




ARTICLE

Cheaters among pollinators: Nectar robbing and thieving vary spatiotemporally with floral traits in Afrotropical forests

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Abstract

Nectar robbers and thieves are common antagonists in plant–pollinator communities, where they deplete nectar without pollinating flowers, substantially affecting plant reproduction. Nevertheless, little is known about the relative abundance of such nectar exploiters in communities, even though spatiotemporal changes in the frequencies of antagonists and mutualists can exert opposing selection pressures on the traits of the interacting species. Although these effects are highly dependent on the community context, interspecific interactions have almost exclusively been studied in interacting species pairs or single-plant studies. We hypothesized that flowers might experience a trade-off between filtering out robbers and thieves. We used an extensive dataset of video-recorded flower–visitor interactions along a complete elevational gradient in wet and dry seasons on Mount Cameroon to assess spatiotemporal changes in robbing and thieving associated with several floral traits. Of the 14,391 recorded visits, ~4.3% were from robbers (mostly bees and birds) and ~2.1% were from thieves (mostly flies, bees, and moths). Only 29 and 39 of the 194 studied plants were robbed and thieved, respectively. We found that specialized floral traits that prevented thieving (such as long floral tubes or spurs) made flowers susceptible to robbing, and vice versa. Cheating behavior was most frequent at mid-elevations, with more frequent robbing during the wet season and thieving during the dry season. These trends were linked to the local floral trait composition and the associations of cheating groups with specific floral traits. Our results suggest that the roles of antagonists and mutualists in shaping partner traits may vary across communities and that they deserve more attention in future studies of interspecific interactions.

KEYWORDS

Afrotropics, cheaters, floral traits, Mount Cameroon, nectar robbing, nectar thieving, spatiotemporal variation

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INTRODUCTION

The evolution of species has been strongly influenced by selection pressures from interspecific interactions. While most species interact diffusely with numerous others in communities, most studies have predominantly focused on pairwise species interactions (Bronstein, 2009). As a consequence, we often interpret morphological and functional traits as outcomes of coevolution within a single interaction type (for instance, an interaction of a flowering plant with its pollinators) while overlooking that these traits may be subjected to opposing selection pressures from both mutualists and antagonists (such as non-pollinating flower visitors; Padyšáková et al., 2013; Strauss & Irwin, 2004). Moreover, these interactions may exhibit substantial spatiotemporal differences, resulting in geographic mosaics of coevolution that profoundly affect species and their communities (Thompson, 2005). Consequently, a comprehensive understanding of species evolution requires the consideration of multiple interaction types in communities, especially those with opposing selection pressures.

Communities of flowering plants and their animal visitors are often viewed as a stereotypical mutualism, where flowers provide rewards such as nectar and pollen in exchange for pollination services (Willmer, 2011). However, the conspicuous advertisement of rewards also attracts non-pollinators (Irwin et al., 2010; Irwin & Maloof, 2002) which may even outnumber pollinators (e.g., up to 78% of visitor species in King et al., 2013; Popic et al., 2013). These non-pollinators, termed as *cheaters*, forage on nectar without touching floral reproductive organs (Irwin et al., 2010; Irwin & Maloof, 2002).

Cheaters in a pollination mutualism can be categorized into *robbers* and *thieves* depending on whether they actively damage flowers during nectar extraction (Inouye, 1980). Thieves are visitors that can extract nectar through the corolla opening without touching the stigmas or anthers while foraging. A common mismatch that leads to thieving is the corolla tube being shorter than the visitors' proboscis, as seen with lepidopterans which often probe for nectar without pollinating the flower (e.g., the butterfly *Eurybia lycisca* on *Calathea crotalifera*; Bauder et al., 2011), although some specialized plants rely on pollination by moths and butterflies (e.g., Balducci et al., 2019; Mertens et al., 2020). Another mismatch that may lead to thieving can be observed in small visitors feeding on open-shaped flowers with exposed stigmas and anthers. For example, small meliponine bees visit large, open Melastomataceae flowers (Murphy & Breed, 2008), and honeybees (*Apis mellifera*) visit *Hypoestes aristata* flowers with protruding stigmas (Padyšáková et al., 2013) without transferring pollen.

Robbers access nectar concealed in tubes or spurs of morphologically specialized flowers through holes in the floral structures, either made by themselves or by previous visitors (Rojas-Nossa et al., 2016). Opening holes in the corolla or calyx, termed *primary nectar robbing*, requires specific adaptations such as strong mandibles (e.g., bumblebees, carpenter bees, and beetles; Inouye 1983), beaks (e.g., sunbirds, hummingbirds, and flowerpiercers; Geerts & Pauw, 2009; Janeček et al., 2011), or teeth (e.g., squirrels and galagoes; Deng et al., 2015). Once these holes are created, they can facilitate *secondary nectar robbing* by enabling other visitors to access nectar through them (Bronstein, 2001; Irwin et al., 2010). Secondary robbing can be more energy-efficient than foraging through the corolla opening, especially for visitors that can access nectar without piercing the flower (Lichtenberg et al., 2018).

Nectar robbers and thieves lower the nectar available for pollinators and may also change their foraging behavior (Irwin et al., 2010; Padyšáková et al., 2013). In addition to inducing secondary robbing, floral damage caused by the robber makes flowers less attractive to subsequent visitors (e.g., Castro et al., 2013). Pollinators may learn to avoid exploited flowers, leading to lower visitation rates for these flowers (Varma et al., 2020). The effects of cheater-induced changes in pollinator behavior can vary across plant species, with some species benefitting from increased outcrossing and others exhibiting reduced pollen deposition and seed set (Irwin et al., 2010). The consequences of nectar exploitation on plant reproduction may depend on the species of cheaters, pollinators, and plants involved in the interactions and the variety of available floral resources. However, the intensity of these effects depends on the amount of nectar removed by cheaters and, therefore, on their visitation rates (Maloof & Inouye, 2000).

While floral traits are often considered to have coevolved with pollinators, they may also be associated with the behavior of nectar exploiters. Open-shaped flowers often attract several generalist visitors, which may increase the deposition of heterospecific pollen, leading to stigma clogging (Arceo-Gómez et al., 2019). Furthermore, the easy access to their nectar rewards makes open-shaped flowers highly susceptible to morphologically mismatched nectar thieves. In contrast, flowers that restrict access to rewards to their specialized pollinators by concealing them in longer nectar tubes (Lázaro et al., 2015) fused petals, and closed shapes such as trap flowers (Gómez, 2005) may improve intraspecific pollen deposition. However, they might be more susceptible to robbers that cannot legitimately access hidden nectar (Rojas-Nossa et al., 2016; Sonne et al., 2016). Thus, floral traits that improve the chances of pollination may

also experience a potential trade-off between excluding nectar thieves and nectar robbers.

Spatiotemporal differences in the intensity of cheating behavior can strongly affect the variance in selection pressure on floral traits (Thompson, 2005). Intraspecific variation in the visitation rates of nectar robbers has been observed at the plant species level (Castro et al., 2013; Cuevas & Rosas-Guerrero, 2016; Irwin & Maloof, 2002; Price et al., 2005), but nectar thieving has gone woefully unnoticed. At the community level, the roles of nectar exploiters also vary spatiotemporally, yet community-wide studies on cheating behavior are scarce. Nonetheless, the few existing studies suggest that the proportion of exploited plant species varies among communities (Cutá-Pineda et al., 2021; Irwin & Maloof, 2002). In particular, Rojas-Nossa et al. (2016) found that the proportion of exploited plant species varies across broad spatial scales (e.g., 51.9% in the Mediterranean, 16.6% in the Alps, 22.2% in the Antilles, and 66% in the Andes). Nevertheless, there is a lack of quantitative assessments of cheating visits for the entire flower–visitor community, which substantially limits our understanding of the role of these antagonistic interactions in evolutionary processes.

Although the spatiotemporal variation in nectar robbing and thieving rates has not been quantified at the community level, it may be reasonable to assume that it mirrors spatiotemporal changes in floral traits of plant communities (Irwin & Maloof, 2002). For instance, the community composition of floral traits varies along elevational gradients (Albrecht et al., 2018; Klomberg et al., 2022), which may be related to the increased energy requirements of pollinators at higher elevations (Classen et al., 2015). This elevation-related variation may increase the importance of traits associated with nectar production and composition for floral visitors (Klomberg et al., 2022). Additionally, floral traits may vary seasonally, as some plants blooming in rainy seasons have closed flowers with narrow tubes (Klomberg et al., 2022) that prevent nectar dilution (Aizen, 2003) and washing away of pollen (Mao & Huang, 2009). In the tropics, ornithophilous plants are more common in the wet season, as seen in sunbird-pollinated plants on Mount Cameroon (Janeček et al., 2022).

Our main aims were to quantify spatiotemporal patterns in nectar exploitation by cheaters along an elevational gradient and between wet and dry seasons in Afrotropical rainforest communities and to understand their relationship to the distribution of floral traits. We addressed the following questions: (1) How frequent are nectar robbing and thieving in the studied communities? (2) Do the nectar exploitation rates vary with elevation or between seasons? (3) Is spatiotemporal variation in visitor behavior associated with floral traits of the studied plants?

(4) Do nectar robbers and thieves differ in their associations with specific floral traits, and do these associations change with their functional groups? (5) Is there any support for a possible trade-off between floral traits that deter nectar robbers and those that restrict nectar thieves?

METHODS

Study area and sites

We studied flower–visitor communities on Mount Cameroon (Southwestern Region, Cameroon; 4°12′10″ N, 9°10′11″ E), the highest mountain in West and Central Africa (4095 m above sea level [asl]). The mountain's southwestern slope represents the only continuous elevational gradient of pristine tropical rainforest extending from the lowland (~350 m asl) to the timberline (~2100–2300 m asl) in continental Africa. Local precipitation is strongly seasonal, with over 2000 mm of monthly rainfall in the foothills during the wet season (June–September) and little to no rainfall in the dry season (November–February; Maicher et al., 2018, 2020). We sampled four elevations along the gradient: lowland (650 m asl), submontane (1100 and 1450 m asl), and montane (2200 m asl), once each in the wet and dry seasons (for details, see Appendix S1: Table S1; Klomberg et al., 2022), with a total of eight elevation–season combinations.

Behavioral observations

We video-recorded flower–visitor interactions for all zoophilous plant species in flower across all vegetation layers, spanning from the forest floor to the canopy using security cameras (VIVOTEK IB8367RT with IR night vision). To ensure representative sampling of the local vegetation heterogeneity, we established six transects (each measuring 200 × 10 m) at each elevation, spaced at least 100 m apart (Klomberg et al., 2022). These transects were operated in both wet and dry seasons. For each plant species flowering in each elevation–season combination, we video-recorded five different plant individuals. Our priority was to separate individual replicates in time (filming on different days) and space (filming only one individual per transect). However, we sometimes recorded more individuals in each transect (if the species was spatially clustered), or we recorded plants in the surrounding vegetation if there were insufficient replicates for a particular observed plant species within the transects. Each recorded individual was filmed continuously for 24 h to document visitor activity during the day and

night. If flowers closed during the recording, we excluded these periods from the analyses.

We processed all video recordings to note flower–visitor interactions. For recordings with minimal background movement, low wind interference, and clear visibility of flowers (either due to their size or distinctiveness in the video), we used semiautomatic motion detection (MotionMeerkat 2.0; Weinstein, 2015). All other videos were watched manually through a sped-up playback. Once the videos were processed to note interactions, specialists used these marked interactions and videos to identify visitors to the best taxonomic resolution, often sorting them into morphospecies. We then assigned identified visitors to 13 functional groups based on the commonly noted pollination syndromes (Willmer, 2011), splitting bees and flies into subgroups that better represent the differences in their reward preferences: sunbirds, bats, small mammals, hoverflies, other flies (hereafter “flies”), honeybees, carpenter bees, other bees, beetles, wasps, butterflies, hawkmoths, and other moths (hereafter “moths”). To account for differences in the sampling effort among individual elevations and seasons (different numbers of plant species in flower), and plant species (differences in the numbers of recorded flowers, flower longevity, technical failures, and/or lack of sufficient replicates for rare plants), we quantified the

visitation frequency for each behavior as the number of visits per flower per minute.

We carefully noted visitor behavior during each visit and made detailed observations regarding whether visitors contacted floral reproductive organs, foraged on floral rewards, and whether the visit was legitimate (through the corolla opening). Based on these details, we noted if visitor behavior for each visit included (1) potential *pollination*, contact with anthers and/or stigmas; (2) *thieving*, nectar accessed through the floral opening without touching anthers or stigmas; and (3) *robbing*, nectar accessed through holes other than the floral opening and without touching any reproductive organs (Figure 1b–e). Thus, for every plant–visitor interaction, we were able to identify *pollinators*, *thieves*, and *robbers*. Additionally, we defined the *main pollinators* of each plant species as the two functional groups with the highest frequency of pollinating visits. Visitors that neither approached floral rewards nor touched reproductive organs were excluded from the analyses.

Floral traits

We measured 10 floral traits (Appendix S1: Table S2; partly used in Klomberg et al., 2022) for all the 195 plant species in our dataset. For each species, we examined one flower

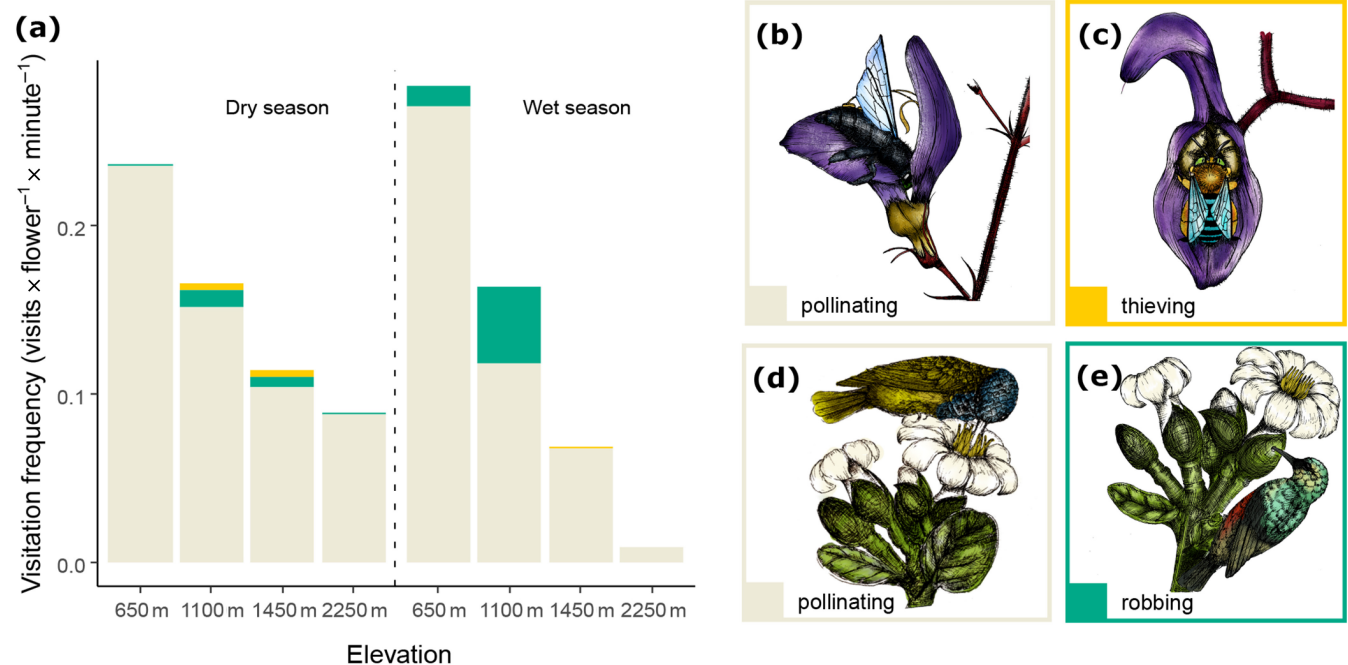


FIGURE 1 Robbers, thieves, and pollinators of flowering plants on Mount Cameroon. (a) Visitation frequencies for pollinators (ivory), thieves (yellow), and robbers (blue) across the elevational gradient and between the dry and wet seasons. Examples of flower visitors: (b) a carpenter bee (*Xylocopa* sp.) pollinating and (c) a blue-banded bee (*Amegilla* sp.) thieving nectar of *Brillantaisia owariensis*; (d) a Cameroon Sunbird (*Cyanomitra oritis*) pollinating and (e) a Northern Double-Collared Sunbird (*Cinnyris reichenowi*) robbing nectar of *Anthocleista scandens* (all drawings by Sailee P. Sakhalkar).

each from five individuals for all the traits except nectar production. Among the traits, seven were qualitative and characterized floral shape (bell, bowl, dish, funnel, gullet, labiate, open, papilionate, salverform, stellate, trumpet, tube, and urceolate), symmetry (zygo- and actinomorphy), orientation (horizontal, pendant, and upright), color (brown, green, orange, pink, purple, red, white, and yellow), nectar guides (presence/absence), brightness (vivid/drab), and odor strength (none, weak, and strong). The qualitative traits were recorded in the field by an experienced botanist. Regarding the quantitative traits, we measured three morphometric traits (corolla size, length, and width of nectar tube) using a caliper in the field. Nectar sugar production was quantified as the amount of sugar in nectar from one flower each from 15 individuals (measured as 24-h production in flowers in situ; the details are described in Janeček et al., 2021 from where the data were taken). For all quantitative traits and nectar production, we used the mean value per plant species.

Data analyses

All statistical analyses were conducted in R 4.1.1 (R Core Team, 2021). We tested if the relative proportions of visitor behavior (robbing, thieving, and pollinating) differed spatiotemporally, that is, across each of the elevation–season combinations, using χ^2 tests (the `chisq.test` function from the `stats` package; R Core Team, 2021). We separately tested for differences between the two seasons, and among the four elevations.

We analyzed interspecific trait–behavior associations using the multivariate RLQ analysis to test whether community-level differences in visitor behavior are associated with floral traits (Dolédec et al., 1996). RLQ is an ordination method that associates matrices **R** and **Q** containing two separate sets of variables (such as environmental variables and species traits) by maximizing their covariance based on a third, central matrix **L** containing variables (such as species composition) that link **R** and **Q**. In our study, matrix **R** ($n \times m$) included a row for each of n sites (characterized by the combination of their environmental variables—elevation and season), with m columns containing data for the frequencies of total visitor behavior (pollination, robbing, and thieving; **L** ($n \times p$) contained presence–absence data each from n sites for p plant species; and **Q** ($p \times q$) had measurements of p plant species for q floral traits.

The RLQ analysis was performed as follows. First, plant species composition at each site (matrix **L**) was ordinated with a correspondence analysis (CA an unconstrained ordination method), which maximizes the correspondence between rows and columns of matrices

that contain count, presence–absence, or abundance data. We then used the row weights (sites) and column weights (plant species) from the CA on matrix **L** to weigh the rows of matrices **R** (sites by visitor behavior) and **Q** (plant species by floral traits). Third, we ordinated matrix **R** with a principal components analysis (PCA, an unconstrained ordination method containing continuous response variables only) and **Q** with Hill and Smith PCA (hs, an unconstrained ordination method combining continuous and categorical response variables). Consequently, in the final step of the RLQ analysis, these separate ordinations were combined by performing a double inertia analysis (a co-inertia analysis for two matrices) of **R** and **Q** linked through **L**. The analysis found those linear combinations of the environmental variables and floral traits that maximized their covariance, thus describing their joint structure (see a conceptual overview of the applied RLQ analysis in Appendix S1: Figure S1). We evaluated the significance of the RLQ analysis using a sequential two-model Monte Carlo test with 9999 permutations to test if species composition was linked to trait composition (by permuting species), as well as to environmental and behavioral variables (by permuting sites). Last, we used ordination diagrams to visually examine the joint structures of the three matrices (Figure 2a) and the associations between sites and visitor behavior (Figure 2b) and between sites and floral traits (Figure 2c). The RLQ analysis was conducted using the `ade4` package (Dray & Dufour, 2007).

Finally, we used separate redundancy analyses (RDA, a constrained ordination method) for robbers and thieves to test whether each of their functional groups had different trait associations. In these independent analyses, robbing and thieving frequencies of functional groups per plant species were Hellinger-transformed (for zero-inflated data with low counts) and used as response variables. In both analyses, floral traits chosen by forward selection were used as explanatory variables. We tested the significance of each RDA using Monte Carlo tests with 999 permutations. The RDAs were performed using the `vegan` package (Oksanen et al., 2022).

We used circular graphs to visualize how exploiters from different functional groups selectively targeted plant species with main pollinators from particular functional groups. Each graph was constructed in the `igraph` package (Csárdi et al., 2023), with nodes representing the number of plant species each functional group of visitors acted as a main pollinator for and arrows indicating instances where a functional group exploits plant species mainly pollinated by another group. We created separate graphs for robbers and thieves to highlight the selectivity exhibited by each functional group in exploiting specific pollinator–resource relationships based on the proportions of exploited plant species.

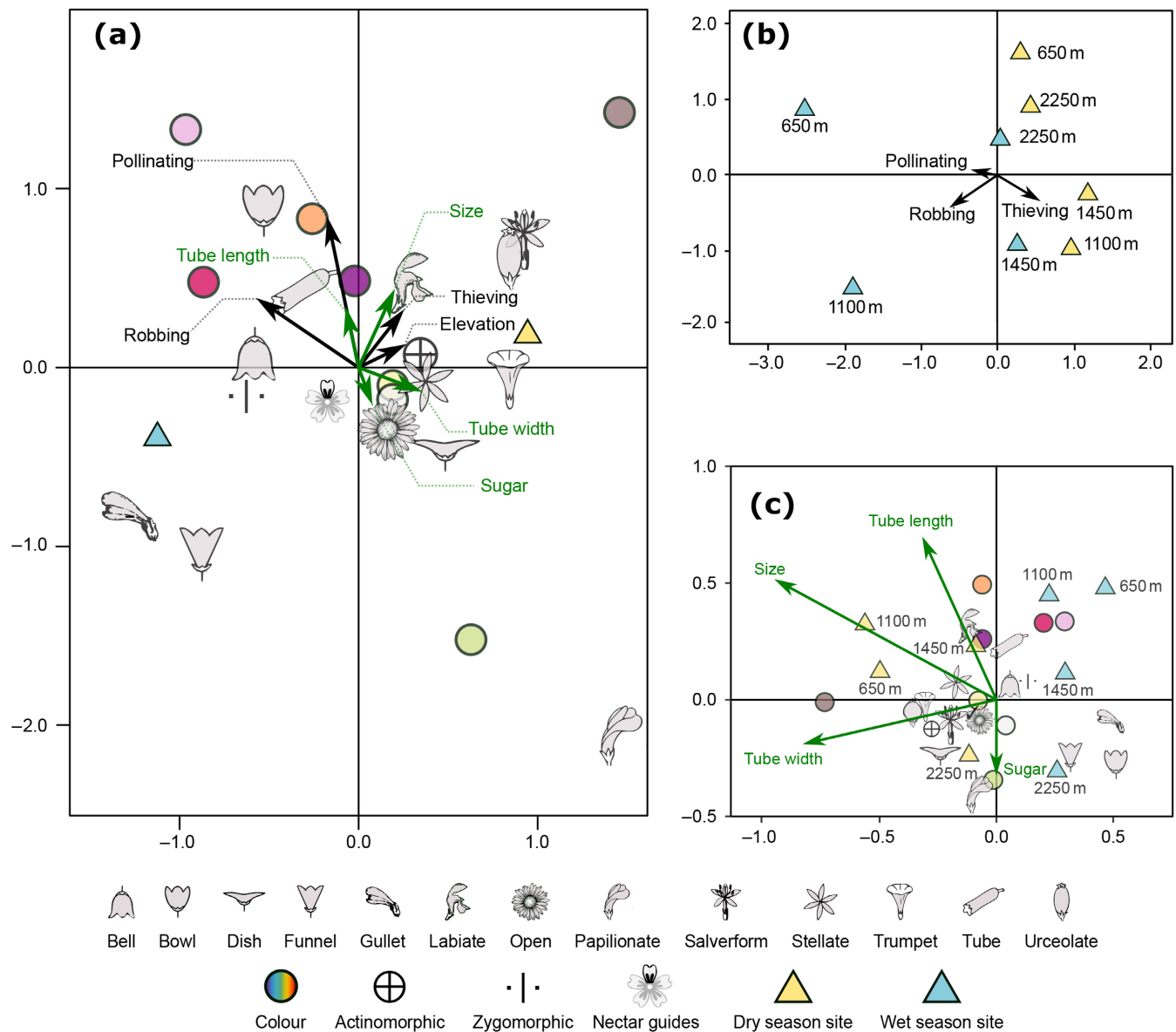


FIGURE 2 Ordination diagrams (biplots) visualizing the associations between environmental variables, visitation frequencies, and floral traits on Mount Cameroon, as resulting from the RLQ analysis. Season, categorical floral traits, and studied site/season centroids are represented by symbols, whereas continuous floral traits (in green) and visitation frequencies (in black) are visualized with arrows. (a) Associations of environmental variables and visitation frequencies with floral traits. (b) Associations of sites with visitation frequencies and environmental variables. (c) Associations of sites and floral traits. Dashed lines are used to label the arrows to improve readability.

RESULTS

We video-recorded flowers from 195 plant species, yielding a total of 26,138 h (i.e., >2.98 years) of footage. The video recordings resulted in a total of 14,391 visits, of which 13,365 visits (92.87%) were by pollinators, 623 visits (4.32%) by robbers, and 304 visits (2.11%) by thieves. Among the recorded 195 plant species, only 26 (14.79%) were robbed and 39 (19.89%) were thieved, while 126 (64.28%) were neither thieved nor robbed (Table 1). No thieves, robbers, or pollinators were observed in 12 plant species.

Furthermore, even exploited plant species differed in the proportion of interactions with exploiters, with an average of 13% of visitors to exploited plants being thieves and 24% being robbers. Some key examples of visitors can be found in our video (Sakhalkar et al., 2022). While *Plectranthus decurrens* had the highest proportion of visits (over 90%) from robbers, *Crassocephalum montuosum* had the lowest (0.12%). Similarly, *Pararistolochia zenkeri* was visited only by nectar thieves, while only 0.03% of visits to *Psydrax dunlapii* were from thieves.

In our study, not all visiting functional groups exhibited exploitative behavior, and a majority of

TABLE 1 Overview of flower visitors on Mount Cameroon.

Taxonomic group	Functional group	Pollinators	Robbers	Thieves	Total
(a) Visitation frequency (no. visits)					
Coleoptera	Beetles	0.0234 (267)	...	0.0036 (33)	0.027 (300)
Chiroptera	Bats	0.0033 (39)	0.0033 (39)
Diptera	Flies	0.1251 (1308)	...	0.0073 (62)	0.1324 (1370)
	Hoverflies	0.3077 (2097)	0.0001 (1)	0.0077 (61)	0.3155 (2159)
Hymenoptera	Carpenter bees	0.0325 (155)	0.0325 (155)
	Honeybees	0.2398 (3397)	0.0071 (123)	0.0034 (58)	0.2503 (3578)
	Other bees	0.5461 (3402)	0.0565 (400)	0.0028 (43)	0.6054 (3845)
	Wasps	0.0711 (450)	0.0032 (24)	...	0.0743 (474)
Lepidoptera	Butterflies	0.0713 (595)	...	0.0011 (17)	0.0724 (612)
	Hawkmoths	0.0113 (6)	0.0113 (6)
	Moths	0.0731 (1408)	0.0004 (5)	0.0018 (30)	0.0753 (1443)
Passeriformes	Sunbirds	0.0357 (229)	0.0075 (58)	...	0.0432 (287)
Other mammals	Small mammals	0.0024 (12)	0.0014 (12)	...	0.0038 (24)
Total		1.543 (13464)	0.0761 (623)	0.0278 (304)	1.647 (14391)
(b) Visiting morphospecies					
Coleoptera	Beetles	38	0	7	70
Chiroptera	Bats	1	0	0	1
Diptera	Flies	29	2	9	31
	Hoverflies	66	0	16	88
Hymenoptera	Carpenter bees	0	0	2	2
	Honeybees	1	1	1	1
	Other bees	19	6	4	19
	Wasps	19	4	0	21
Lepidoptera	Butterflies	77	0	8	80
	Hawkmoths	26	0	0	26
	Moths	257	5	19	283
Passeriformes	Sunbirds	4	5	0	5
Other mammals	Small mammals	3	4	0	8
Total		540	27	66	635
(c) Visited plant species					
Coleoptera	Beetles	19	0	7	48
Chiroptera	Bats	1	0	0	1
Diptera	Flies	62	2	18	96
	Hoverflies	41	0	20	88
Hymenoptera	Carpenter bees	9	0	0	20
	Honeybees	27	3	1	47
	Other bees	73	15	2	100
	Wasps	12	4	0	30
Lepidoptera	Butterflies	22	0	3	59
	Hawkmoths	31	0	0	31
	Moths	39	3	6	80

(Continues)

TABLE 1 (Continued)

Taxonomic group	Functional group	Pollinators	Robbers	Thieves	Total
Passeriformes	Sunbirds	12	7	0	23
Other mammals	Small mammals	3	2	0	6
Total		180	29	39	195 ^a

Note: Visitation frequencies (i.e., number of visits per flower per minute), numbers of visits, numbers of visiting morphospecies, and numbers of visited plants are listed separately for pollinators, robbers, and thieves in each functional group of flower visitors.

^aTwelve were not visited by cheaters or pollinators.

TABLE 2 Visitation frequencies (i.e., number of visits per flower per minute) and numbers of visits (in parentheses) for pollinators, robbers, and thieves at each of the four elevations and two seasons sampled on Mount Cameroon.

Behavior type	Dry				Wet				Total
	650 m	1100 m	1450 m	2250 m	650 m	1100 m	1450 m	2250 m	
Pollinators	0.2477 (1936)	0.2029 (1755)	0.1650 (2405)	0.1160 (2540)	0.2913 (1935)	0.2340 (954)	0.2480 (1526)	0.0378 (413)	1.543 (13464)
Robbers	0.0008 (6)	0.0097 (173)	0.0057 (59)	0.0011 (6)	0.0128 (119)	0.0459 (259)	0.0001 (1)	0.0000 (0)	0.0761 (623)
Thieves	0.0040 (38)	0.0060 (100)	0.0062 (79)	0.0000 (0)	0.0006 (4)	0.0013 (4)	0.0080 (67)	0.0014 (12)	0.0278 (304)
Total	0.2525 (1980)	0.2186 (2028)	0.1769 (2543)	0.1171 (2546)	0.3048 (2058)	0.2813 (1217)	0.2562 (1594)	0.0393 (1425)	1.647 (14391)

morphospecies (540) were observed visiting flowers legitimately (a summary of all visiting groups is shown in Table 1, with additional details in Appendix S2: Table S1). Although nectar robbing (0.0761 visits flower⁻¹ min⁻¹) was four times more frequent than thieving (0.0278 visits flower⁻¹ min⁻¹), 66 morphospecies thieved flowers compared with 27 morphospecies that robbed. Interestingly, the two functional groups that were the most frequent pollinators, other bees and hoverflies, also emerged as the most frequent exploiters. All 19 recorded morphospecies of other bees served as pollinators of at least some of the visited plants, and 73 plant species in our study relied on them as on their main (i.e., the first or second most frequent) pollinator. Remarkably, despite their role as pollinators, other bees were the most frequent robbers. Hoverflies, on the other hand, were the second most frequent group of pollinators, nearly all morphospecies potentially pollinated flowers, and 62 plant species depended on them as on their main pollinators. Strikingly, hoverflies also exhibited the highest frequency of thieving behavior. Interestingly, despite being the richest in terms of morphospecies, moths served as the main pollinators for only 39 plant species. It is also important to highlight that although sunbirds and honeybees were equally frequent robbers, honeybees robbed only three of the 47 plant species they visited,

while sunbirds robbed seven of 23 visited plant species. After hoverflies, the most common thieves were flies, honeybees, and beetles. While 19 morphospecies of moths and 8 morphospecies of butterflies thieved flowers, they were the least frequent nectar thieves (Table 1).

Spatiotemporal variation in visitor behavior

The total visitation and pollination frequencies declined with increasing elevation and were lower in the dry season than in the wet season (Figure 1a, Table 2). However, this pattern differed for robbing and thieving. In the dry and wet seasons, robbing frequency increased from 650 to 1100 m asl and then declined to 2250 m asl. However, on average, robbing was 3.4 times more frequent in the wet season than in the dry season. On the other hand, the thieving frequency peaked at 1450 m in both seasons and, on average, was 1.5 times more frequent in the dry season (Figure 1a, Table 2). The χ^2 tests confirmed that these spatiotemporal differences were also statistically significant for the relative ratios of visitor behavior between seasons ($\chi^2 = 474.63$, $df = 3$, $p < 0.001$) and elevations ($\chi^2 = 2946.3$, $df = 9$, $p < 0.001$).

Association of visitor behavior, floral traits, and spatiotemporal variation

Overall, the RLQ analysis revealed no significant association between environmental variables (elevation and season) and visitor behavior frequency (PCA: $F_{4,3} = 4.365$, $p = 0.11$) and a significant association between environmental variables and floral traits (PCA: $F_{25,156} = 1.289$, $p = 0.01$). As summarized in Appendix S1: Table S3, the first RLQ axis explained 96.67% and 62.92% of the first-axis variation from the separate analyses of the variation in environmental variables and visitor behavior (Figure 2b) and in floral traits (Figure 2c), respectively. The two RLQ axes explained 81.22% (Figure 2a; Appendix S1: Table S3) of the joint structure, with the first axis capturing most of the variation. This showed that their joint structure was strongly associated with plant species composition across the sites.

The ordination diagrams (Figure 2) show that the first axis separated the communities according to the two seasons (Figure 2b). Nectar robbing was associated with the wet season and flowers that were zygomorphic, bell-shaped or tubular, orange or red, and with long tubes (Figure 2a). Nectar thieving was closely associated with trumpet-shaped, urceolate, and open flowers, increasing towards larger flowers with wider nectar tubes. Pollination was more frequent during the wet season (Figure 2b) and was closely associated with actinomorphic flowers that were salverform, stellate, or dish-shaped (Figure 2a). There was no apparent elevational pattern in the association of floral traits and visitor behavior.

Floral trait associations of floral cheaters

Robbers had clearer associations with plant species with specific pollinating groups than thieves (Figure 3a,c), although this pattern varied among the functional groups of cheaters. As nectar robbers, moths exploited plant species mainly pollinated by honeybees, other bees, butterflies, and sunbirds. However, moths were less selective while thieving, exploiting plants with main pollinators from all functional groups, except hawkmoths, wasps, bats, and small mammals. Hoverflies robbed plant species with flies, hoverflies, and sunbirds as their main pollinators, whereas they thieved plants that were mainly pollinated by flies, butterflies, moths, carpenter bees, honeybees, and small mammals. Unlike hoverflies and moths, other bees were more selective while thieving plants rather than while robbing them. Other bees were robbers of plants whose primary pollinators included all functional groups besides flies, small mammals, and

honeybees. However, other bees only thieved plants mainly pollinated by themselves, carpenter bees, and hoverflies.

Floral traits were significantly associated with the frequencies of nectar robbing and thieving by different functional groups of visitors (RDA for robbing: pseudo- $F = 3.22$, $p = 0.001$, 16.56% of explained variation; RDA for thieving: pseudo- $F = 2.30$, $p = 0.001$, 12.00% of explained variation; Appendix S1: Table S4). However, these associations were clearer for some groups of cheaters than for others. The functional groups of nectar robbers differed in their associations to flower shape, tube length, and tube width, with the relationship being clearer for other bees and sunbirds (Figure 3b). Sunbirds mainly robbed tubular flowers and flowers with wide and long nectar tubes. Other bees did not have a strong association to robbing flowers with larger nectar tubes, but they appeared to rob gullet-shaped and labiate flowers. Although nectar thieving groups had different associations with flower brightness, shape, and tube length (Appendix S1: Table S4, Figure 3d), these associations were strongest for flies and hoverflies. In general, flowers with longer tubes were not associated with thieving by any functional group, with floral shape influencing which functional group would thieve the flower. Flies thieved funnel-shaped and papilionate flowers, hoverflies thieved labiate flowers, and other bees thieved gullet and salverform flowers. Drabness separated flowers thieved by beetles from those thieved by other groups. The traits associated with thieving by butterflies and moths were not apparent in the ordination diagram (Figure 3d).

DISCUSSION

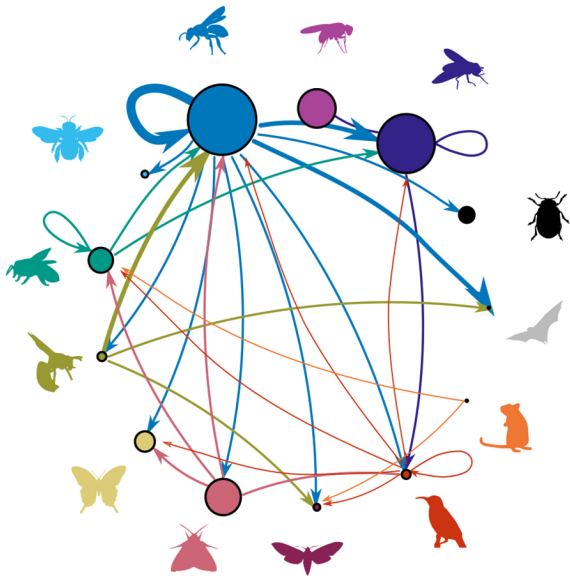
To our knowledge, this is the first quantification of spatiotemporal variation in nectar robbing and thieving at the level of a flower–visitor community. Although we found nectar robbing and thieving to be rare in the tropical communities on Mount Cameroon, their interaction frequencies fluctuated spatiotemporally in concert with the floral trait distribution in these communities. Our results suggested that floral traits in these communities may be influenced not only by their pollinators but also by their antagonists.

Rare cheaters in flower–visitor communities

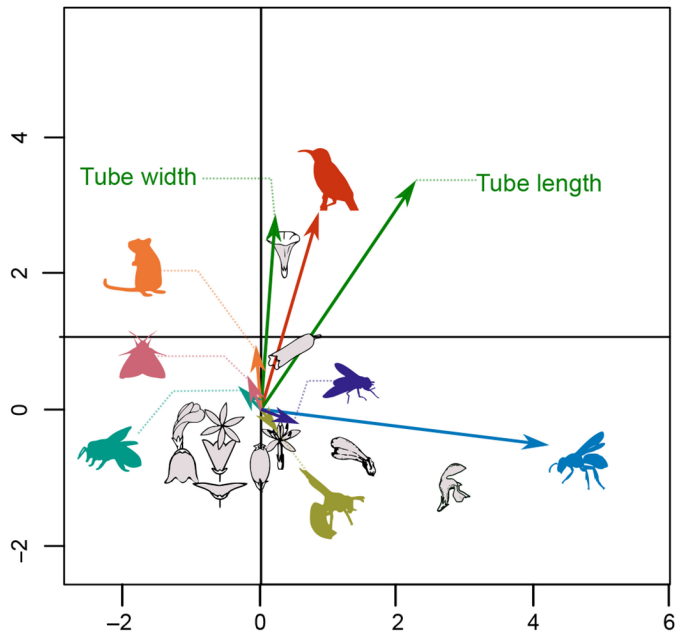
Theoretical models predicted that while cheaters evolve and persist in numerous plant–pollinator mutualistic interactions, they are typically found in low proportions

Nectar robbers

(a)

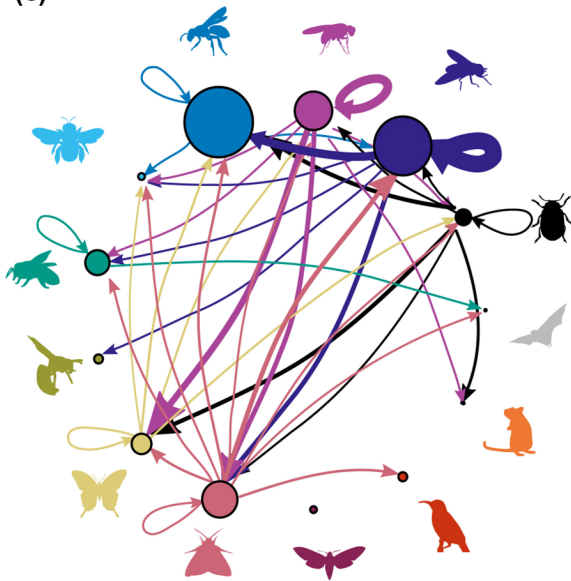


(b)

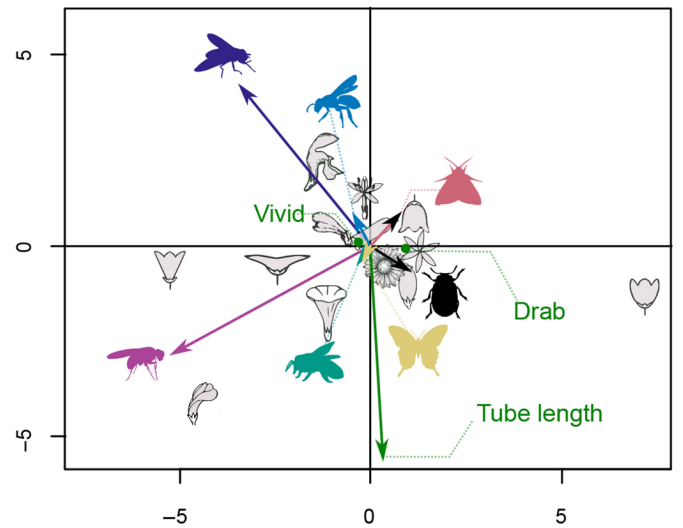


Nectar thieves

(c)



(d)



Flower shapes



Visitor groups



FIGURE 3 Legend on next page.

in communities (Jones et al., 2015). Although empirical quantifications of cheating in flower–visitor communities are rare, studies focusing on a single plant species (Castro et al., 2013; Cuevas & Rosas-Guerrero, 2016; Padyšáková et al., 2013) or on a subset of the plant community that was robbed (Rojas-Nossa et al., 2016) found that cheaters are common and may even outnumber pollinators. However, these studies included only species morphologically vulnerable to nectar robbing. Thus, the proportion of robbed species when considering the entire plant community is probably much smaller, as 14.79% in our study. Although we found that robbers and thieves were present in all studied communities, their frequency was consistently lower than of pollinators (Figure 1a). Our findings support the suggestion that cheaters are ubiquitous but rare. Thus, while floral antagonists might influence the evolution of plant–pollinator interactions (e.g., Irwin et al., 2010; Irwin & Maloof, 2002), their frequency may be too small to exert a significant selection pressure at the community level, and their influence should not be overestimated.

Cheating pollinators

Bees are among the most important pollinators in a majority of communities (Willmer, 2011), yet they were the most frequent nectar robbers in our study, especially on flowers with longer tubes (e.g., *Bertiera racemosa*) and labiate and gullet shapes (e.g., *Impatiens niamniemensis* and *Plectranthus kamerunensis*). Nevertheless, all six morphospecies of robbers in the functional group “other bees” also behaved as potential pollinators in our study, suggesting that for some plant species, bees can be antagonists (robbers) as well as mutualists (pollinators). We expected smaller bees (such as halictids) to thief open flowers successfully. However, such bees only robbed two plant species (*Brillantaisia owariensis* and *P. kamerunensis*) where they did not touch the reproductive organs adapted for larger bees (see our video in

Sakhalkar et al., 2022). Another notable mismatch due to the small size of bee visitors was observed with the large and trumpet-shaped flowers of *Kigelia africana*, commonly visited by relatively smaller honeybees without touching the long, filamentous anthers. Further, the nectar of gullet flowers of *Brillantaisia owariensis* was often thieved by small pollinators, such as blue-banded bees (*Amegilla* spp.) and skippers (Lepidoptera: Hesperinae), too small to touch the reproductive organs of this plant that is usually pollinated by large carpenter bees (*Xylocopa* spp.) (Figure 1b,c; see our video in Sakhalkar et al., 2022).

Sunbirds were the second most frequent robbers in our study, in concordance with other studies (Geerts & Pauw, 2009; Padyšáková et al., 2013). Although flowers can often be adapted to ornithophily, sunbirds are attracted to flowers with high amounts of nectar, regardless of other floral traits (Chmel et al., 2021). Thus, when their bills were too short to access nectar within long-spurred flowers, they often resorted to nectar robbing. Interestingly, sunbirds also robbed larger flowers with accessible nectar, such as *Kigelia africana*, *Costus dubius*, and *Anthocleista scandens* (Figure 1d,e; see our video in Sakhalkar et al., 2022), even though such flowers usually allow sunbirds to feed legitimately and with relatively short handling times (Temeles & Pan, 2002).

The most frequent nectar thieves in our study were hoverflies and flies, similar to numerous single-species studies (e.g., Bartoš et al., 2015; Klomberg et al., 2019). Our observation that the frequency of thieving by nonspecialized flies and hoverflies declined with nectar tube length was predictable (Branquart & Hemptinne, 2000), considering that they would be unable to feed on nectar with small proboscides (Doyle et al., 2020). Despite this, deeper flowers were still thieved by small-sized flies and hoverflies if their nectar tubes (e.g., *Aframomum* spp.) or spurs (*Impatiens* spp.) were wide enough (Zhang et al., 2014), or if they produced enough nectar to accumulate in the tube (Vlašánková

FIGURE 3 Floral preferences of nectar robbers and nectar thieves based on the main pollinators of the exploited plants (circular graphs), and trait associations for functional groups of robbers and thieves (ordination diagrams). (a, c) Robbers are more selective than thieves in their choice of exploited plant species. The circular graphs visualize how functional groups of cheaters differ in their choice of robbing (a) or thieving (c) plants with main pollinators from specific functional groups. All functional groups are visualized as silhouettes; each circle represents the number of plant species for which a particular functional group serves as the main pollinator. Arrows indicate the number of plant species that a functional group exploits, where the exploited plant species are primarily pollinated by another functional group; their thickness corresponds to the number of exploited plant species. (b, d) Ordination diagrams (redundancy analyses) visualizing the association between floral traits and the frequency of exploitation for different functional groups of robbers (b) and thieves (d). Arrows visualize the frequencies of robbing or thieving for each functional group (colored as the silhouettes) and continuous floral traits (in green). Dashed lines are used to label the arrows to improve readability. The centroids for flower shapes and the labels for functional groups are marked with symbols.

et al., 2017). Similarly, small beetles were also common nectar thieves of generalized open flowers (e.g., *Begonia* spp.), as reported by numerous other studies (Bartoš et al., 2015; Gómez, 2005; Sayers et al., 2019). We also observed small beetles thieving nectar of some closed flowers with large chambers (e.g., *Aframomum* spp.). None of the beetles in our study robbed flowers, although an older study reported nectar robbing by weevils (Clement, 1992). Surprisingly, we found that moths and butterflies were not frequent nectar exploiters (Mertens et al., 2021). Although lepidopterans can be efficient pollinators (de Araújo et al., 2014; Schemske, 1976), many lepidopterans have a long proboscis and can feed on diverse flowers, generalized or specialized, without pollinating them (Bauder et al., 2011). All flowers thieved by butterflies and moths in our study were either large and trumpet-shaped (e.g., *Pararistolochia zenkeri*) or had exposed reproductive organs that allowed bypassing pollination (e.g., *Clematis simensis*) resulting in a morphological mismatch (Irwin et al., 2010).

Spatiotemporal variation in cheating and floral traits

An inter-biome-scale study by Rojas-Nossa et al. (2016) found that the key determinants of nectar robbing among communities could be morphological adaptations of flowers for their specialized pollinators. On Mount Cameroon, morphologically generalized flowers prevail in the dry season and specialized flowers in the wet season (Janeček et al., 2022; Klomberg et al., 2022). Mirroring this, nectar robbing was more frequent in the wet season, whilst the opposite pattern was observed for thieving. We found nectar thieving to be more common in flowers with open and trumpet shapes, larger sizes, and wider tubes, which prevailed during the dry season (Figure 2b). Such flowers are prone to morphologically mismatched nectar thieves (Irwin et al., 2001). Flowers with longer nectar tubes and generally narrower corollas were prevalent in the wet season (Figure 2a), where their morphology could help avoid nectar dilution (Aizen, 2003) or specialize to their pollinators with higher energetic needs (Chmel et al., 2021), while making them more susceptible to robbing by small-tongued visitors unable to reach their nectar through the flower opening (Bronstein, 2001; Maruyama et al., 2015; Navarro & Medel, 2009). It is important to note that although our study examined floral traits that increased floral susceptibility to robbing, we did not measure some other floral traits defending against nectar robbing. These traits include petal thickness, calyx density, inflorescence structure, and corolla stickiness (McCarren et al., 2021; Rojas-Nossa et al., 2016).

Trade-off in floral traits

We found empirical support for the expected (Bronstein et al., 2017; Inouye, 1980) yet never studied trade-off in floral traits attracting nectar robbers and nectar thieves. Floral specialization, especially through concealing nectar in long and/or narrow tubes and spurs, helps reduce the number of thieves and ineffective pollinators (Lázaro et al., 2013), but such unexploited nectar can attract robbers (Irwin et al., 2010), and vice versa. In our study, morphologically specialized flowers were robbed by other bees, sunbirds, and honeybees, whereas generalized flowers were more susceptible to nectar thieving (see specific examples above), particularly for flowers with open and trumpet shapes, larger sizes, and broader tubes, similar to Irwin et al. (2001). Our observations emphasize the complications that prevent plants from following any simple strategy in the evolution of floral traits to avoid exploitation of floral rewards without efficient pollination.

CONCLUSIONS

We found that nectar thieving and robbing were generally uncommon in the Afrotropical forests we studied. Nevertheless, we observed spatiotemporal variation in visitor behavior, which can arise from the uneven distribution of floral traits in communities. The higher prevalence of closed flowers in the wet season was associated with robbing, whilst that of open flowers in the dry season was related to nectar thieves being more common. This lends support to the trade-off between floral traits that deter robbers and those that restrict thieves. Furthermore, we identified specific floral traits associated with the robbing and thieving behavior of particular functional groups of nectar exploiters. Altogether, we demonstrated that floral traits, commonly known to shape plant–pollinator interactions, also have a significant relationship with nectar robbers and thieves.

AUTHOR CONTRIBUTIONS

Sailee P. Sakhalkar and Robert Tropek conceived the idea. Robert Tropek and Štěpán Janeček designed the study. Štěpán Janeček, Robert Tropek, Yannick Klomberg, and Jan E. J. Mertens sampled the data. Yannick Klomberg, Jan E. J. Mertens, and Robert Tropek supervised processing of the video recordings. Jiří Hodeček identified the floral visitors. Sailee P. Sakhalkar, Yannick Klomberg, Jan E. J. Mertens, and Robert Tropek assessed the visitor behavior. Sailee P. Sakhalkar analyzed the data. Sailee P. Sakhalkar, Robert Tropek, and Štěpán Janeček interpreted the results and wrote the

manuscript draft. All authors commented the manuscript and approved its submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT


Data and code are available from Zenodo: <https://doi.org/10.5281/zenodo.8398202>.

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