

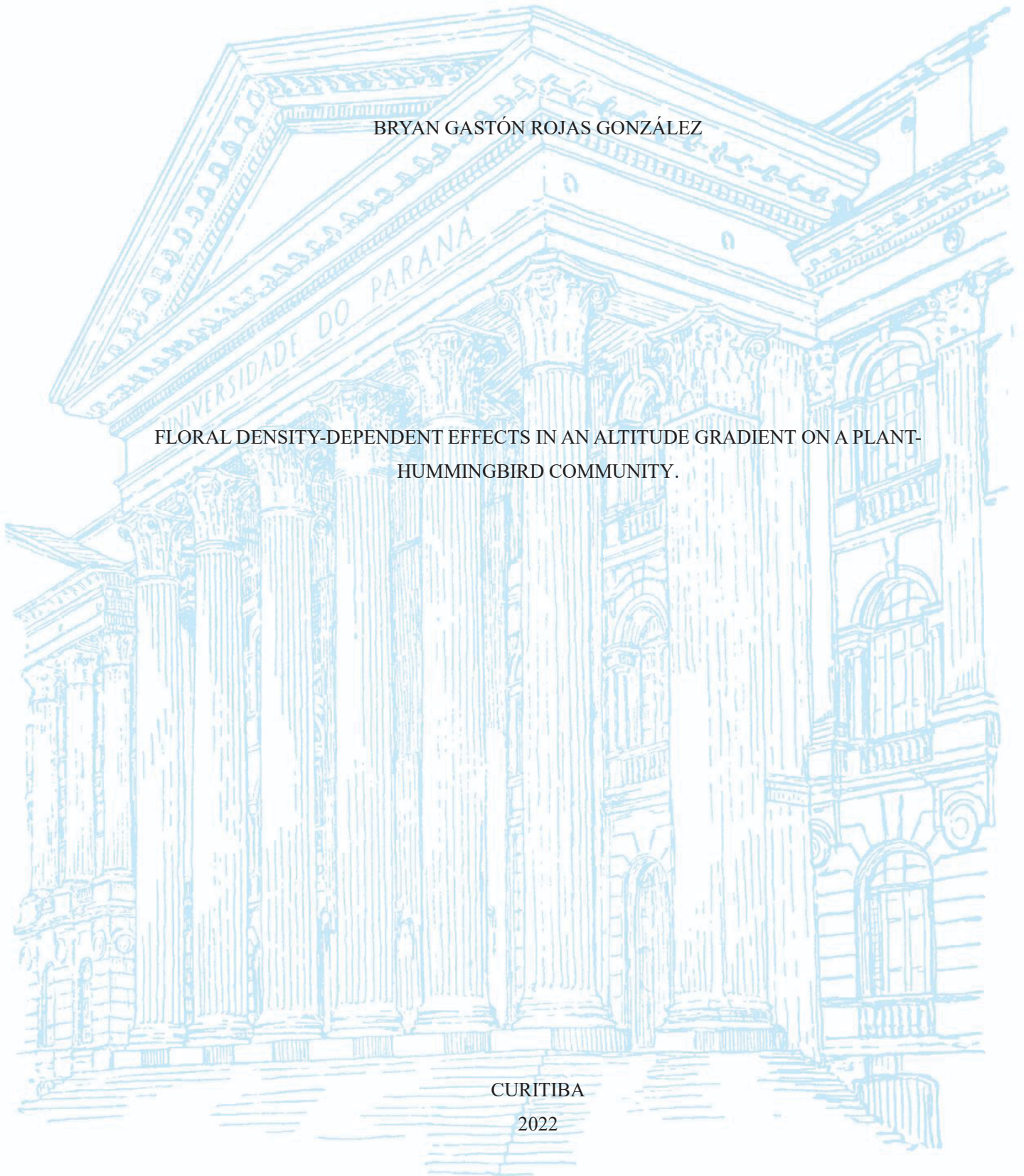
UNIVERSIDADE FEDERAL DO PARANÁ

BRYAN GASTÓN ROJAS GONZÁLEZ

FLORAL DENSITY-DEPENDENT EFFECTS IN AN ALTITUDE GRADIENT ON A PLANT-  
HUMMINGBIRD COMMUNITY.

CURITIBA

2022



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FLORAL DENSITY-DEPENDENT EFFECTS IN AN ALTITUDE GRADIENT ON A PLANT-  
HUMMINGBIRD COMMUNITY.

Dissertação apresentada ao Curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, da Universidade Federal do Paraná, como requisito parcial à obtenção do título de Mestre em Ecologia e Conservação.

Orientadora: Profa. Dra. Isabela Galarda Varassin

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“ Toda a poesia reflete o que a alma não tem.  
Por isso, a canção dos povos tristes é alegre e a canção dos povos alegres é triste”  
(Fernando Pessoa)

## RESUMO

A polinização é um serviço ecossistêmico fundamental de grande importância para a reprodução das plantas, produção agrícola e manutenção da biodiversidade. A denso-dependência negativa (*i.e.*, desvantagem no fitness quando uma espécie se torna abundante) e facilitação assimétrica (*i.e.*, vantagem no fitness por meio da facilitação de espécies raras em relação às comuns) são processos que promoveram a coexistência planta-polinizador em sistemas biodiversos. No entanto, eles são influenciados pela escala espacial, partição de nicho e gradientes ambientais. Devido às condições ambientais, em contraste com outros polinizadores, os beija-flores têm uma maior contribuição para a polinização de comunidades vegetais de altitude. Com isso, o estudo do sistema planta-beija-flor pode melhorar a compreensão dos diferentes cenários ecológicos onde a coexistência de plantas possa ser mantida por processos de denso-dependência negativa e facilitação assimétrica. Neste estudo, objetivamos compreender a relação entre os efeitos dependentes da densidade floral e as taxas de visitação de beija-flores em diferentes escalas e em um gradiente de elevação. Descobrimos que as taxas de visitação de beija-flores foram maiores quando plantas raras coocorreram com heteroespecíficos, mas menores quando plantas abundantes coocorreram com heteroespecíficos, em escala regional. Em contraste, em escala local, as taxas de visitação de beija-flores foram maiores quando as espécies de plantas eram localmente abundantes e cercadas por poucos heteroespecíficos. Ao longo de um gradiente de elevação, processos denso-dependentes ocorreram apenas em comunidades de média e alta altitude, sugerindo que comunidades com baixa disponibilidade de flores e altas interações especializadas podem ser mais propensas a apresentar efeitos denso dependentes florais. Além disso, a presença de um beija-flor (*R. naevius*) que atua como “organizador da comunidade” na elevação baixa poderia ter contribuído com esse padrão. Nosso estudo destaca a importante relação entre elevação e partição de nicho com efeitos denso dependentes em sistemas planta-beija-flor e seus mecanismos potenciais para contribuir para a coexistência.

Palavras-chave: Polinização planta-beija-flor. Partição de nicho. Gradiente de elevação. Especialização. Efeitos denso-dependentes.

## ABSTRACT

Pollination is a key ecosystem function, which is of great importance for plant reproduction, crop production and biodiversity maintenance. Negative density dependence (i.e. fitness disadvantage when a species become abundant) and asymmetric facilitation (i.e. fitness advantage of facilitation to rare species in relation to common ones) are both processes that have shown to foster plant-pollinator coexistence in biodiverse systems. However, they are influenced by spatial scale, niche partitioning and environmental gradients. Due to environmental conditions, in contrast with other pollinators, hummingbirds have a higher contribution to the pollination of high elevation plant communities, thus, plant-hummingbird system is a good object of study to give us a better understanding of under which different ecological scenarios one can expect plant coexistence to be maintained by negative density-dependence and asymmetric facilitation processes. In this study, we aimed to understand the relationship between floral density-dependent effects and hummingbird visitation rates on different scales and in an elevational gradient. We found that hummingbird visitation rates were higher when rare plants co-occurred with heterospecifics, while lower when abundant plants co-occurred with heterospecifics, at a regional scale. In contrast, at local scale hummingbird visitation rates were higher when plant species were locally abundant and were surrounded by few heterospecific neighbors. Across an elevation gradient, such density-dependent processes occurred only at mid- and high-elevation communities, suggesting that communities with low flower availability and high specialized interactions might be more prone to show flower dense-dependent effects. Besides, the presence of a hummingbird (*R. naevius*) acting as a “community organizer” in the low elevation community might have contributed to this pattern. Our study highlights the important relationship between elevation and niche partitioning with dense-dependent effects on plant-hummingbird systems and its potential mechanisms to contribute to coexistence.

Keywords: Plant-hummingbird pollination. Niche partitioning. Elevational gradient. Specialization. Dense-dependent effects.

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## INTRODUCTION

The relevance that pollination have for plant maintenance has lately raised interest about its role on plant coexistence. Pollination is a key ecosystem function, which is of great importance for plant reproduction, crop production and biodiversity maintenance, as approximately 80% of plant species worldwide are dependent on animal pollination (Rodger et al., 2021; Ollerton et al., 2011). Negative density dependence (i.e. fitness disadvantage when a species become abundant) and asymmetric facilitation (i.e. fitness advantage of facilitation to rare species in relation to common ones) are both processes that have shown to foster plant-pollinator coexistence in biodiverse systems (Bergamo et al., 2020; Wei et al., 2021). Nevertheless, density-dependent processes are influenced by spatial scale; with foraging behavior and plant spatial distribution influencing in the local scale, whereas, overall available flower resources being more important at regional scales (Goulson, 2000; Nottebrock et al., 2013). Since environmental gradients entail changes in species composition, spatial distribution and interactions, such gradients are important to understand plant-pollinator community processes and its maintenance (Ghazoul, 2005; Nottebrock et al., 2017; Totland, 2001). Thus, the study of environmental gradients is key to give us a better understanding of under which different ecological scenarios one can expect plant coexistence to be maintained by negative density-dependence and asymmetric facilitation processes. In this study, we aimed to understand the relationship between floral density-dependent effects and hummingbird visitation rates on different scales and in an elevational gradient.

Facilitation and competition for pollination, as well as and their interplay, are the interactions forces thought to govern main ecological processes in plant-pollinator communities. Recent studies shows that plant coexistence, in rich plant-pollinator systems, can be promoted by asymmetric facilitation, and intraspecific competition when in high flower abundance, processes that are strongly influenced by pollination niche partitioning (Bergamo et al., 2020; Wei et al., 2021). On one hand, due to high intraspecific competition, negative dense-dependent effects can allow coexistence conferring fitness advantages to rare species and disadvantages to common ones (Chesson, 2000; Levine & HilleRisLambers, 2009). Pollinator attraction by high flower abundance can also lead to a positive density effect, conferring an advantage to common plants potentially destabilizing coexistence (Nottebrock et al., 2017; Sánchez-Castro et al., 2021). On the other hand, facilitative interactions, which are more predominant in high elevation and adverse environmental conditions, can also favor rare plant species when the advantage of heterospecific presence benefit more rare species than common ones (Tur et al., 2016; Wei et al., 2021).

It has been shown that spatial context is an important factor affecting pollinator abundance, richness and behavior (Steffan-Dewenter et al., 2002). In fact, pollinator foraging behavior has been suggested to partly explain shifts in pollinator visitation between spatial scales, where high pollinator visits on small spatial scales are diluted on larger scales (Goulson, 2000). For instance, bumblebee visitation rates on *Trifolium pratense* increased with flower conspecific and heterospecific density (facilitation) in small spatial scales, while at coarser scales, visitation rates decreased as flower abundance increased (competition) (Hegland, 2014). Thus, competition and facilitation are also dense-dependent processes, and may show

different and even contrary trends depending on spatial scale. Even though such dense-dependent effects have shown to be positive in small scale and negative in regional ones allowing coexistence (Bergamo et al., 2020a), more studies are necessary to reveal a more consistent pattern of spatial scale changes of plant-pollinators dense-dependence effects and how they behave in other important pollinator groups.

Plant-hummingbird interactions vary in composition and structure along environmental gradients and resource availability (Sonne et al., 2020; Weinstein & Graham, 2017). Several studies have shown that groups of pollinators vary on pollination efficiency among elevation, because high precipitation, windy conditions and lower temperatures in high elevations physiologically limit insect groups, while remaining hummingbirds are able to provide efficient pollination services (Conrad et al., 2021; Cruden, 1972; González et al., 2009; Stiles, 1978). Moreover, changes on the number and composition of coexisting pollinators (Brosi & Briggs, 2013) as well as changes on resource availability, can affect pollinator' niche overlap (Pimm et al., 1985; Tinoco et al., 2016). Consequently, changes in pollinator niche may affect hole network interaction partitioning, for this, network level specialization ( $H_2'$ ) has shown to be a valuable tool to assess partitioning of interactions and differences across distinct pollination interaction webs (Blüthgen, et al., 2006; Sonne et al., 2020). Since species richness, composition and interactions, as well as abiotic conditions change with elevation, we can also expect changes on the underlying mechanisms structuring these communities (McCain & Grytnes, 2010; Patsiou et al., 2021). In fact, elevation gradients have been pointed out as important models to understand the assembly of plant-hummingbird communities and pollination niche partitioning (Maglianesi et al., 2015; Ramos-Jiliberto et al., 2010). Pollination niche partitioning is an important mechanism for plant diversity maintenance (Benadi, 2015; Benadi & Pauw, 2018; Pauw, 2013; Wei et al., 2021); hence, its variation in elevational gradients is important to understand how coexistence persists under different scenarios.

The aim of this study was to assess the variation of flower dense-dependent effects in plant-hummingbird communities in different scales and across an elevational gradient. We expected flower negative dense-dependent effect and asymmetric facilitation to be the major processes explaining flower visitation rates at high elevation, whereas for mid and low elevation we expected less or none dense-dependent effects. Among scales, we expected positive density-dependence effect on visitation rates on local spatial scale, negative density-dependence effect and asymmetric facilitation at regional scale at high elevations, whereas we expected less, none dense-dependent effects or a dense-dependent effect configuration not favoring plant coexistence (i.e. advantages for common over rare species in both scales) on mid and low elevations. Lastly, we expected high elevations communities to experience higher specialization (niche partitioning) and that high specialization would also promote flower dense-dependent effects favoring plant coexistence.

## METHODS

The study was conducted across an elevation gradient in southeastern Brazil. The area is part of the tropical Atlantic forest which harbors exceptional levels of diversity and endemism (Marques & Grelle, 2021). Data collection took place in three different elevations: low elevation (0 – 50 m), mid elevation (1000 – 1100 m) and high elevation (1900 – 2200 m) and in each elevation three transects were set. The different elevation sites were distributed in five localities: Parque Estadual da Serra do Mar (PESM) - núcleo Picinguaba (0 – 400 m), Fazenda Bananal (0 – 400 m), PESM – Núcleo Cunha (950 – 1560 m), Parque Nacional do Itatiaia (1800 – 2200 m) and Instituto Alto Montana (1850 - 2000). The low elevation localities (23°21' S 44°51' W) have a mean annual precipitation of 1369 mm and encompass various forest types such as the Brazilian “restinga” (sandy forest), mangrove and Atlantic tropical forest. The mid elevation locality (23°10' S, 44°55' W) has a mean annual precipitation of 2120 mm and is characterized by high humidity, composed mostly by cloud forest vegetation, subtropical and tropical forests (Buzato et al., 2000). The high elevation localities (22°21' S, 44°40' W) have a mean annual precipitation of 2200 mm and are characterized by highland Atlantic forests and high-elevation grasslands (Ribeiro et al., 2007).

We monthly visited the three different elevations from December 2019 until November 2021. Due to the COVID-19 global situation, we did not sample eight months (from April 2020 to September 2020 and March 2021 to April 2021), in low and mid elevation and three months (from April 2020 to June 2020) in high elevation. We had 16 months of sampling at low elevation, 15 at mid-elevation and 19 for high elevation.

To obtain hummingbird-flower visitation data, we used time-lapse cameras. We placed six cameras along a 1.5 km transect using 10 m as a minimal distance between them; each camera had their own GPS coordinate. They were placed from dawn to dusk, and recorded an image every second for three days, which was considered as a first event, generating a total of ~43,200 images per camera per day. After three days, we changed batteries and memory cards and set for another three days of recording on a different plant along the same transect, completing two events. Thus, cameras filmed 12096 hours. We processed pictures using Deep Meerkat Software (Weinstein, 2015) which only return frames with presence of a hummingbird. We manually revised the frames which were used to identify and quantify hummingbird visits. We considered only legitimate visits, that is when hummingbirds had contact with plant reproductive whorls, and we counted the total number of visits per event.

To estimate flower abundance, all flowers potentially visited by hummingbirds were counted along the transect in monthly censuses; for this, only plants with hummingbird visitation and ornithophilous syndrome (i.e. tubular shaped and bright colored corollas; Faegri and Van der Pijl, 1979) were considered. We directly counted all flowers if the plant displayed less than 50 flowers. For plants with more than 50 flowers, we estimated flower abundance by counting all flowers from five flower units (aggregations of flowers, mainly inflorescences). We then estimated the average number of flowers per unit and multiplied this average by the total number of flower units.

To assess differences between local and regional scale, we calculated conspecific and heterospecific flowers at two scales. We quantified conspecific and heterospecific flower density for each recorded flowering plant with time-lapse cameras. In local scale if species A was recorded, all flowers from individuals A along the transect accounted for local conspecific density of A. Thus, flowers that does not belong to species A were counted as local heterospecific density. For regional scale, we considered the sum of the three transects of each elevation. Therefore, we considered the number of flowers of species A present on the three transects on every elevation as regional conspecific density, and again flowers that were not from species A were considered as regional heterospecific density.

A quantitative interaction matrix was built to represent plant-hummingbird interactions. Hummingbirds were set on columns and plants in rows, each cell represents the number of legitimate visits performed by hummingbirds through all sampling time. We built one interaction matrix for each elevation, so in total we had three matrices. In order to describe how species partition their interactions in the network, we calculated network specialization of each elevation, quantified by the  $H_2'$  index, (Blüthgen, et al., 2006).

In order to test how flower dense-dependent effects affect hummingbird visitation rates, we used GLMMs to test such relationship. Hummingbird visitation was used as a response variable in all models. To obtain a comparable response variable across sites, we included the sampling effort of each observed plant (number of hours the plant was recorded) as an offset; as a result, the response variable is expressed in visitation rate (visits per hour). For flower density counts, data was log and z-transformed to improve model convergence (Benadi & Pauw 2018). We removed one month from mid elevation due to an extremely abundant flower display, and due to a bootstrap analysis of outliers made with DHARMA Package (Hartig, 2021) we also removed two months from high elevation that also had extreme flower abundance values (Supplemental material Figure 1). Three models were fit (one for each elevation); each model had local conspecific, local heterospecific floral density and their interaction, regional conspecific, regional heterospecific and their interaction as explanatory variables, resulting in six fixed variables per model. All models followed a Negative Binomial error structure and log link, with months and species as random effects, and in the case of high elevation, transect was included as a random effect, given the lower AIC value for this model. Model selection was done based on the AIC values. GLMMs were fitted with `glmer.nb()` from *lme4* package in R (Bates et al., 2015).

## RESULTS

Across the elevation gradient, we registered 17833 interactions between 85 plants and 12 hummingbird species. We found 7 hummingbird and 37 plant species at low elevation; 5 hummingbird and 35 plant species at mid elevation and 4 hummingbirds and 20 plant species at high elevation. Network specialization ranged from less specialized at low elevation ( $H_2' = 0.39$ ), followed by the mid elevation ( $H_2' = 0.45$ ) and more specialized at high elevation ( $H_2' = 0.59$ ).

In low elevation site, flower visitation rate was not affected neither by conspecific density, heterospecific density nor by their interaction in both scales (Table 1). At the local scale, flower visitation rates increased with the increase of conspecific density in the mid ( $X^2 = 6.24$ ,  $P = 0.012$ ) and high ( $X^2 = 8.94$ ,  $P = 0.003$ ) elevations (Figure 1a, c), whereas flower visitation rates decreased with the increase of heterospecific density in the mid elevation ( $X^2 = 5.8$ ,  $P = 0.016$ ) (Figure 1b). At the regional scale, there was an interaction between conspecific and heterospecific density components (Table 1), resulting in similar patterns for both mid ( $X^2 = 4.69$ ,  $P = 0.03$ ) and high ( $X^2 = 4.04$ ,  $P = 0.044$ ) elevation. Regional conspecific density had a negative effect on visitation rates when plants were in mid and high regional heterospecific density while conspecific density showed no effect on visitation rate for plants with low heterospecific density (Figure 2). Regional heterospecific density had a positive effect on visitation rates when the plant species presented low regional conspecific density (i.e. it was a rare species at the regional scale) while heterospecific density showed no effect on visitation rates for plants with medium and high regional conspecific density (i.e. abundant species) (Figure 3). Given that we did not find any density-dependent effects on low elevation and that these effects depend on the dissimilarity of species abundance, we calculated Pielou's evenness index (Pielou, 1966) for each month in each elevation and then, we performed an ANOVA to test the differences between sites (Supplemental material, table 1). We did not find any difference between evenness among elevations.

## DISCUSSION

We found evidence of flower density-dependence on visitation rates at different scales and elevations. Negative density-dependence (i.e. disadvantages of abundant species) and asymmetric facilitation (i.e. greater benefits of heterospecifics to rare species than for abundant ones) were found on regional scale, whereas positive density-dependence was found on local scale (i.e. advantages of local abundance) and negative effect of heterospecifics (i.e. local competition). Interestingly, such complex interactive effects between conspecifics and heterospecifics density were found at mid and high elevation sites, where network specialization was highest. This suggests that in high elevations, higher niche partitioning plays an important role on supporting flower dense-dependent effects on these plant-hummingbird communities. We did not find any effect of flower density at the low elevation site where specialization resulted to be the lowest.

Negative density dependence and asymmetric facilitation seems to be the main processes in regional scale at the mid and high elevation sites. The interaction between conspecific and heterospecific density suggests that abundant common species were negatively affected by the presence of high abundant heterospecifics (Figure 2), while rare ones experienced higher visitation rates as heterospecific density increases (Figure 3). Thus, rare species are experiencing an advantage due to high intraspecific competition within common species and a disproportionate advantage of facilitation, which are known mechanisms fostering plant coexistence when plant species share pollinator resources (Bergamo et al., 2020; Wei et al., 2021). Moreover, we found opposite trends between regional and local scales, represented by the benefits of local conspecific density and costs of local heterospecific density. Thus, the asymmetric facilitation for rare species and negative density dependence at regional scales could be compensating such advantages of common species at local scales, in order to promote rare species maintenance, as seen in Bergamo et al. (2020).

At local scale the higher visitation rate that focal plants experienced when conspecifics were more abundant suggest a positive density dependence effect on mid and high elevation. Moreover, at mid elevation, we also found a disadvantage for focal plants surrounded by heterospecifics indicating interspecific competition for pollinators (Figure 1, b). Hummingbird's resource preference should mirror their adaptive foraging strategy which seeks to maximize their fitness, consequently hummingbirds visiting flowers more intensively when they were surrounded by more conspecifics, at local scale in mid and high elevation, might reflect this behavior (Revilla & Křivan, 2016). A possible explanation for this relies on the optimal foraging theory which, at first instance, predicts that when pollinators are at low abundance (common on harsh environmental and higher elevation sites) they opt for resource specialization (Fontaine et al., 2008; Revilla & Křivan, 2016). In fact, hummingbird's preference for well trait-matched resources results in lower foraging costs when compared with more abundant but poorly matched resources (Weinstein & Graham, 2017). Consequently, we hypothesize that hummingbirds at mid and high elevations are foraging more efficiently when abundance of one plant species is high. Hummingbirds are likely using only one strategy instead of attempting to extract nectar from several flower species (representing different foraging efforts) thus, reducing energy costs (Emlen, 1966; McArthur & Pianka, 1966).

Another explanation for the positive relationship between visitation frequency and conspecific density might be spatial patterning of resources (Nottebrock et al., 2017). Dispersal limitation and heterogeneous spatial constraints could lead to a spatial aggregation of conspecifics and therefore higher probability of being visited by hummingbirds (Lara-Romero et al., 2016). Conspecific aggregation may result in higher fitness on local scale, since aggregation could help avoiding heterospecific pollen receipt and conspecific pollen loss and this can feedback and promote spatially clustered conspecifics (Morales & Traveset, 2008; Waser & Fugate, 1986).

Specialization (i.e. niche partitioning) seems to have significant implications on flower density-dependence at mid and high elevations. Network specialization can promote plant coexistence under certain conditions (Benadi, 2015; Pauw, 2013). This might be possible because a high partitioning of interactions may reduce interspecific competition, mechanism shown to promote co-occurrence (Chesson, 2000; Maglianesi et al., 2015). The low niche partitioning in the low elevation site could be driven by the presence of a peculiar hummingbird species: *Ramphodon naevius*, which only occurs in low elevation sites. *Ramphodon naevius* is considered a “community organizer” (Sazima et al., 1995). It is known to be a high resource demanding species, which visit plant species with high nectar rewards (Sazima et al., 1995). Aside these specific demands, it is also known for visiting a great number of species regardless of floral density in its environment, converting it into a generalist and in an important node in the network, capable of shaping an important part of the plant composition (Wolowski et al., 2017). Thus, the presence of this species can likely lowers the specialization of the network and increases niche overlap.

Since we did not find any difference in species evenness between sites (supplemental material table 1) we hypothesize that the lack of flower density-dependent effects on hummingbird visitation on the low elevation site might be linked to a lower network specialization, a homogenizing effect of *R. naevius* (visiting both low and high density species) and presence of other pollinators. Studies have shown that birds are more efficient providing pollination services for plants at higher elevations in contrast with bees, which are less abundant and provide lower visitation rate (Conrad et al., 2021; Cruden, 1972; Dellinger et al., 2021). Consequently, a higher abundance of pollinators other than hummingbirds coupled with mixed pollination systems (hummingbirds + insects) in lower sites (Lehmann et al., 2019) may cause a dilution of flower density effects on hummingbird visitation. In fact, hummingbird mean visitation per month was higher in higher elevations (high=377, mid= 354, low= 269). Moreover, higher flower availability (Supplemental Figure 2) would also result in an increased niche overlap among hummingbirds, as found for latitudinal gradients (Schleuning et al., 2012), leading to a reduction of network specialization in low elevation sites.

Hummingbird visitation rates were higher when rare plants co-occurred with heterospecifics, while lower when abundant plants co-occurred with heterospecifics, at a regional scale. In contrast, at local scale hummingbird visitation rates were higher when plant species were locally abundant and were surrounded by few heterospecific neighbors. Across an elevation gradient, such density-dependent processes occurred only at mid- and high-elevation communities, suggesting that communities with low flower availability and high

specialized interactions might be more prone to show flower dense-dependent effects. Those effects are benefiting common species, by positive density-dependence effects on local scale, and rare species maintenance by negative density-dependence effects and asymmetric facilitation on regional scale. Nonetheless, flower availability and foraging behavior may play important roles and need to be incorporated on the plant coexistence research framework, since these can unveil complex processes that can help to understand the maintenance and permanence of highly biodiverse ecosystems.

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## FIGURE LEGENDS

**Figure 1.** Local scale effects in mid (a and b) and high (c) elevations, of conspecific (a and c) and heterospecific density (b) on visitation rate (visits/hour). Dots represent the model partial residuals (after fixing the effect of other explanatory variables).

**Figure 2.** Regional scale interaction of conspecific and heterospecific flower density effects in a) mid and b) high elevation - Dots represent the model partial residuals (after fixing the effect of other explanatory variables). Blue dots and lines represent regional conspecific density effect for species with low regional heterospecific density (at the 10<sup>th</sup> quantile). Yellow dots and lines represent regional conspecific density effect for species with medium regional heterospecific density (at the 50<sup>th</sup> quantile) and red dots and lines represent regional conspecific density effect for species with high regional heterospecific density (at the 90<sup>th</sup> quantile).

**Figure 3.** Regional scale interaction of conspecific and heterospecific flower density effects in a) mid and b) high elevation. Dots represent the model partial residuals (after fixing the effect of other explanatory variables). Blue dots and lines represent regional heterospecific density effect for species with low regional conspecific density (at the 10<sup>th</sup> quantile). Yellow dots and lines represent regional heterospecific density effect for species with medium regional conspecific density (at the 50<sup>th</sup> quantile) and red dots and lines represent regional heterospecific density effect for species with high regional conspecific density (at the 90<sup>th</sup> quantile).

## TABLES

Table 1. GLMM coefficients of the visitation rate (negative binomial error structure) models of three different elevations: low elevation mid-elevation and high elevation. Bold values show significant effects, a P value < 0,05.

Fixed effects	Low elevation		Mid elevation		High elevation	
	Estimate	$X^2$ (P-value)	Estimate	$X^2$ (P-value)	Estimate	$X^2$ (P-value)
Local conspecific	0.092	0.73 (0.394)	<b>0.274</b>	<b>6.24 (0.012)</b>	<b>0.263</b>	<b>8.94 (0.003)</b>
Local heterospecific	0.112	2.48 (0.116)	<b>-0.179</b>	<b>5.8 (0.016)</b>	0.068	1.61 (0.204)
Regional conspecific	-0.058	0.28 (0.598)	-0.216	2.27 (0.132)	-0.165	3.27 (0.07)
Regional heterospecific	-0.004	0.002 (0.963)	0.061	1.47 (0.225)	0.108	0.68 (0.409)
Local interaction	-0.006	0.01 (0.916)	0.050	0.4 (0.527)	0.041	1.15 (0.283)
Regional interaction	-0.006	0.009 (0.923)	<b>-0.144</b>	<b>4.69 (0.03)</b>	<b>-0.087</b>	<b>4.04 (0.044)</b>

**FIGURES**

Figure 1

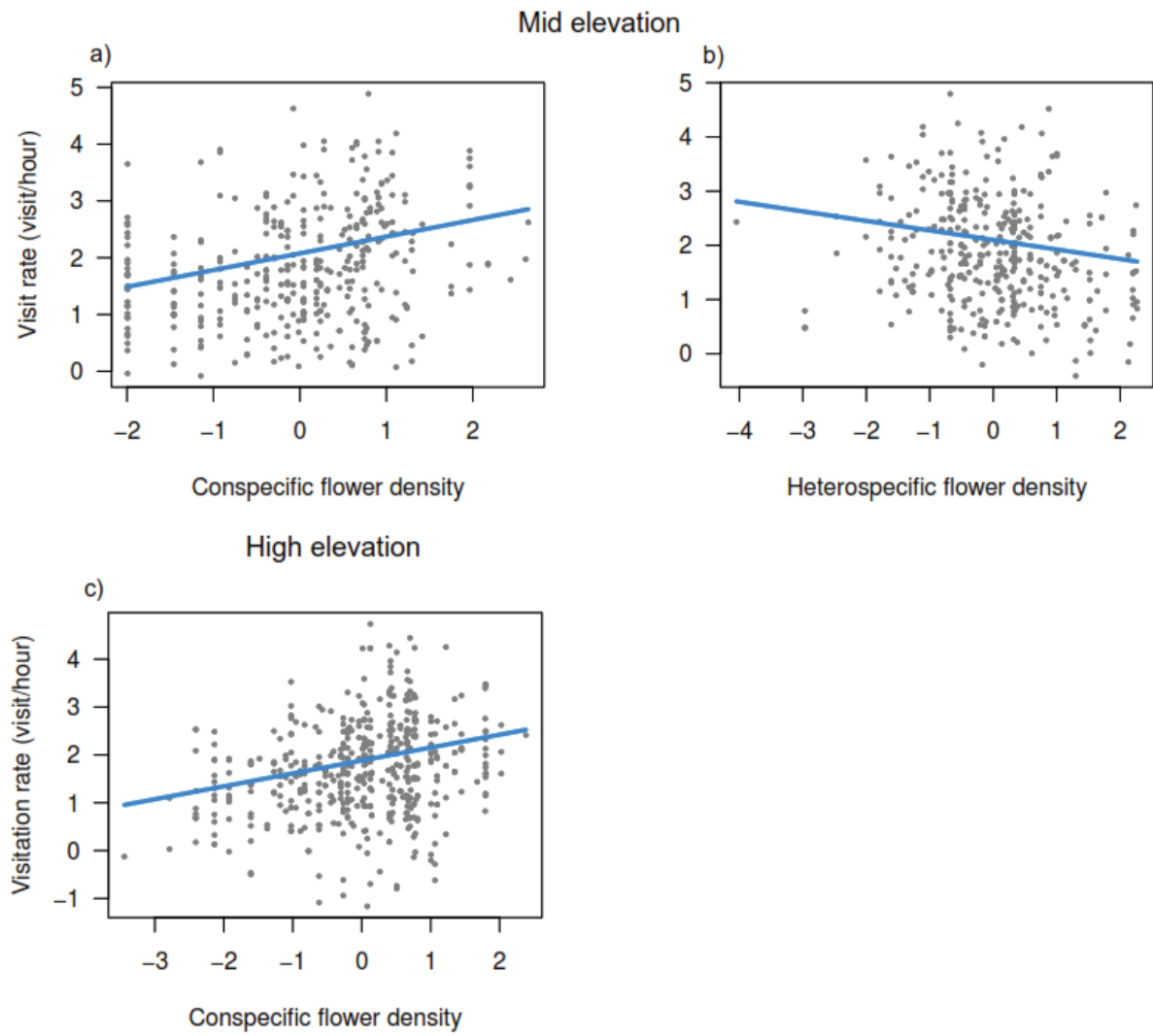


Figure 2

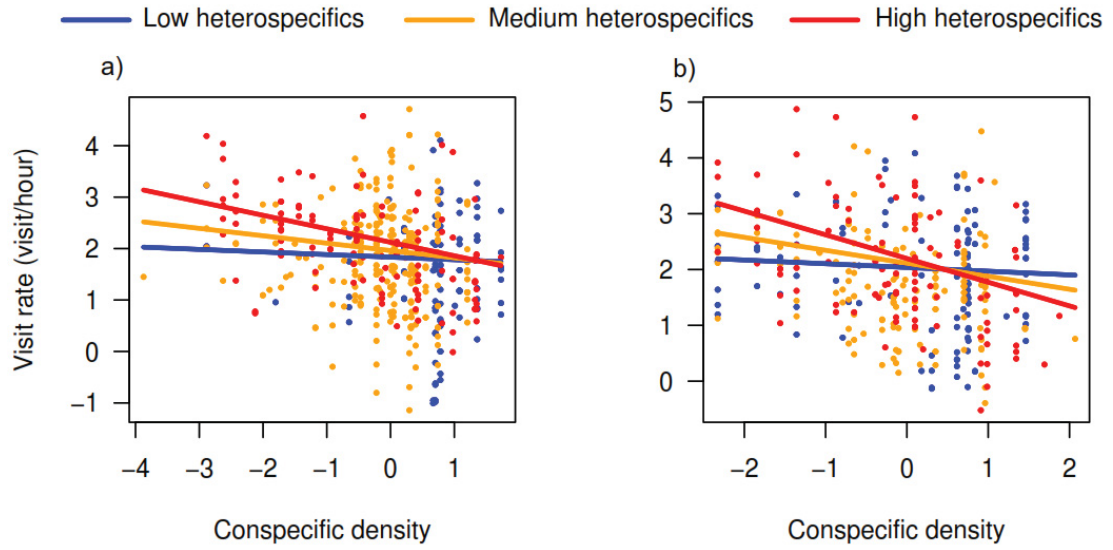
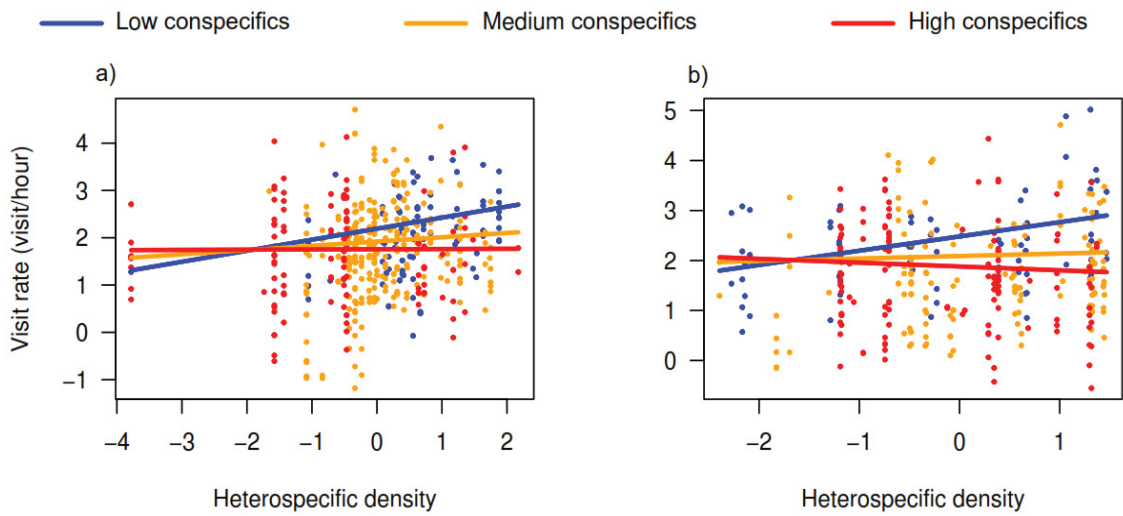
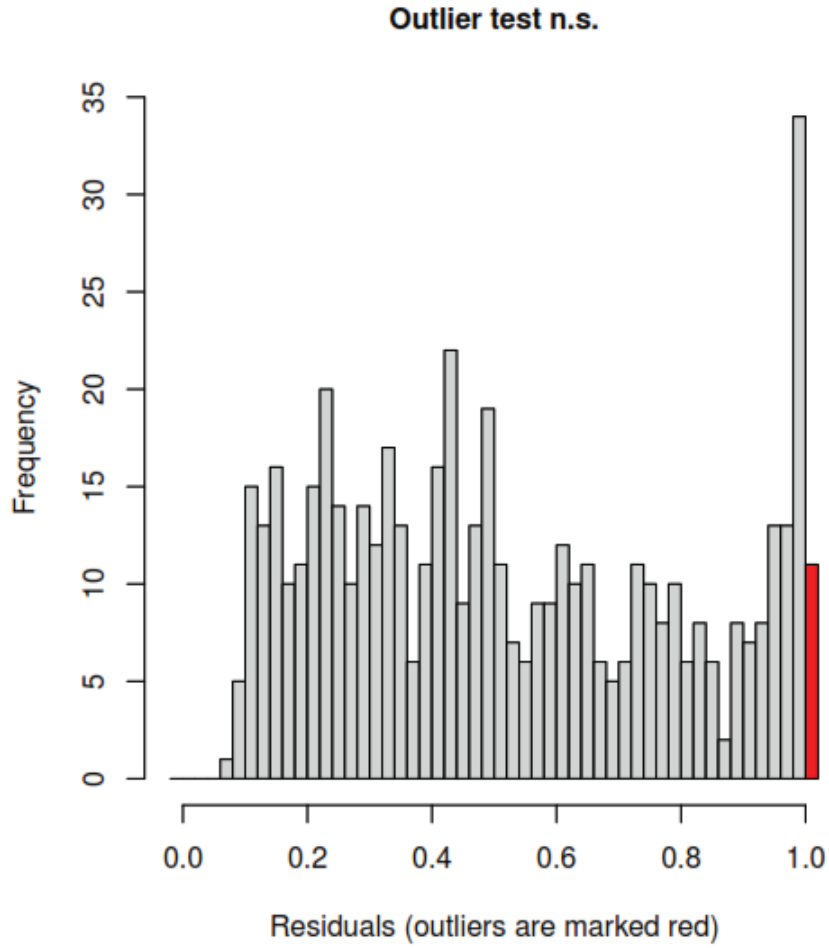


Figure 3



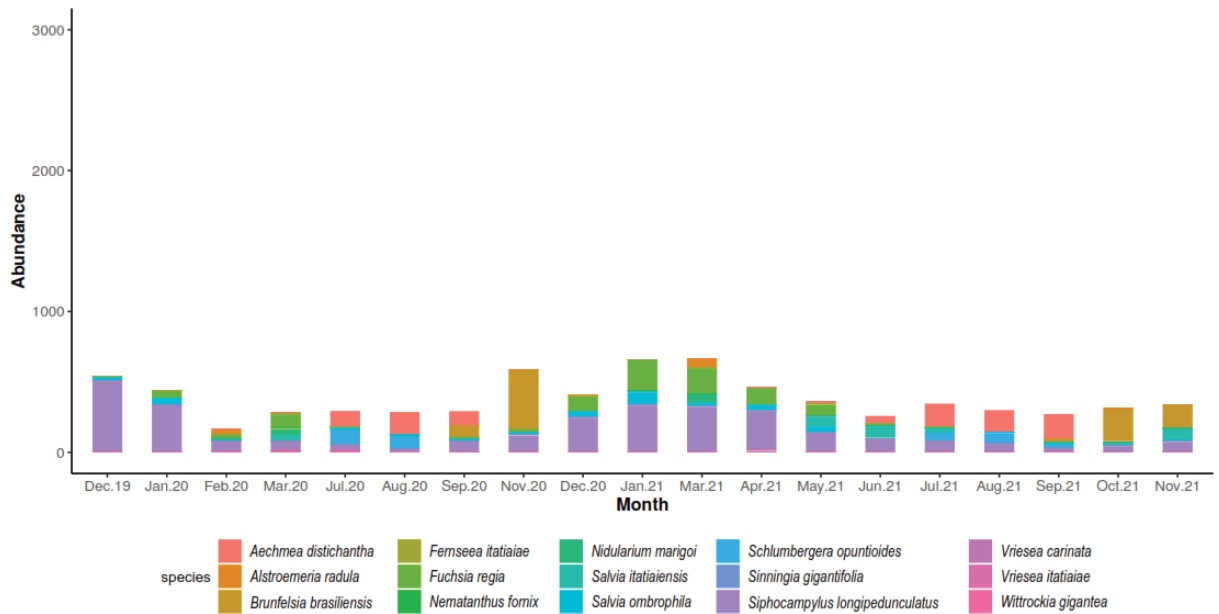
### SUPPLEMENTAL MATERIAL

Supplemental figure 1. Residual outlier marked in red on high elevation negative binomial GLMM. Model residuals on x axis and frequency on y axis.

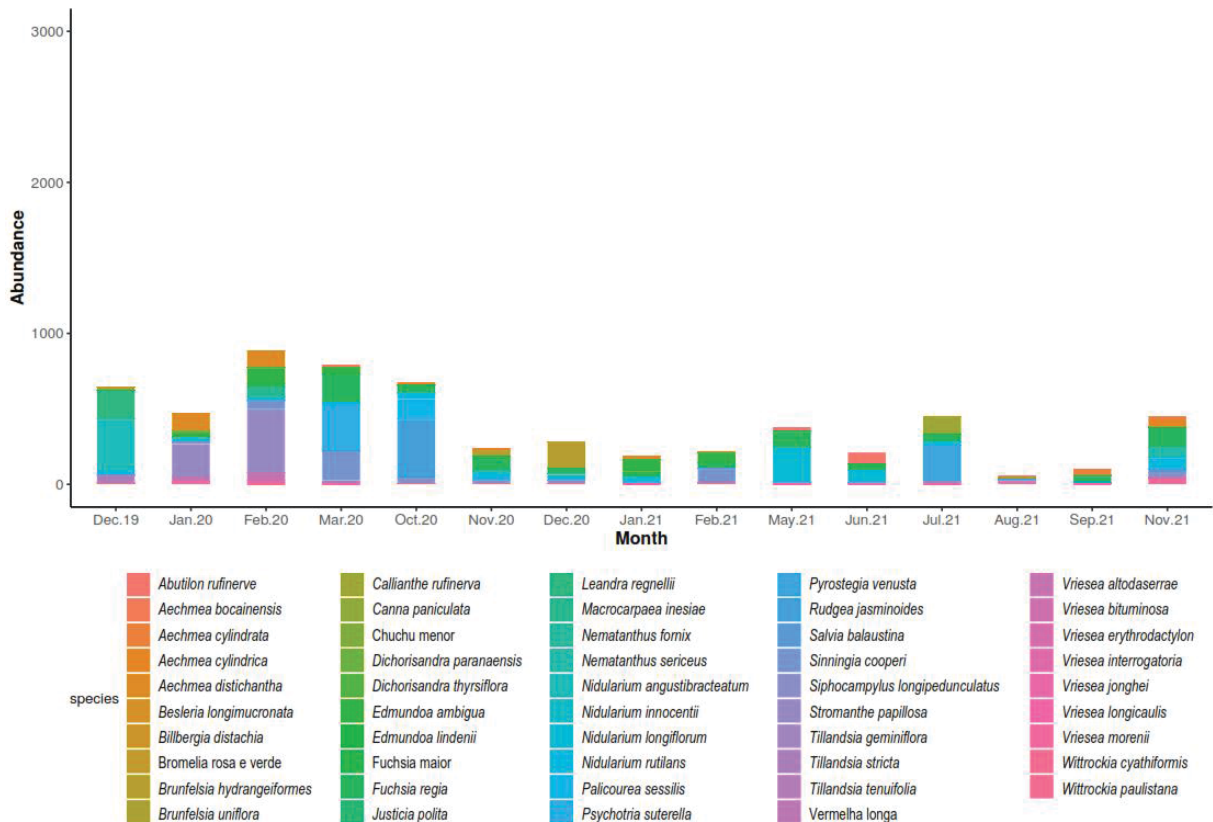


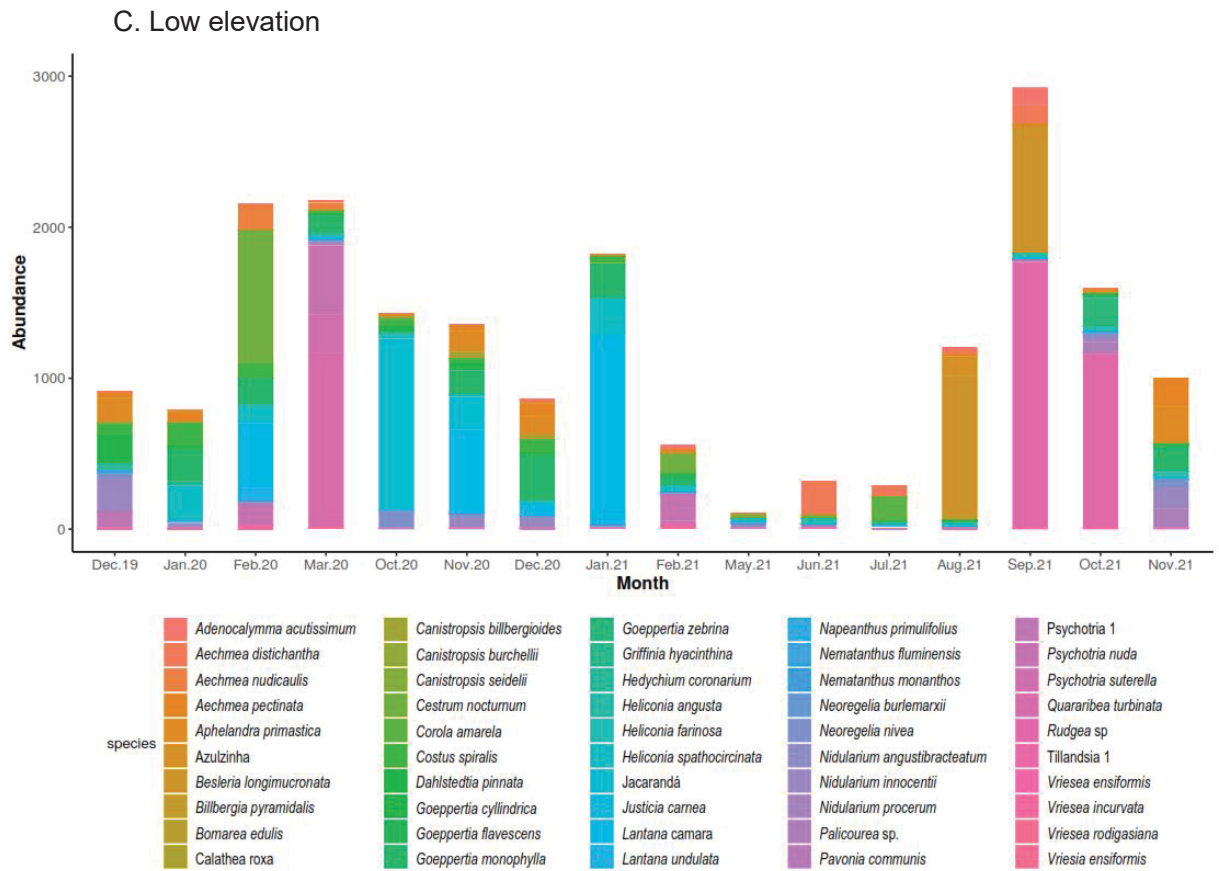
Supplemental figure 2. Flower availability on high elevation (A), mid elevation (B) and low elevation (C). Sampled month on x axis and abundance of raw counts of flowers on y axis. Each bar color represents a different species.

A. High elevation



B. Mid elevation





Supplemental table 1. ANOVA results comparing monthly evenness index for three elevations (low, mid and high).

	Estimate	Std. Error	t value	Pr(> t )
(Intercept)	0.671	0.035	19.336	<2e-16
elevationlow	-0.074	0.051	-1.445	0.155
elevationmid	0.002	0.052	0.043	0.966