ORIGINAL PAPER

Bumblebee floral neighbors promote nectar robbing in a hummingbird-pollinated plant species in Patagonia

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Abstract
Nectar robbers are common cheaters of plant-pollinator mutualisms by making holes in flower tissues to attain floral rewards often without providing pollination service. Most studies have focused on the consequences of nectar robbing on plant reproduction, whereas the underlying drivers of spatiotemporal variation in nectar robbing have been comparatively less explored. We assessed variation in nectar robbing of *Campsidium valdivianum*, an endemic hummingbird-pollinated climber species from the temperate forests of Southern South America, which currently is subjected to nectar robbing by the alien short-tongued *Bombus terrestris*, and determined if this variation is related to characteristics of the floral neighborhood. We located plants of *C. valdivianum* and estimated the proportion of flowers with holes. We recorded the presence, identity and distance to the nearest bumblebee-pollinated plants with open flowers. Results showed that the proportion of robbed flowers in *C. valdivianum* increased almost seven times in the presence of bumblebee flowering plants in the neighborhood. No evidence was found that the proportion of robbed flowers differs between neighborhoods with *Berberis darwinii* only vs. *B. darwinii* and *Cytisus scoparius*, the co-flowering plant species typically visited by bumblebees during the study. Finally, the proportion of robbed flowers increased not only with the presence but also with the proximity of these bumblebee-pollinated plants. Our results suggest that floral neighborhoods attractive to bumblebees can operate as magnets, potentially increasing the intensity of nectar robbing on nearby hummingbird-pollinated species. This study provides novel insights into understanding spatio-temporal variation in nectar robbing.

Keywords *Bombus terrestris* · *Campsidium valdivianum* · Floral larceny · Magnet effect · Mutualism cheaters · Temperate rainforest

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Introduction

Exploiters of plant–pollinator mutualisms are widespread in nature, being common among both plants and floral visitors (Bronstein 2001). On the animal side, some floral visitors behave as nectar-robbers, getting nectar rewards illegitimately by making holes in flowers' corollas (Inouye 1980). Nectar robbing is a taxonomically and geographically widespread phenomenon occurring in various communities containing nectariferous plants (Irwin and Maloof 2002; Irwin et al. 2010; Rojas-Nossa et al. 2016). The effect of nectar robbing on plants range from being highly negative (e.g., Irwin and Brody 1999; Fitch and Vandermeer 2021; Mackin et al. 2021; Chalcoff et al. 2022), neutral (e.g., Ye et al. 2017a; Varma and Sinu 2019; Rojas-Nossa et al. 2021) to positive (e.g., Maloof and Inouye 2000; Singh et al. 2014). However, two meta-analyses suggest that nectar robbing is, on average, detrimental to plant reproduction (Irwin et al.

2001; Burkle et al. 2007). The net outcome and the magnitude of the interaction along the antagonism-mutualism continuum depend on several factors such as the identity and behavior of the nectar-robbers, their life-history traits, and the reproductive biology of the plant (Maloof and Inouye 2000; Irwin et al. 2001, 2010; Burkle et al. 2007; Navarro and Medel 2009; Carrió and Güemes 2019; Varma and Sinu 2019; Varma et al. 2020; Rojas-Nossa et al. 2021).

Nectar robbing exhibits considerable spatio-temporal variation (Irwin and Maloof 2002; Rojas-Nossa 2013; Cuevas and Rosas-Guerrero 2016; Rojas-Nossa et al. 2016; Carrió and Güemes 2019; Varma et al. 2020; Fitch and Vandermeer 2020, 2021). Yet, the vast majority of studies have attributed this variation to intrinsic factors associated with the plant and animal species involved, either to floral traits (floral morphology and nectar quality and quantity), flower visitors' traits (proboscis length and body size), or both. For instance, numerous studies have shown that long, tubular, narrow flowers usually exhibit high nectar robbing levels (Lara and Ornelas 2001; Urcelay et al. 2006; Navarro and Medel 2009; Rojas-Nossa 2013; Maruyama et al. 2015; Eliyahu et al. 2015; Rojas-Nossa et al. 2016, 2021; Valdivia et al. 2016). In addition, the incidence of nectar robbing has been related to nectar quantity and quality (Rojas-Nossa et al. 2016). However, a subject that requires further study is the evaluation of extrinsic factors, particularly the community context that may also underlie spatio-temporal variation in nectar robbing among and within populations (Cuevas and Rosas-Guerrero 2016; Fitch and Vandermeer 2021). In turn, this community context can affect the relative abundance and visitation frequency of nectar robbers vs. legitimate pollinators that may greatly influence the effect of nectar robbing on plant fitness across populations (Rosenberger 2018; Chalcoff et al. 2022).

A largely overlooked ecological community dimension potentially affecting nectar robbing is the characteristics of the floral neighborhood (Cuevas and Rosas-Guerrero 2016; Martínez-Pérez and Faife-Cabrera 2019; Fitch and Vandermeer 2021). Despite possible dilution effects, i.e. when per flower visitation decreases with increasing floral densities (Wenninger et al. 2016), pollinators generally act as optimal foragers and select patches with high floral densities (Hegland and Boeke 2006; Fowler et al. 2016). Ultimately, dense floral patches and diverse floral neighborhoods are more likely to attract more pollinators that eventually may benefit the entire plant community (Ghazoul 2006; Hansen et al. 2007; Lázaro et al. 2009). However, these patches can also attract more antagonistic partners, such as herbivores (Kim 2017) and nectar robbers (Cuevas and Rosas-Guerrero 2016; Martínez-Pérez and Faife-Cabrera 2019; Fitch and Vandermeer 2021). Interestingly, floral visitors may shift their foraging strategy and their ecological role from mutualism to antagonism depending on

flower characteristics (Ye et al. 2017b) and the ecological context, for instance, the presence and abundance of other flower visitors (Rosenberg 2018). Regarding flower characteristics, Pyke (1982) reported that the short-tongued bumblebee *Bombus occidentalis* shifted from pollination to nectar robbing when foraging on flowers with long corolla tubes (Pyke et al. 2012). Accordingly, floral visitors may behave as legitimate pollinators of some plant species and, simultaneously, act as nectar robbers of other nearby plant species in the floral neighborhood. In fact, the ecological context can determine the extent of nectar robbing of plant species that are prompted to be robbed. This would be the case when certain flowering species occurring in the neighborhood act as flower visitor magnets and promote nectar robbing of target plant species.

The short-tongued bumblebee *Bombus terrestris* has invaded Southern South America and nowadays interacts with the plant communities of the Andean Patagonian region (Morales et al. 2013). These plant communities are typically composed of a mixture of species that produce flowers that can be legitimately pollinated by the invasive *B. terrestris*, and species with long or tubular shaped flowers whose nectar *B. terrestris* can access only by robbing (Morales et al. 2013). Indeed, *B. terrestris* has been reported robbing nectar from several plant species in its native range in Eurasia (Dafni and Shmida 1996; Navarro and Guitián 2000) as well in its invaded range in Japan (Kenta et al. 2007; Dohzono et al. 2008), Australia (Hingston and McQuillan 1998a), Tasmania (Hingston and McQuillan 1998b, 1999), and Southern South America (Ruz and Herrera 2001; Valdivia et al. 2016; Sáez et al. 2017; Rosenberger 2018; Chalcoff et al. 2022).

An ideal model system is *Campsidium valdivianum* (Bignoniaceae) (Fig. 1A), an endemic hummingbird-pollinated climber species from the temperate rainforests of Patagonia (Fig. 1B) that produces long tubular flowers and exhibits high levels of nectar robbing by bumblebees (Urcelay et al. 2006) (Fig. 1C, D). A previous study in *C. valdivianum* showed that the proportion of robbed flowers per plant and the number of holes per flower made by the native long-tongued bumblebee *Bombus dahlbomii* (Apidae) were positively related to corolla length (Urcelay et al. 2006). At present, the native bumblebee has been largely replaced by the invasive short-tonged *B. terrestris*, which has become the most abundant and widespread *Bombus* species in the temperate forests of Southern South America (Morales et al. 2013). Following up the study by Urcelay et al. (2006), here we explored spatial variation in nectar robbing of *C. valdivianum* by *B. terrestris* and determined if this variation is related to the surrounding floral neighborhood. We hypothesized that those floral neighborhoods that are attractive to bumblebees foster and augment nectar robbing in nearby hummingbird-pollinated flowers. Accordingly, we expected an increase in the proportion of robbed flowers in
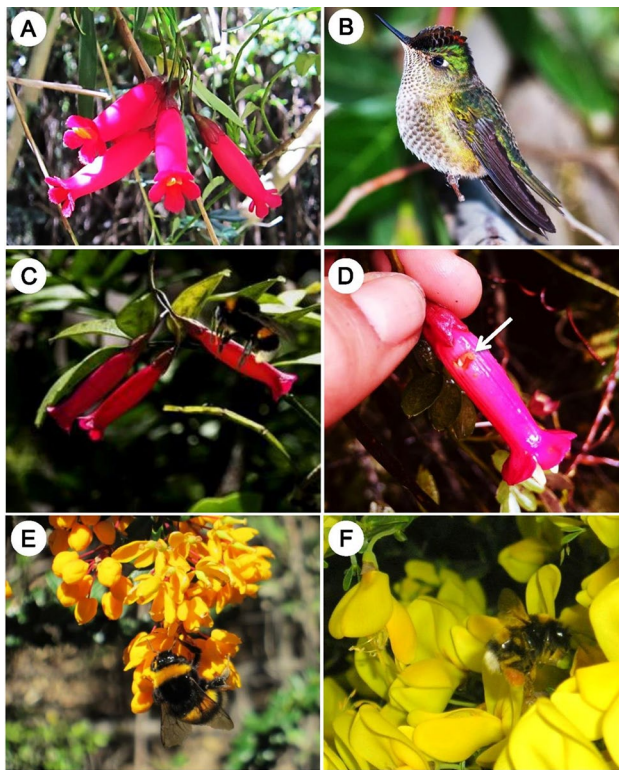
Fig. 1 The study system, including **A** the flowering plant *Campsidium valdivianum*, **B** the legitimate hummingbird pollinator *Sephanoides sephaniodes* (photo credit: Facundo Vital, used with permission), **C** the alien short-tongued and current nectar robber *Bombus terrestris*, **D** a robbed flower (the arrow points the hole made by a bumblebee), **E** the native shrub *Berberis darwinii,* and **F** the alien scotch broom *Cytisus scoparius* being visited by *Bombus terrestris*

C. valdivianum with the presence and increasing proximity of co-flowering bumblebee-pollinated neighbors.

Materials and methods

Study site and species

The study was carried out in Puerto Blest (41°02′S, 71°49′W, 760–850 m a.s.l.), Nahuel Huapi National Park (Patagonia, Argentina), one of the easternmost relics of Valdivian rain forest. This site is characterized by a mean annual precipitation of ~3000 mm (Barros et al. 1983). The vegetation comprises high, open, evergreen multilayered forest being dominant tree species *Nothofagus dombeyi* (Nothofagaceae), including also *Fitzroya cupressoides* (Cupressaceae), *Weinmannia trichosperma* (Cunoniaceae), and *Drimys winteri* (Winteraceae), among others (Calvelo et al. 2006). Among the over half a dozen ornithophilous species occurring in this area, *Campsidium valdivianum* (Bignoniaceae) blooms the earliest in the austral spring, and

its flowering phenology spans approximately from early September to December (Fraga et al. 1997; Aizen and Rovere 2010; Chalcoff et al. 2014). *Campsidium valdivianum* is a climbing liana, observed hanging from branches of different tree species. It has hermaphrodite flowers characterized by long, pink, tubular corollas (Fig. 1A) pollinated by *Sephanoides sephaniodes* (Trochilidae) (Riveros 1991; Fraga et al. 1997), the only hummingbird that inhabits the temperate forests of southern Argentina and Chile (Fig. 1B). The native bumblebee *B. dahlbomii* has been previously observed visiting *C. valdivianum* flowers and behaves as both pollinator and nectar robber (Riveros et al. 1991; Urcelay et al. 2006). However, *B. dahlbomii* declined abruptly across the region in the last decade after the invasion of introduced European bumblebees (Morales et al. 2013); consequently, the short-tongued *B. terrestris* is now the most common bumblebee in the region (Aizen et al. 2019). Unlike *B. dahlbomii, B terrestris* acts exclusively as a nectar robber in *C. valdivianum* (Fig. 1C, D).

During the study, the main co-flowering species in moderately disturbed areas included the native shrub *Berberis darwinii* (Berberidaceae) (Fig. 1E) and the alien scotch broom *Cytisus scoparius* (Fabaceae) (Fig. 1F). Both species are mainly pollinated by bumblebees (Morales and Aizen 2002, 2006; Cavallero et al. 2018) and visited by *B. terrestris* (Gavini and Farji-Brener 2015). Field observations show that *C. scoparius* is invading the forest area, yet bushes are still not very large (< 1 m tall) and mostly restricted to trail edges and other human disturbed habitats.

Sampling design

In November of 2019, we sampled 64 plants of *C. valdivianum* along a 1.5 km, ca. 5 m wide trail from Puerto Blest to Puerto Frias and determined for each plant the incidence of nectar robbing. Specifically, in each plant we estimated the proportion of robbed flowers per plant (i.e., number of robbed flowers/total number of flowers). We considered the presence of, at least, one hole in the corolla as evidence of nectar robbing. Because of the prolonged flowering phenology of this plant species, we inspected corollas of both all fresh and senescent flowers still attached to the plant and also of all corollas shed on the ground from flowers that opened earlier in the season to cover a period of nectar robbing as long as possible. We characterized a focal plant's floral neighborhood within a 10×5 m plot, with its major axis parallel to the trail. Plants of *C. valdivianum* were always located at the edges of the trail, and each focal plant was centered along one of the two 10-m sides of the plot. Thus, the sampling area of each plot extended 5 m at both sides of the target plant along the trail edge and 5 m inside the forest. Beyond that distance from the trail edge the chance

of finding a plant in flower in the understory was almost nil because of the shady conditions. Within the plot, we recorded the presence, identity, the number of species of all bumblebee-pollinated plants in flower, plant density (i.e., number of plants of each bumblebee-plant species) and proximity, measured as the distance between the focal *C. valdivianum* plant under observation and the closest flowering bumblebee plant.

Data analysis

All analyses were performed in the R environment v3.4.4 (R Development Core Team, 2018). We used a generalized linear mixed effect model, with binomial error distribution, using the function "*glmer*" from the package "lme4" (Bates et al. 2015), to assess the effects of floral neighborhood on the proportion of robbed flowers per plant. In general, we found one plant only, a *B. darwinii* plant, or two neighboring plants, one *B. darwinii* and one *C. scoparius*, within a plot. Hence, we did not observe appreciable variation in plant density independent of species composition in order to consider this variable any further. Therefore, in a first analysis we tested the effect of the bumblebee-pollinated neighborhood on the proportion of robbed flowers by considering floral neighborhood as a binary variable (presence/absence of at least one bumblebee-pollinated plant). In this analysis, we also evaluated the effect of the floral display of the target plant, by considering the total number of *C. valdivianum* flowers we sampled in each plant as a covariate. Some of the sampled *C. valdivianum* plants were nearby and had overlapping neighborhoods, thus we assigned them to the same plot, reason why we considered "plot" as a random effect to control for spatially nested data. Using a similar model structure as before, we also analyzed the effect of floral neighborhood composition on nectar robbing, with composition coded as "absence of bumblebee-pollinated plants", "presence of *B. darwinii* only", or "presence of both *B. darwinii* and *C. scoparius*". There were no cases of neighborhoods composed solely by *C. scoparius*, probably because *C. valdivianum* does not occur in highly disturbed areas dominated by *C. scoparius*. Post-hoc tests (Tukey HSD) were used for comparisons across floral neighborhood composition levels. Finally, we analyzed the proportion of robbed flowers using the distance to the closest flowering bumblebee plant as a fixed effect, restricting this analysis to data where there was at least one flowering bumblebee plant in the neighborhood ($N = 24$). We also performed a Mantel test to check for potential spatial autocorrelation in the data, using the function "*mantel.rtest*" from the package "ade4" (Dray and Dufour 2007) in the R environment.

Results and discussion

In total, we observed 708 flowers from 64 *C. valdivianum* plants. On average, we inspected 11.0 ± 0.9 flowers per plant (range from 2 to 32). Overall, mean proportion ($\pm$ SE) of robbed flowers per plant was $15.2 \pm 2.6\%$, moreover 34 (53%) plants had at least one robbed flower. The proportion of robbed flowers increased almost seven times, from 5.2 to 34%, in the presence of flowering bumblebee plants in the neighborhood ($\chi^2 = 64.47$, df = 1, $P < 0.0001$, Fig. 2A). There was no evidence that the total number of flowers per focal plant, i.e., the floral display size, affect the probability of a flower being robbed ($\chi^2 = 0.023$, df = 1, $P = 0.879$, Fig. 2B). In addition, floral neighborhood composition had a significant effect on the proportion of robbed flowers ($\chi^2 = 75.67$, df = 2, $P < 0.0001$, Fig. 2C). However, there was no evidence that the proportion of robbed flowers differs between neighborhoods composed by *B. darwinii* only and by *B. darwinii* and *C. scoparius* (mean = 29 vs. 37%; z-ratio = -1.27, $P = 0.413$; Tukey's HSD post-hoc test). Finally, the proportion of robbed flowers increased with the proximity to the nearest bumblebee flowering plants occurring in the neighborhood ($\chi^2 = 10.6$, df = 1, $P = 0.001$, Fig. 2D). This trend persisted even when data were analyzed separately; neighborhoods with *B. darwinii* only ($\chi^2 = 5.1$, df = 1, $P = 0.02$) and with both *B. darwinii* and *C. scoparius* ($\chi^2 = 4.5$, df = 1, $P = 0.03$). There was no evidence of spatial autocorrelation in our data (Mantel statistic, $r = 0.015$, $P = 0.35$), indicating that proximity between focal plants by itself does not necessarily translate into similarity in the proportion of robbed flowers. Therefore, results support our hypothesis that the presence of flowering bumblebee-pollinated plants in the neighborhood increases nectar robbing in a hummingbird-pollinated plant species.

Most studies on nectar robbing have assessed the consequences on plant reproductive success rather than its drivers or causes (Maloof and Inouye 2000; Irwin et al. 2010, but see Fitch and Vandermeer 2020, 2021). Our findings provide evidence of some likely drivers of spatial variation in nectar robbing in hummingbird-pollinated plant species. Our results suggest that floral neighborhoods can operate as pollinator magnets (Molina-Montenegro et al. 2008), for instance increasing the arrival and activity of bumblebees (e.g., Liao et al. 2011; Yang et al. 2013), which in the context of our study system are known to act as antagonistic partners of *C. valdivianum*. Ultimately, bumblebee-pollinated flowering neighbors can potentially increase robbing levels of nearby plant species. Taken together with the results from Urcelay et al. (2006), our study suggests that both intrinsic (i.e., corolla length) and extrinsic (i.e., floral neighborhood) factors contribute to determine spatial

Fig. 2 Patterns of nectar robbery in *Campsidium valdivianum*: proportion of robbed flowers as a function of **A** the presence of a bumblebee floral neighborhood, **B** the total number of flowers in the plant (i.e., floral display of the focal plant), **C** composition of the floral neighborhood, and **D** distance (cm) to the nearest flowering bumblebee plant. Model predicted values (solid line) with 95% confidence intervals (shaded area) are shown. Different letters indicate significant differences ($P < 0.05$) according to a Tukey's HSD post-hoc test
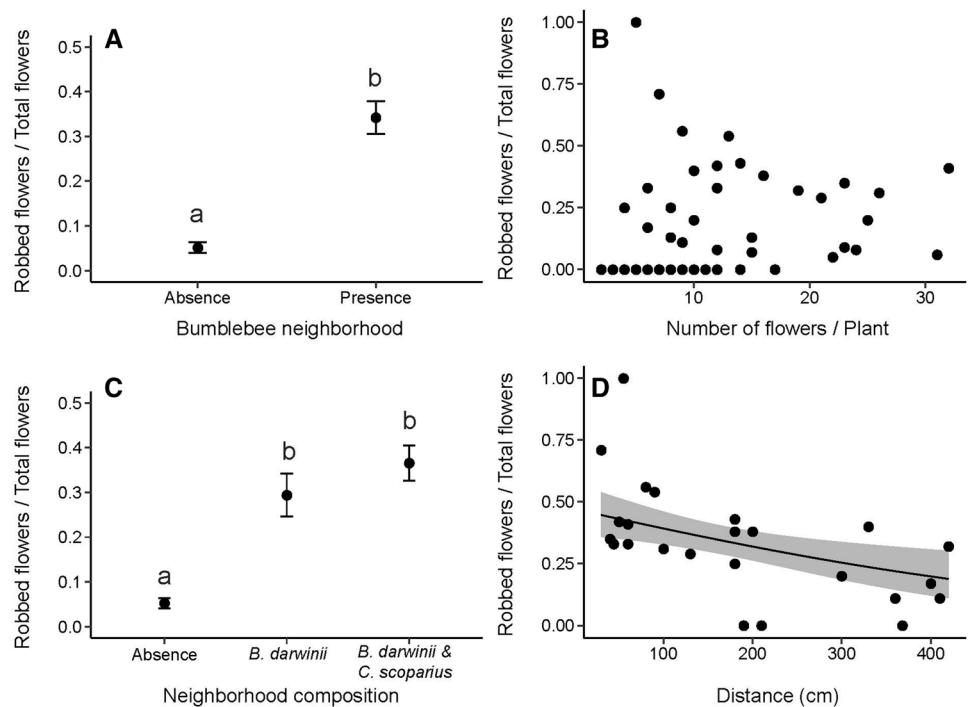
variation in nectar robbing in *C. valdivianum*. Likewise, a study conducted in Cuba reported a positive association between the frequency of nectar robbery in *Guettarda clarensis* (Rubiaceae), by the bee *Xylocopa cubaecola*, with the increasing floral display of neighboring species (Martínez-Pérez and Faife-Cabrera 2019). Furthermore, these authors also found that not all flowering neighbor species contribute to an increase in the robbing levels in *G. clarensis* (Martínez-Pérez and Faife-Cabrera 2019), which resembles the apparent lack of an effect of *C. scoparius* presence here. Similar nectar robbing levels in neighborhoods of only *B. darwinii* with those with both *B. darwinii* and *C. scoparius* may be attributed to some redundancy between these two species (Walker 1992). Nonetheless, the strictly high pollen-rewarding strategy of *C. scoparius* compared with the mixed pollen and nectar rewarding of *B. darwinii* does not suit with the redundancy hypothesis. However, the lack of floral neighborhoods composed solely of *C. scoparius* hinders testing this idea.

An interesting finding was the considerably overall low magnitude of flower robbery, either in terms of the proportion of plants with damaged flowers in the population (53%) or the proportion of robbed flowers per plant (15%) compared to the previous study (Urcelay et al. 2006) that showed that the majority of plants (95%) suffered from some level of nectar robbing, with a mean proportion of robbed flowers per plant of 41%. In their study, however, only senescent flowers (i.e., those shed on the ground) were analyzed, whereas here the flowers still attached on their plants were also inspected. If robbery makes flowers more likely to be

shed promptly, a sampling based exclusively on senescent flowers may lead to higher nectar robbery values than those seen in this study. In addition, flowers still attached to the plant could have been exposed to nectar robbers for a shorter time, while senescent flowers reflect the accumulation of nectar robbing events along their life span. Alternatively, differences in nectar robbery between these two studies could be due to differences in bumblebee abundance, even though *B. terrestris* is much more abundant than *B. dahlbomii* used to be (Morales et al. 2013).

There is another intriguing possibility, that differences between our and Urcelay et al.'s study (2006) are related to a new ecological context, in which *B. terrestris* is now the main nectar robber. Although *B. terrestris* is an important nectar robber of other hummingbird plant species in the study area like *Fuchsia magellanica* (Rosenberg 2018), being a smaller species it may not be as efficient at piercing the thick corollas of *C. valdivianum* as *B. dahlbomii*, one of the largest bumblebees in the world. Differences in body size could explain the lower primary nectar robbing levels we recorded (see also Newman and Thomson 2005). Despite being a poor primary robber of *C. valdivianum*, *B. terrestris* could be engaged into active secondary robbing (i.e., collecting nectar from existing holes; Stout et al. 2000), which was not assessed in this study. Nevertheless, it has been observed that ca. 97% of the visits to the flowers of *Vicia nigricans* (Fabaceae) by *B. terrestris* result in secondary robbing (Chalcoff et al. 2022). Similarly, when *B. terrestris* become moderately frequent visitors of *Fuchsia magellanica* (Onagraceae), they end up collecting

nectar almost exclusively by secondary robbing (Rosenberger 2018). These findings indicate that secondary robbing by this bumblebee species is highly frequent in the region. In the study plant, the number of holes we found among flowers with evidence of robbery ($N = 127$) ranged between one to four. However, the mean number of holes was 1.35 ± 0.06 ($\pm$ SE) with 77.2% of the flowers presenting one hole in the corolla, 11.8% two, 10.2% three, 0.8% four holes. Certainly, this result suggests little primary robbery at the flower level.

In conclusion, we found that the incidence and magnitude of nectar robbing in *C. valdivianum* flowers is strongly context-dependent. Considering that nectar robbing can have diverse effects on plant fitness (Maloof and Inouye 2000; Irwin et al. 2001, 2010; Eliyahu et al. 2015; Varma and Sinu 2019; Varma et al. 2020; Rojas-Nossa et al. 2021), more studies are needed to determine the net outcome of nectar robbing in *C. valdivianum*. Specifically, further studies on this system could examine whether nectar-robbing affects plant reproductive output, and if so, whether direct or indirect pathways come into play, for instance, through changes in hummingbird behavior triggered by nectar robbing. Regardless of the ultimate outcome, this study provides evidence that interspecific floral neighborhoods have the potential of promoting nectar robbing.

Author contributions Study conception and field data collection was performed by SSG, EM and FZM, with considerable feedback from MAA and CLM. Data analysis was performed by SSG. The first draft of the manuscript was written by SSG and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest All authors declare that they have no conflicts of interest.

Ethical approval This article does not contain any studies with human or animal performed by any of the authors.

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