust flies. Sweet scented flowers were significantly more attractive to bees and ants, while flowers with undetected scents were visited most by ants, bees and flies, although rates were not statistically different from those of other groups in most cases. Within visitor groups, visitation rates were not significantly different among scent categories except for the flies: delicate flies were more frequent visitors to flowers with fermented rather than sweet scents, while robust flies were more frequent visitors to fermented scents than to either sweet or undetected scent flowers. Among groups, beetles had the lowest (<1 visit/h) and least variable overall rates, followed by bugs, while in other groups, visitation rates were higher and more variable, particularly among species within certain scent groups. Tests of significant differences are in the Supporting Information Table S3.

How well did scent traits capture variation in floral visitation?

Comparing tree species-level visitation rates across groups, we found that Hymenoptera (ants and bees) were broadly similar, in terms of median rates and species visited (Fig. 4); however, ants as a group visited more species. Bees showed the most consistently elevated visitation rates to sweet-scented tree species, with more

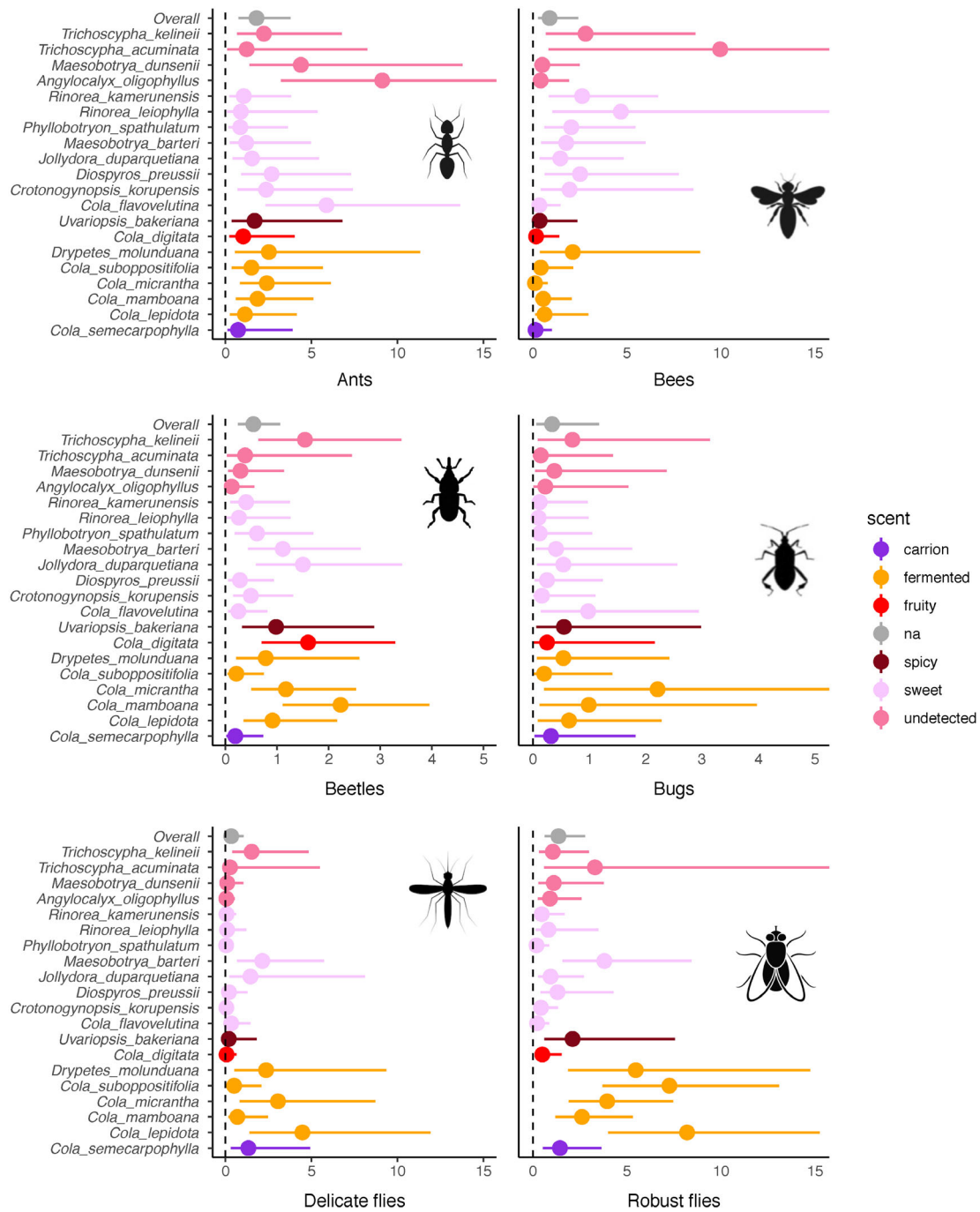


Fig 4. Visits per hour: posterior median estimates (dots) and 95% CI (bars) for visitation rate to tree species (tree species random intercepts) for each visitor group, coloured by scent trait. Note x-axis scale differs for middle panel. Estimates with medians at zero indicate no observations were made for the visitor group to this tree species. (Comparisons of variability within and among tree species are illustrated in the Supporting Information Fig. S2.) Estimates are from Model 3: random-intercepts only.

variable rates to other scent categories. Broad similarities in visitation rates likewise existed between beetles and bugs, although beetles were much more generalised as a group, visiting tree species in five of the six scent categories at comparable rates. The two suborders of flies also broadly resembled one another in foraging preferences and

overall rates, although the robust flies were more generalised as a group. For flies, the fermented scent category did a good job of capturing the highest visitation rates. Overall median rates across groups differed very little, suggesting such averaging was not useful for understanding insect group-level differences in this study.

Variation in visitation to tree species compared to individual trees

There was less variation in visitation rates among individual trees than among tree species, suggesting that visitation rates were dictated more by the attractiveness of species-level traits than by individual tree differences (e.g., in attractiveness, resource quantity, or spatial–temporal location) (Supporting Information Fig. S2). The high variability in delicate fly (nematocera-like) visitation rates among tree species can be seen here also in their relatively wider and lower peaks compared to other groups.

Correlations across visitor groups in visitation patterns to tree species and individuals

The correlation matrix of the random effects in our models estimated the correlation (positive or negative) in visitation rates between pairs of insect groups to tree species and tree individuals. Correlations were considered significant if the area between the upper and lower probability intervals did not contain zero. There was a significant positive correlation (0.46) between delicate flies and robust flies at the level of tree species, suggesting substantial overlap in floral preferences among Diptera (Supporting Information Fig. S3). All other correlations had 95% probability intervals that spanned both negative and positive correlations; for correlation values that are otherwise fairly high (>0.3), this means that there is uncertainty in these values.

Probability of zero-inflation due to ecological mismatch

All visitor groups had a significant amount of zero-inflation, but it differed across groups (Fig. 5). It was highest for bugs (Hemiptera: Miridae, Tingidae), suggesting that a large proportion of the zero observations were structural and would not disappear with increased sampling effort. However, bugs were also the smallest dataset so these results should be interpreted with caution. Ants, bees, and delicate flies showed similar zero-inflation probabilities suggesting more than half the zeros were random while the rest had biological causes. Ants, like robust flies, were found on all but three tree species, but ants differed by having a more variable presence on individual trees, likely leading to a higher zero-inflation estimate. Beetles and robust flies had the lowest zero-inflation, reinforcing their ubiquity in this community, despite (in the case of beetles) their low visitation rates, suggesting a high probability of missed observations (random zeros) that could be improved by longer observations.

Discussion

Plant–pollinator interactions in African rainforests are understudied, leaving us without baselines against which to measure how accelerating environmental change is affecting insect populations and pollination ecology. In this study from Korup National

Park, we aimed to provide a window into the structure of diurnal floral resource use by diverse insect groups to woody species in understory. Most flowers in our study provided exposed floral rewards and this lack of morphological specialisation in the flowers was reflected in the broad foraging overlap among insect groups. Despite this overlap, insect groups exhibited important differences, quantified in terms of visitation rates, in their overall foraging, in their visits to certain scent trait groups or tree species, and over time. As has been found in other studies (e.g. Herrera 2020), insect group visitation rates varied more among tree species than among individual trees, suggesting that tree species trait differences are important for structuring plant–pollinator interactions in the Korup woody understory.

The role of floral traits

Multisensory signalling by flowers and the ability of floral visitors to process information on multiple types of floral traits is to be expected, as more information allows visitors to better discriminate among floral choices (Leonard & Masek, 2014; Kantsa *et al.*, 2017). However, the environment in which a floral cue is perceived influences its effectiveness (Kaczorowski *et al.*, 2012). We found that in an environment characterised by calm air, relatively low light and visibility, and stable temperatures, scent was an important floral trait that structured visitation rates, particularly among bees and flies, where it effectively partitioned sweet and fermented-smelling floral resources between them. Floral scents may be less important in other environmental contexts; however, few studies have included scent traits in analyses of diurnal plant–pollinator communities (but see: Junker *et al.*, 2010; Kantsa *et al.*, 2017). We suggest, as others have, that scents may be critical, possibly dominant, floral functional traits for some diurnal as well as nocturnal communities and that tropical understories are ripe for community analyses of floral scents (Raguso, 2008a; Knudsen, 1999).

Further study will be needed to uncover the key chemical similarities in the scents of ‘sweet’ vs. ‘fermented’ tree species in this community that may explain visitor overlap among human-perceived scent categories. Previous studies have found that particular scent compounds can partition visitation, for example between fly- and wasp-pollinated *Eucomis* species (Shuttleworth & Johnson, 2010); however, scent profiles can also be complex and diverse, and unrelated blends of compounds can be associated with the same general scent and attract the same visitor groups (e.g. small beetles and ‘fruity’ scents in Annonaceae; Jürgens *et al.*, 2000). Our results suggest that even qualitative studies of scent traits, limited as they are by the range and bias of human perception, can be useful starting points for understanding the role of scent in structuring floral visitation at the community level.

Compared to other insect groups, bees had the highest visitation rates to sweet-scented flowers; however, their preference for such scents was far from absolute. While many bee-visited flowers are described as sweetly scented, bees are capable of detecting and foraging from flowers with scents that encompass a very broad range of volatiles (reviewed by Dötterl & Vereecken, 2010). In contrast to bees, some fly groups may have evolutionarily conserved, innate preferences for fermented scents: this has been found among

Drosophilidae where floral scents mimic food and breeding substrates, which may often be one and the same (Stökl *et al.*, 2010). Fermented-scented flowers are not uncommon in tropical systems and may honestly signal food and/or breeding substrates, as well as be non-rewarding mimics (Goodrich & Jürgens, 2018). In this study, fermented-scented species belonged to the unrelated genera *Cola* (Malvaceae) and *Drypetes* (Putranjivaceae): all produced accessible nectar rewards that attracted diverse floral visitors. Other fly groups, such as Muscidae, Calliphoridae and Tachinidae (which include species less dependent on decaying flowers and fruit to complete their life cycles) are attracted to a wider range of floral scent profiles (Zito *et al.*, 2013). Many insects, however, including bees and at least some flies, are also capable of modifying their innate preferences through learning in order to exploit rich resources (Menzel, 1985; Troje, 1993).

Floral scent has been associated with ant deterrence as well as pollinator attraction (Willmer *et al.*, 2009; Galen *et al.*, 2011); however, we found that while the tree species with the highest ant visitation and nectar robbing rate was one with undetected scent (*Agylocalyx oligophyllus*), there was not a significant preference by ants for species with undetected scents over other scent groups. Tree species with undetected scents were otherwise heterogeneous in terms of floral traits: flowers were red, white or yellow in colour, with either accessible (often visible) nectar or none. This variation suggests that the ‘undetected’ scent category grouped those with the absence of a trait rather than by their trait similarity. However, our methods relied on human detection of scent, and flowers that are scentless to humans may be emitting aliphatic volatiles (Kantsa *et al.*, 2017), or carbon dioxide, innate attractants to many insects (Peach *et al.*, 2019). Additionally, carbon dioxide may be a signal of nectar availability in scentless flowers (Dötterl & Vereecken, 2010).

The absence of strong associations between floral colour traits and particular visitor groups may suggest that human-coded colour categories were not useful for understanding the role of floral colour in structuring pollinator visits in this community (Arnold *et al.*, 2009). Colour perception is highly conserved and well understood in bees, and somewhat well understood in flies; however, much less is known about colour perception in other groups (Briscoe & Chittka, 2001; Lunau, 2014). One commonality is that ultraviolet light is perceived by all insect groups, though not by humans: white flowers absorb UV and will appear blue green in trichromatic insect colour space, making ‘human white’ translatable. Pigmented flowers on the other hand may or may not reflect UV light, making the translation from human to insect colour space more variable (Kevan *et al.*, 1996; Arnold *et al.*, 2009). Further study of this system could benefit from modelling floral colour traits based on floral reflectance spectra. Nevertheless, some support for ‘pollinator syndromes’ was apparent, in that certain colours were predictably, though not exclusively, correlated with certain scents and insect groups, specifically: fruity-scented red flowers and beetles, and carrion-scented maroon flowers and flies (Fenster *et al.*, 2004).

Temporal trends

Incorporating time into our analysis proved important – both fly groups increased marginally in visitation rate throughout

the sampling period, as their preferred host plants came into flower and rainfall become more frequent (House, 1989). Flowers are integral to the life cycle of some groups: diverse Drosophilidae require flowers for breeding substrates as well as for adult food, and populations show strong fluctuations in response to floral resources and correlated rainfall (Pipkin, 1965; Pipkin *et al.*, 1966; Coutourier *et al.*, 1986). The observed marginal decrease in bee visitation over time may represent a shift to denser, more attractive floral resources in the canopy, particularly for honeybees. For other less-specialised groups, flowers may represent one of various alternating food sources. The marginal negative temporal trend in ant visitation may have to do with increased food choice with increasing rainfall, in the form of extrafloral nectaries and honeydew production by homopteran insects; we have no data to support this for Korup, but this correlation has been found in other forests (Rico-Gray, 1993). Lastly, trends at higher taxonomic levels may obscure more varied temporal responses at the species level (Kishimoto-Yamada & Itioka, 2015) and future studies would benefit from higher insect taxonomic resolution.

Visitation rates in relation to pollination

When visitors have contact with the reproductive parts of the flower, their visitation rate relative to that of other visitors can be indicative of their importance as pollinators (Vázquez *et al.*, 2007; Herrera, 2020). Robust flies and bees are likely to be important pollinators to most species in this study, due to their high visitation rates: many species belonging to these groups have high pollen transfer potential due to their large body size and/or pollen collecting behaviour. For insects that carry little pollen and the probability of pollination per visit is low, a high visitation rate can still result in effective pollination (Mesler *et al.*, 1980; House, 1989). By this logic, delicate Diptera such as fungus gnats may be important pollinators of several species in this study. Many tree species require cross-pollination, and when tree species are at low local densities, cross-pollination will be difficult for small, non-volant pollinators (House, 1989). Ants can be good pollinators in the right context, with pollination increasing with higher visitation (Ashman & King, 2005; Reddi & Reddi, 1985). In our sample, this may be the case only for ant-dominated *Cola flavovolutina*, which had flowers that were a morphological fit for ants and was locally abundant, however work on its pollination success suggests it is pollen-limited (Drager *et al.*, in review). Given their low visitation rates, beetles and bugs may have a low trophic impact in terms of floral resource use and are likely important pollinators only to species where they are a dominant visitor group (e.g. beetles: *Cola digitata* & *Cola mamboana*). Hemiptera are considered opportunistic floral visitors, transferring little pollen (Wheeler, 2001), and the Miridae and Tingidae observed here are mainly plant pests (Grazia *et al.*, 2015). However, adults are winged, allowing them potentially to cross-pollinate; they also have a relatively long labium that could allow them to reach less-accessible nectar. While phytophagous bugs likely contribute little to pollination when main pollinators are abundant, having a diverse suite of floral visitors may buffer pollination services from fluctuations in the population abundance of main pollinators (Wheeler, 2001).

Restricted vs. cosmopolitan groups

Observations of interactions in nature typically involve long waiting periods where no observations are recorded. While increasing observation time should increase sample size, this will only occur if a certain ecological interaction exists to begin with. The low zero-inflation rates of beetles and robust flies suggest they would benefit the most from increased observations. Ants, despite visiting most tree species, did not have low zero-inflation, and we can speculate that two traits, social foraging that recruits others to resources, combined with being non-volant and thus having a smaller foraging range, resulted in spatially structured visits, where some individual trees did not get visited, as can be seen in their higher visitation rate variability among trees than among tree species (Fig. 5). Additionally, in this study, we identified zeros as only either random or structural; however, there is also the possibility of zeros due to observational error, but given the coarse taxonomic resolution used, we do not anticipate it is high for these data.

Correlations in visitation patterns

Correlations in visitation patterns suggest either similarities or differences in interaction patterns at the level of tree species or individual trees. Positive tree species-level correlations suggest similar resource use at similar rates, while correlations at the level of individual trees may signify either directly shared resources – and the potential for interactions among visitors – (positive correlations) or resource partitioning (negative correlations) in time or space. In this study, insect visitors were divided into traditional taxonomic groups, except for the Diptera, that due to their richness and abundance we were able to model as two groups, separated at the most basal split. The strong positive correlation between the two dipteran groups in terms of the tree species they were attracted to may be expected if flower visiting Diptera have conserved innate preferences. This suggests that there is interesting work to be done on floral resource competition among the highly diverse Diptera in this community (14 families identified from our subsample of specimens). Other visitor groups overlapped in non-significant ways; however, uncertainty in the estimates could conceal further interaction structure in terms of visits to certain tree species and individuals.

Cross-continental comparisons

Across continents, lowland rainforests differ in ways that may affect pollinator community composition. The understory is structurally similar between Korup, Cameroon and Neotropical plots, being rich in flowering trees of small stature; this is unlike South East Asian plots where the understory is dominated by non-reproductive juveniles of canopy trees (LaFrankie *et al.*, 2006). Greater floral resources in the understory may support a higher diversity of pollinators. Climatic differences lead to phenological differences in floral resource availability: despite being one of the wettest places in Africa, Korup has a distinct dry season that ends with a peak flowering period; in contrast, La Selva, Costa Rica is an aseasonal wet forest where up to a

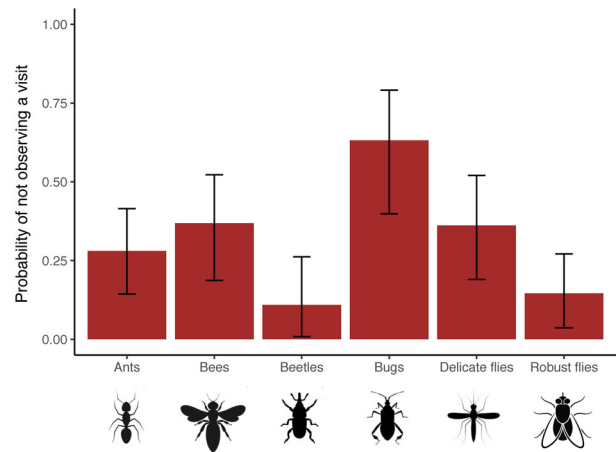


Fig 5. The mean zero-inflated probabilities of not observing visits due to ecological mismatch with 95% CIs, from Model 1: full model. (Note probability of no observation is actually higher, as the probability of a random zeros has been modelled by the Poisson part of the model.)

third of the species flower all year (Newstrom *et al.*, 1994; Thomas *et al.*, 2003). Malaysian forests are aseasonal but also unpredictable, offering low levels of floral resources punctuated by resource peaks that vary greatly among years (Sakai *et al.*, 1999). Korup's predictable but seasonal abundance peak of floral resources should select for pollinators with life histories that can exploit these peaks as well as deal with floral scarcity and extremely wet conditions the rest of the year. Pollinators with short life cycles and that enter diapause, that migrate, that are social and stock resources, or that can exploit alternative food sources should be favoured. More constant resource availability, such as is found in wet Neotropical forests, should facilitate larger and more specialised pollinators (Bawa, 1990; Corlett, 2004).

Previous work on the plant-pollinator ecology of other tropical understory communities suggests that generalised interactions are common, with 'small diverse insects' visiting many tree species (Bawa *et al.*, 1985; House, 1989; Momose *et al.*, 1998). However, the degree of generalisation and the dominant pollinator groups may differ among forests. If we compare visitors to the woody understory only (no herbaceous species), then in a Malaysian rainforest (Lambir Hills NP; tree species = 38), social bees and beetles were the main groups, visiting 44% of species, and 45% species, respectively (Momose *et al.*, 1998). In Costa Rica (La Selva; tree species = 84), bees were the dominant group, main pollinators of 42% of species, and visitors to 54%, with other groups each visiting no more than 20% (Bawa *et al.*, 1985; Kress & Beach, 1994). Species visited by 'small diverse insects', a category with no dominant group but that included beetles and flies, among others (the way this was calculated was not indicated in either study) amounted to 24% for Lambir and 12% for La Selva. Ants were not considered. Korup (n tree species = 20) paints a more generalised picture, where flies visited 90% of tree species, bees 85% and beetles 80%. For flies, this is in strong contrast to their visiting 24% of species in Lambir and 14% of species in La Selva, despite our study having left out the smallest and most cryptic flowers that may depend on microdipteran

visits (e.g. *Dorstenia* spp.). If, for comparative purposes, we assign dominant pollinators to the tree species we studied (defined here as composing more than 60% of visits and excluding ants), then bees are the main visitors for 25% of species, beetles 5%, flies 35% with robust flies (Brachycera) being the main visitors to half of these. Butterflies and birds, important lowland Neotropical groups, were at very low abundance (Table 1). Birds, rarely observed in this study, are important visitors to some herbaceous species (e.g. Marantaceae, Ley & Claßen-Bockhoff, 2009) and increase in importance at higher altitudes (Nsor *et al.*, 2019). Moth pollination is likely very important in this understory, as we observed the consecutive and abundant flowering of species with white, narrow, tubular corollas and no diurnal visitors (e.g. Rubiaceae, Apocynaceae; Supporting Information Table S4) (Maicher *et al.*, 2018). It is also possible that nocturnal pollinators are important to some of our focal species – cockroaches and grasshoppers, for example, are nocturnal pollinators to an Annonaceae species in the region (Mertens *et al.*, 2018).

The diurnal understory assemblage that visits woody species in Korup may be distinct in terms of the abundance, diversity, and ecological niche breadth occupied by flies. Korup also appears to have a greater percentage of tree species with taxonomically generalised interactions, with overlap in insect group visits between the highly abundant and diverse ‘fly attractive’ *Cola* (Malvaceae) and *Drypetes* (Putrangivaceae) species, and the ‘bee attractive’ *Rinorea* (Violaceae) species in this forest. While this study evaluated fewer tree species than the studies we cited, the species were representative of the bulk of floral resources available. Our sample contained 22% of the woody species flowering in the understory in 2016; yet they represented ~85% of the flowering trees >1 cm dbh. This suggests that we have captured the main floral resources available to diurnal pollinators, if not their full phylogenetic or functional diversity. It also suggests we have described the dynamics of the main diurnal visitor groups of understory trees during peak flowering. However, to definitively compare plant–pollinator communities among tropical lowland forests, we will need observations that encompass the full diversity of the forest during both day and night, throughout the entire year. To fully understand the dynamics of the plant–pollinator community, we will need longitudinal studies which will help address the role that climate and resource availability play in driving insect community composition. We predict that towards the end of the peak flowering period, as the rainy season becomes more intense, and breeding substrates increase, the abundance and diversity of flower-visiting Diptera will also continue to increase (Pipkin, 1965; Kishimoto-Yamada & Itiola, 2015).

Conclusions

Anthropogenic drivers are increasingly perturbing insect communities; however, little data exist from tropical regions, particularly from the Afrotropics (Janzen & Hallwachs, 2019; van Klink *et al.*, 2020). It is unclear how predicted changes to precipitation patterns will affect plant–pollinator interactions in Equatorial Africa (e.g., Feng *et al.*, 2013), although changes in flowering phenology have already been detected (Bush *et al.*, 2020). African rainforest

trees play major roles in the global water cycle and climate change mitigation, they support some of the planet’s richest biodiversity, and provide food, medicine, cultural value and income for rural populations across equatorial Africa, and they are nearly all adapted for insect pollination (Watson *et al.*, 2018). Agroforestry and shifting cultivation are the main farming systems in these forest zones and are also largely dependent on insect pollinators (Gockowski & Sonwa, 2008). This study of a biodiversity hotspot provides novel baseline data on plant–floral visitor interactions and the floral traits that help structure them. Studies such as this one, quantifying wild plant–pollinator assemblages and dynamics, are a first step towards managing pollination as a critical ecosystem service.

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Author Contributions

A.P.D. generated the ideas and designed methodology; A.P.D., R.T.W. and W.A.N. collected the data; G.C., D.K., and D.W.T. established the K.F.D.P.; A.P.D. analysed the data; A.P.D. and A.E.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflicts of Interest

All authors state they have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data and R scripts are publicly available at <https://github.com/APDrager/Korup-plant-poll>; Specimen images and metadata: <https://www.inaturalist.org/projects/pollinators-of-korup-national-park> and at project KVIS at <https://www.boldsystems.org>, public data portal.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix 1

Figure S1. Distribution of observation times throughout the day, by tree species.

Figure S2. Comparison of posterior distributions of standard deviations in visitation among tree species vs. among individual trees, for each visitor group, from each model.

Figure S3. Correlations in visitation rate between visitor groups at the level of tree species (left) and individual trees (right). Heavy black outline indicates 95% CI did not overlap zero. Estimated using Model 3: random-intercepts only.

Appendix 2

Figure S4. Plant-visitor network for the Korup Forest Dynamics Plot during peak flowering 2016. NB: All interactions observed are included here despite very low observation times for some tree species (marked with an asterisk and not included as focal species in the study). ‘Unspecified observations’ correspond to observation records that do not include an insect specimen and were only identified broadly to functional group.

Appendix 3

Table S1a. Results from NMDS analysis: scaling of the aggregated visitation data as a matrix of proportion of visits by insect group to tree species. **Table S1b.** Results from NMDS analysis: the floral trait matrix fitted onto the ordination as vectors.

Table S2. Model comparison statistics showing Models 1 & 2 fit the data better than Model 3, with Model 2 possibly fitting slightly better than Model 1.

Table S3. Pairwise significance tests of differences among and within visitor groups with respect to visitation rate to scent categories, using Model 2 estimates. Pairwise significance tests of differences in zero-inflation among visitor groups, using Model 1 estimates.

Table S4. List of the ninety reproductive tree species observed in 2016, including number of individuals, reproductive stage, observation hours, and where possible, educated guesses about pollinator groups.

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