

# Nectar robbing: a common phenomenon mainly determined by accessibility constraints, nectar volume and density of energy rewards

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Nectar robbers use a hole made in the perianth to extract nectar. Since robbers may modify plant fitness, they play an important role by driving evolution on floral traits, shaping population structure and influencing community dynamics. Although nectar robbing is widespread in angiosperms, the causes and ecological implications of this behaviour on large ecological scales are still unexplored. Our aim is to study the frequency of nectar robbing in plants of temperate and tropical regions and examine its association with plant traits. We characterised the levels of nectar robbing in 88 species of Mediterranean, Alpine, Antillean and Andean plant communities and identified the most important nectar robbers. We analysed associations between the levels of robbing and floral morphology, production and density of energy rewards, mechanisms of protection against nectar robbers, plant life form and geographic origin. Nectar robbing was present at all sampling sites. Within communities two patterns of robbing levels related to the diversity and specialization of robbers were detected. In most communities one plant species presented very high levels of robbing while other species had intermediate to low robbing levels. There, nectar robbers are opportunists, robbing highly rewarding plants. In the Andean community the high specialization of several co-existing flowerpiercers produced an even pattern of robbing levels in the plant community. Plants with long flowers, abundant nectar and a high energy density are more likely to be robbed by both insects and birds. A high aggregation of the flowers within the plants and the presence of long calyxes and bracts are associated to low robbing rates by insects and to a lesser extent by birds. Besides the morphological constraints that operate on a single flower basis, nectar robbing is a phenomenon dependent upon the density of energy rewards reflecting the presence of mechanisms on higher ecological scales.

Nectar robbers are animals that obtain nectar through perforations in the flower's perianth made either by the animals themselves or by other robbers (Inouye 1980). This particular feeding behaviour has diverse consequences for plants' reproductive success, which may differ in strength and direction, ranging from zero to high impact and may be negative to positive for plant fitness (see Maloof and Inouye 2000, Irwin et al. 2010 for detailed reviews). For this reason, nectar robbers are considered to be one of the selective forces that drive the evolution of plants, shaping floral characteristics, population structure and community dynamics (Irwin et al. 2001, Urcelay et al. 2006, Navarro and Medel 2009).

Nectar robbing is common in angiosperms and has been observed in many systems around the globe (Irwin and Maloof 2002). It occurs mostly in long tubular flowers or flowers with spurs in which nectar is kept out of the reach of animals with short proboscides (Lara and Ornelas 2001, Irwin et al. 2010, Maruyama et al. 2015). However, not all plants with concealed nectar are robbed equally, and a great variation among individuals, species, sites, seasons and years occurs (Arizmendi 2001, Irwin et al. 2001). Although some

plant species are only robbed occasionally, other plants are more prone to experience robbing and in some systems the impact is so high that nearly all open flowers in a population present holes made by these floral visitors (Maloof and Inouye 2000). Such differences in the proportion of robbed flowers among species are attributable to temporal or spatial changes in the abundance of robbers or the floral resources offered, and also to the particular characteristics of the plants that make them more susceptible to robbing (Navarro 2000, Irwin and Maloof 2002). However, the factors that determine the differences in the frequency of robbing within communities are practically unexplored. The evidence suggests that corolla length, orientation and the abundance of flowers determine robbing in tropical plant communities (Rojas-Nossa 2007, 2013). Considering the relevance of these exploiters in terms of plant reproduction and evolution and hence their impact on the dynamics of entire ecosystems, the plant traits that explain the variation in robbing frequency require particular attention in order to understand the causes that trigger this particular feeding behaviour in animals that often make legitimate visits to other flowers.

Although nectar robbing has been observed in diverse taxonomical groups, the most common robbers are insects and birds. Several species of hymenopterans (particularly of the genera *Xylocopa* and *Bombus*), and coleopterans in different ecosystems have been observed behaving as nectar robbers of bird- or insect-pollinated plants (Utelli and Roy 2001, Irwin et al. 2010). Several different groups of birds, including hummingbirds, tanagers, white-eyes and sunbirds, among others, behave commonly or occasionally as nectar robbers (Traveset et al. 1998, Navarro 1999, Geerts and Pauw 2009, Anderson et al. 2011, Maruyama et al. 2015). However, the flowerpiercers (*Diglossa* genus) are specialized nectar-robbing birds (Schondube and Martínez Del Rio 2004). They have a particular bill and tongue morphology that allows them to hold the flower with their hooked maxilla while piercing with the sharp mandible and repeatedly introduce the tongue to extract nectar efficiently (Schondube and Martínez Del Rio 2003). These birds live in sympatry with hummingbirds in the mountain forests of South and Central America, competing for nectar resources (Arizmendi 2001, Navarro 2001, Navarro et al. 2008).

Even though both groups of robbers (insects and birds) feed on floral nectar, their cognitive, behavioural, sensory, morphological and physiological traits related to nectarivory differ. As a consequence, they can use different plant traits as cues to find nectar and discriminate among less- or more-rewarding flowers and species, driving selection on different characteristics of the plants they visit. For example, floral morphology is a character strongly associated with the quality of the reward and the frequency of nectar robbing by both animal groups. However other traits such as floral orientation and flower density have been also related to a higher frequency of robbing either by birds or insects (Lara and Ornelas 2001, Rojas-Nossa 2007, 2013, Castro et al. 2009).

Plants have mechanisms to reduce nectar robbing. The presence of extrafloral nectaries or certain chemical compounds in nectar and flower tissues reduces visits by nectar-robbing insects (Adler 2000, Adler and Irwin 2005, Kessler et al. 2008). It has also been suggested that densely arranged flowers, modifications of floral parts and the presence of structures, such as thick floral parts or bracts, might act as efficient physical constraints to protect nectar from larcenists (Stiles 1981, Inouye 1983, Whitney et al. 2009). However the association of such mechanical barriers with the incidence of nectar robbing has not been properly evaluated at community scale.

Despite the importance of nectar robbers in understanding the evolution and stability of pollination interactions, few biological systems have been studied from different perspectives at the same time (but see Irwin and Brody 2011). Thus, the information on nectar robbers is at present still too scarce, fragmented and limited to particular geographic areas, and therefore hinders the inference of common patterns. Only a few empirical and theoretical approaches have attempted to unravel the ecological complexity of plant-pollinator-larcenist interactions at community or system levels (Arizmendi 2001, Rojas-Nossa 2013, Maruyama et al. 2015, Wang et al. 2015). However, even more remarkable is the lack of studies that compare the variation of the characteristics among robbed and non-robbed plants within

communities that could lead to generalizations regarding the causes of this phenomenon in broader ecological and evolutionary contexts. Therefore, our aims are: 1) to study and compare the frequency of nectar robbing in plant species in four temperate and tropical communities in which nectar robbers are mainly insects or birds, and 2) to detect which floral and plant traits, including morphology, nectar reward, density of the energy reward offered, presence of protection mechanisms against nectar robbers, plant life form and geographic origin, are associated with the frequency of robbing by each animal group within these communities.

## Methods

### Study sites

We conducted this study on four communities of plants in two different biogeographical regions and at two different altitudes: Mediterranean (temperate lowlands), Alps (temperate highlands), Antilles (tropical lowlands) and Andes (tropical highlands). We analysed the species whose flowers produce or store nectar in a spur, cup or tube  $\geq 3.6$  mm length formed by the corolla, calyx or both. We set this value as the minimum threshold based on the minimum length of the proboscis or beaks for the legitimate pollinators as has been reported for these communities (Herrera 1989). This threshold allowed for the exploration of floral morphologies that are prone to being robbed, while excluding species with open dish-shaped corollas, which would yield a large number of non-informative zeros (i.e. 0 = non-robbed), thus reducing the power of the statistical models.

The Mediterranean community was studied at three sites of the Iberian Peninsula. Two sites were located in the Natural Park Serra da Enciña da Lastra, municipality of Rubiá, Ourense, Spain (567 m a.s.l.; 42°28'19"N, 6°50'17"W and 438 m a.s.l.; 42°28'15"N, 6°49'26"W). The third site was located in La Barosa, León, Spain (590 m a.s.l.; 42°29'50"N, 6°48'52"W). The region presents a Mediterranean climate with a mean annual temperature of 12.3°C and a mean rainfall of 901 mm. The landscape is composed of crops and native vegetation, such as holm oak woodlands (predominantly *Quercus ilex*, *Arbutus unedo* and *Quercus suber*), and scrub communities (Gutián et al. 1993). The field work spanned from May to June in 2010, 2011 and 2012.

The alpine community was studied on two sites of the northeastern Calcareous Alps. Both sites were located in the Rax mountain, one in Reichenau an der Rax, and the other in Schwarza im Gebirge, Lower Austria, Austria (1625 m a.s.l.; 47°43'02"N, 15°45'42"E and 1820 m a.s.l.; 47°42'54"N, 15°42'11"E respectively). The mean annual temperature is 1°C and annual precipitation averages 2000 mm (Dullinger et al. 2011). The area is covered by natural vegetation and consists of a matrix of alpine meadows with scattered patches of different sizes dominated by small shrubs and trees, such as *Pinus mugo*, *Picea abies* and *Larix decidua*. In this community the field work was conducted in August 2012.

The Antillean community was studied at two locations in Cuba. The first in Tapaste, La Habana (250 m a.s.l.;

23°00'44"N, 82°06'10"W), and the second site in La Laguna, Mayabeque (71 m a.s.l.; 23°08'34"N, 81°49'05"W). The region has a mean annual temperature of 25.5°C and the mean annual rainfall is 1300 mm. The landscape is karstic and covered by heterogeneous vegetation including littoral microphyllous forests, mesophyllous semideciduous forests, evergreen forests, riparian forests, secondary forests and scrublands mixed with fields and pasturelands (Vale et al. 2011). In this community the field work was carried out in August 2010.

The Andean community was sampled in the northern Andes at two sites. Both sites are located in the Cerros Orientales of Bogotá, Cundinamarca, Colombia (2700–3150 m a.s.l.; 4°49' 22"N, 74° 01' 10"W and 2800–3190 m a.s.l.; 4°48'41"N, 74°00'36"W). The region has a mean annual temperature of 14°C and the annual precipitation is 1038 mm (Rojas-Nossa 2007). The high Andean forest is present in the lower and humid areas of the hills dominated by trees such as *Weinmania tomentosa* and *Clusia multiflora*. The elfin forest occurs at higher altitudes and is characterised by shrubby vegetation dominated by composites and ericads. In this community the field work took place from March 2003 to April 2004 and from November 2011 to June 2012.

### Identity of nectar robbers

To identify the species that behave like primary nectar robbers, we made observations of the floral visitors and their behaviour along transects of 300–1000 m in length at each site. Nectar robbers were identified by capturing insects or by the visual observation with binoculars (10×25) of birds from 6 a.m. to 6 p.m. in the tropical communities, and from 8 a.m. to 8 p.m. at the temperate communities. Because in the Mediterranean and Antillean communities some of the plant species were likely to have nocturnal floral visitors, our observations there took place from 10 p.m. to 1 a.m. Moreover, we characterised the type of hole made by robbers, which was useful in differentiating robbing by certain species and helped us to accurately determine cases of nectar robbing from florivory. We carried out 70 h and 9 min of observations in the Mediterranean community, 21 h 19 min in the Alpine community, 14 h and 25 min in the Antillean community, and 148 h and 28 min in the Andean community.

### Levels of nectar robbing

To assess the frequency of primary nectar robbing (sensu Inouye 1980) in each plant species (hereafter 'levels of nectar robbing') we carefully observed the presence of perforations made by robbers in a sample of flowers randomly selected along transects. We inspected a total of 10 838 flowers of 88 plant species. On average  $123.2 \pm 20.1$  flowers per species were analysed for perforations. The level of nectar robbing was calculated as the number of flowers with one or more holes divided by the number of flowers analysed per species. Although secondary nectar robbing is a common phenomenon in plant–larcenist interactions (Irwin et al. 2010), the assessment of the levels of secondary robbing was out of the range of our study.

### Plant traits

To characterise floral morphology, a sample of  $40 \pm 10$  fresh flowers of each species was randomly selected. We measured a total of 3915 flowers. The floral characters assessed were: total corolla length, tube length and tube diameter at the opening. The width of the corolla tube was calculated as the ratio diameter / length of the tube. Thus, lower values of this variable correspond to narrow floral tubes, while numbers around 1 or more correspond to broad corollas. The flower orientation was measured in 1–10 flowers per species by measuring the angle with respect to a line perpendicular to the ground. For this purpose we placed a small pendulum attached to a line near the flower, then we measured the angle with a protractor and later transformed it to radians (Supplementary material Appendix 1 Fig. A1); flowers oriented totally upwards have 0 rad; flowers horizontally oriented have 1.57 rad and flowers perfectly pendent have 3.14 rad. We also characterised floral symmetry (zygomorphous or actinomorphic) and corolla type (dialipetalous or gamopetalous).

To test the association between the presence of chemical barriers and nectar robbing levels we recorded the presence or absence of substances (such as latex) secreted by floral tissues when the corolla is mechanically damaged. Also, we recorded the presence or absence of protective structures, such as calyx, hairy calyxes, or bracts, that covered at least the basal part of the corolla where nectar is concealed, and classified the flowers based on the thickness of the perianth as follows: thin ( $\leq 1$  mm) or fleshy ( $> 1$  mm thickness). We characterised the aggregation of flowers in inflorescences and plants using a semi-qualitative scale with three values: low aggregation for flowers with distances  $\geq 30$  mm; medium aggregation for flowers with distances between 5–29 mm; and high aggregation for flowers with  $\leq 5$  mm distance from each other.

For reasons related to energetic costs, perching robber-birds may prefer foraging in plants with strong branches that support their weight. Therefore, we characterised each species' life form as tree, shrub, herb, parasite or epiphyte. In addition, in locations where exotic plants occur, we included this variable (i.e. exotic or native) in the analysis.

### Flower density and nectar rewards

We quantified the density of flowers (no. of flowers  $\text{m}^{-2}$ ) of each plant species at each site. For this purpose we delimited one transect per site measuring 10 m width and 300 to 1700 m length according to the environmental complexity of the vegetation. In each transect we counted all open flowers of each species. Finally we averaged the flowers  $\text{m}^{-2}$  of all sites for each community.

To assess the volume and sugar concentration of nectar we bagged an average of  $20 \pm 4$  fresh flowers randomly selected from each species (one per plant) with mosquito net bags. After 24 h we extracted and measured all nectar accumulated in the flower with 0.5, 1, 2, 5, or 10  $\mu\text{l}$  capillary micropipettes, according to the size of the flower and the produced volume. Sugar concentration was characterised with a portable refractometer (0–32°Brix). For flowers with a nectar concentration higher than 32°Brix, we diluted

the nectar with a known volume of distilled water, recorded the measurement and then calculated the original concentration. To calculate the kilojoules produced per flower in 24 h we used the method described in Corbet (2003). The mean energetic value per flower ( $\text{kJ flower}^{-1}$ ) was multiplied by the density of flowers ( $\text{flowers m}^{-2}$ ) to express the density of energy reward offered by each plant species in terms of kilojoules per  $\text{m}^2$  ( $\text{kJ m}^{-2}$ ).

## Data analysis

We used an arcsine-root transformation for flower orientation. All other variables were non-transformed. We then performed a principal component analysis (PCA) for all quantitative and qualitative variables in each community using the FactoMineR package ver. 1.28 for R (Lê et al. 2008). Finally, we analysed the relationship between the levels of nectar robbing as a response, and the first factors of the PCA that explained more than 72% of the variance in the data as predictors. With this aim we fitted generalized linear models (GLM) for each community using binomial error structure and log link function in R software (Dobson 2002).

To assign a positive or negative association for certain plant traits and the levels of nectar robbing in each community, we first analysed the contribution of each variable for the first three PCA factors. To determine the highest contributions of traits to each factor, we used the following criteria: for continuous variables we considered traits with contributions higher than 10; for categorical variables we considered traits with a  $p \leq 0.05$  for the  $\chi^2$ -test (Supplementary material Appendix 1 Table A1–A4). We used the sign of the coordinate to determine the direction of the association among traits and that particular factor. Then, we used the sign of the estimates of the factors that contributed significantly (i.e. with a  $p \leq 0.05$ ) to the GLM models. Finally, to assess the direction (positive or negative) of the influence of each factor on the robbing level, the signs were multiplied.

## Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.5s06n>> (Rojas-Nossa et al. 2015).

## Results

### Levels of nectar robbing and identity of nectar robbers

The Mediterranean community was composed of 27 species belonging to 14 families (Fig. 1a). A total of 51.9% plant species presented very low levels of nectar robbing (proportion of robbed flowers  $\leq 0.2$ ). The main primary nectar robbers were *Bombus terrestris* and *Xylocopa violacea* (Fig. 2a–b). The frequency of robbing in *Lonicera etrusca* was higher than for all other species of the community with more than the half of the flowers presenting one or more holes made by several insect species (level of robbing = 0.54), such as the hymenopterans *Xylocopa cantabrita*, *X. violacea* and *B. terrestris*,

or the coleopterans *Oxythyrea funesta* and *Tropinota hirta*. We did not detect any sign of nectar robbing in 44.4% of the nectariferous species of this community (Fig. 1a).

The Alpine community was represented by 12 species from seven families (Fig. 1b). Unlike the Mediterranean community, most species did not show any sign of floral larceny by primary nectar robbers. Only *Anthyllis vulneraria* presented high levels of robbing (0.6) by the bumblebee *Bombus terrestris* (Fig. 2c), while *Gentiana nivalis* exhibited very low levels of robbing (0.1). In species such as *Gentianella campestris*, *Aconitum napellus*, *Dianthus alpinus*, *Campanula alpina*, *Euphrasia officinalis*, *Rhinanthus serotinus* or *Pedicularis rosea* we did not detect signs of nectar robbing in the flowers (Fig. 1b).

In the Antilles only nine species from six families fulfilled the characteristics defined to be included in the sampling at the time the study was conducted (Fig. 1c). The robbing pattern was similar to that of the Mediterranean and the Alpine communities with one species (*Tecoma stans*) having intermediate levels of robbing (0.54) and another (*Ipomoea nil*), very low levels (0.1). In this community the primary robbers were one carpenter bee (*Xylocopa cubaecola*) and one hummingbird (*Chlorostilbon ricordii*) (Fig. 2d). Other common species in this community such as *Ipomoea angulata*, *Rhytidophyllum wrightianum*, *Hamelia patens* or *Rondeletia odorata* did not present holes in their flowers (Fig. 2e).

The Andean community was highly diverse and comprised 40 nectariferous species belonging to 18 families. A total of 66% of the species were robbed in varying degrees ranging from 0.12 to 1 (Fig. 1d). Two species (*Thibaudia grandiflora* and *Bejaria resinosa*) presented very high levels of robbing (1 and 0.84 respectively, Fig. 2f). Plants such as the exotic *Digitalis purpurea* or the native *Macrocarpaea glabra* had high levels of robbing (0.64 and 0.62 respectively). *Fuchsia* sp. had intermediate levels of robbing (0.43). 42.5% of the species exhibited low to very low levels of nectar robbing ( $\leq 0.4$ ). In the Andes the main primary nectar robbers were the passerines *Diglossa humeralis* (Fig. 2g), *D. albilatera*, *D. lafresnayii*, *D. caerulescens* and *D. cyanea*. Although the flowers of some species were abundant (e.g. *Gaiadendron punctatum* or *Clusia multiflora*), and/or produced large amounts of nectar (e.g. some Bromeliaceae), we did not detect any sign of nectar robbing in their flowers.

## Floral characteristics associated with nectar robbing

### Mediterranean community

The levels of robbing in the Mediterranean plants were significantly associated with the three first principal components (factors) which explained 72.8% of the variance (Table 1). The first factor was mostly defined by positive associations with morphological variables, such as tube diameter, corolla length, tube length and orientation (Table 2, Supplementary material Appendix 1 Table A1). Remarkably, the presence of long calyxes or bracts and a high aggregation of the flowers were negatively associated with the first factor and thus with robbing, which would suggest that these features act as mechanical barriers against nectar robbing. Species with long flowers oriented horizontally to a downward inclination without any mechanical barrier were robbed more frequently. The second factor was mainly determined by the



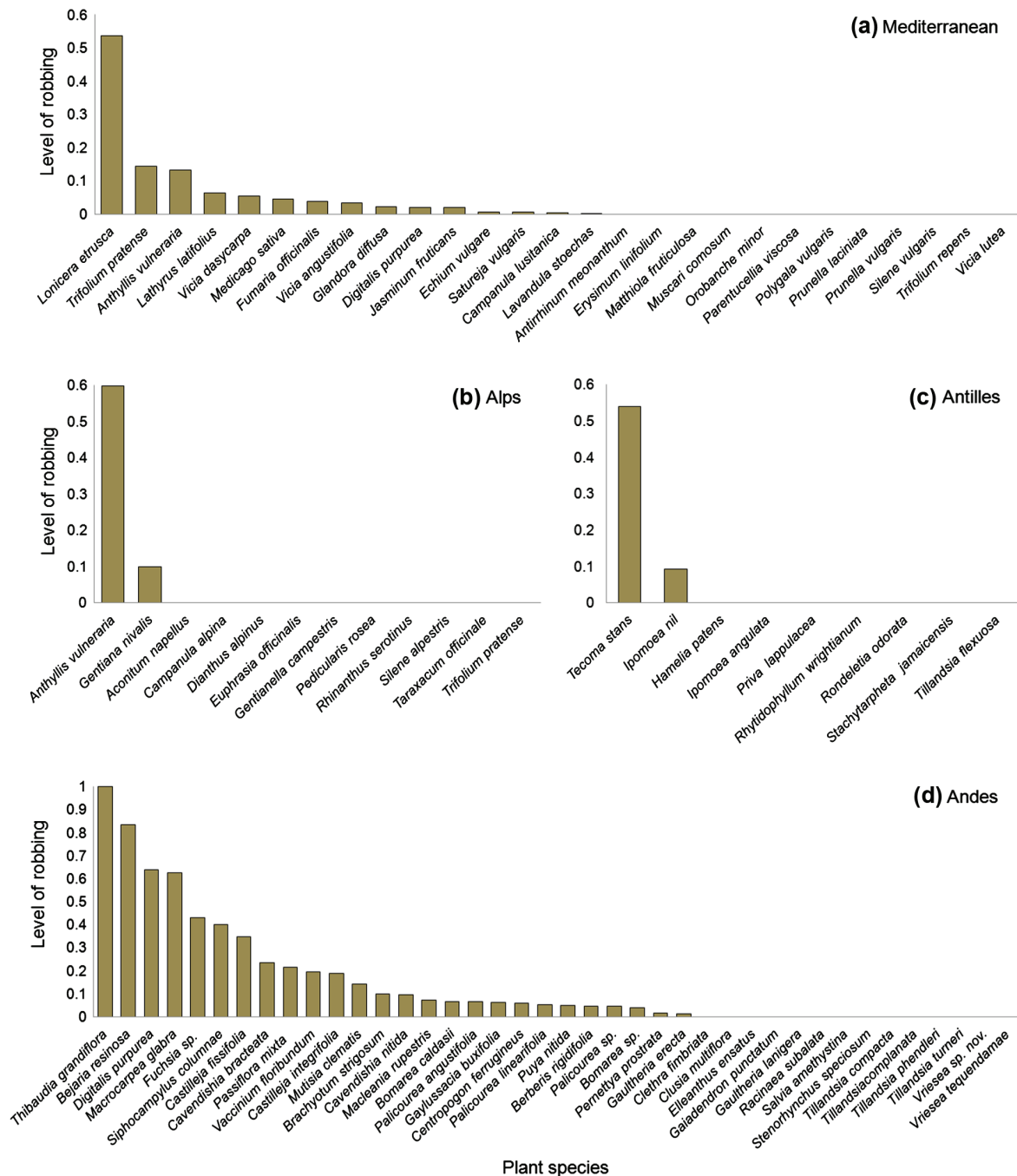


Figure 1. Levels of nectar robbing (number of flowers with  $\geq 1$  holes made by primary nectar robbers/total number of inspected flowers) in (a) 27 species of the Mediterranean community, (b) 12 species of the Alpine community, (c) nine species of the Antillean community and (d) 40 species of the Andean community.

narrowness of the tube and the characteristics of the energy reward offered, such as the volume of nectar produced per flower, the quantity of flowers per unit area or the energy offer in the environment ( $\text{kJ m}^{-2}$ ). This factor is also significantly associated with robbing levels (Table 1), meaning that the plants that offer dense and high nectar rewards, in narrow flowers, are more prone to being robbed (Table 2).

The tube diameter and the particular morphology and behaviour of robbers were relevant in determining the levels of nectar robbing in certain plants regardless of the

flower length or nectar production. For instance, *Digitalis purpurea* and *Lonicera etrusca* had very long flowers (mean  $\pm$  SD =  $46.9 \pm 4.1$  and  $32.9 \pm 4.6$  mm respectively) and a copious nectar production ( $5.9 \pm 9.4$  and  $5.2 \pm 3.7$   $\mu\text{l}$  respectively). However, the large diameter of *D. purpurea* ( $14.9 \pm 5.6$  mm) allowed *Bombus terrestris* to visit the flower legitimately, while *Xylocopa violacea* behaved like a robber. In contrast, the narrow aperture of *L. etrusca* ( $2.5 \pm 0.4$  mm) forces medium and small visitors to get illegitimate access.

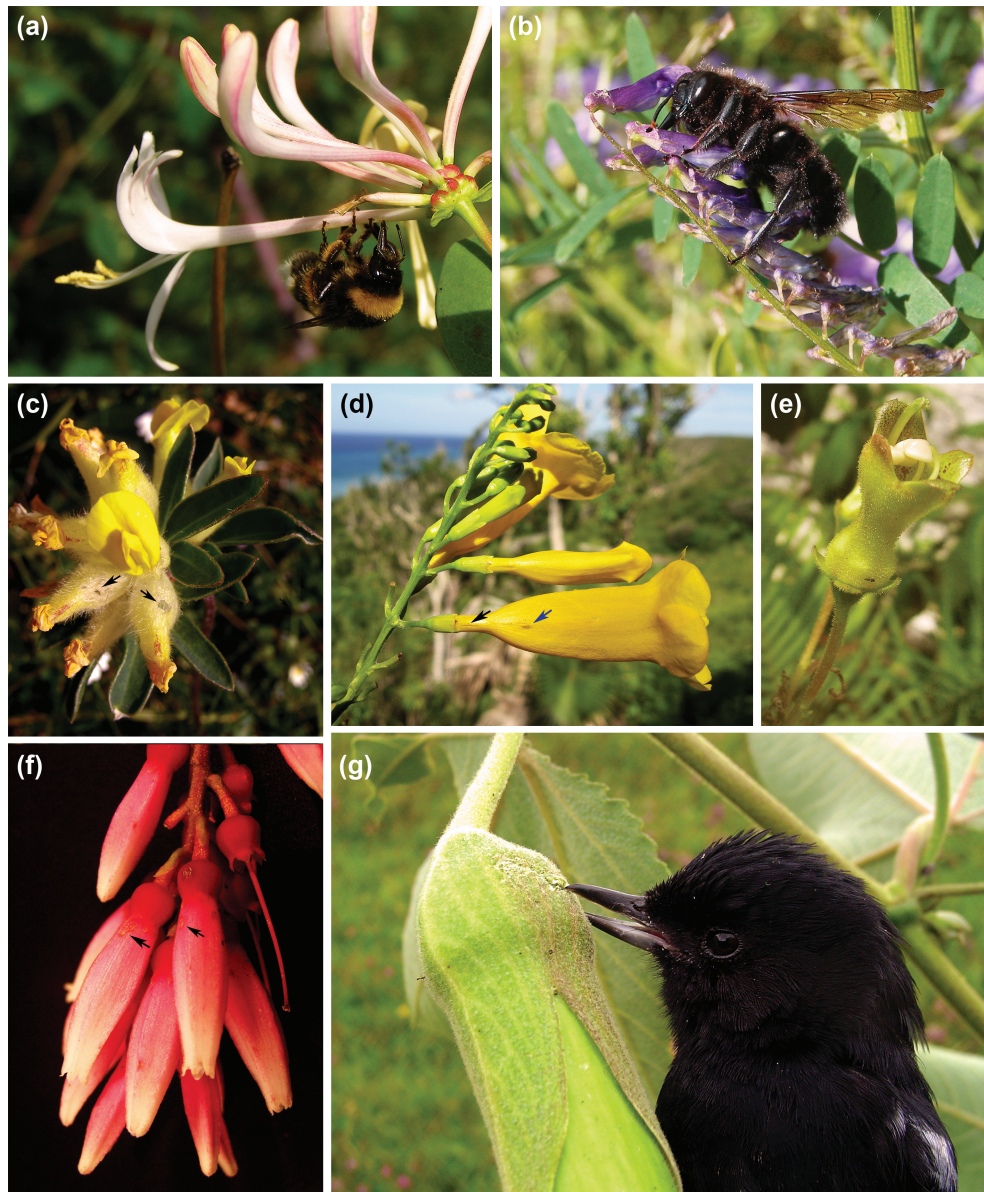


Figure 2. Nectar robbing is a common phenomenon in temperate and tropical plants with concealed nectar. In the Mediterranean the species *Lonicera etrusca* was highly robbed by coleopterans and particularly by hymenopterans, such as *Bombus terrestris* (a). Other nectariferous species such as *Vicia dasycarpa* were robbed to a lesser extent by hymenopterans, such as *Xylocopa violacea* (b). In the Alpine community *Anthyllis vulneraria* was frequently robbed by *Bombus terrestris* (c). In the Antilles the tree *Tecoma stans* (d) presented slits made by *Xylocopa cubaecola* (black arrow) and holes made by the hummingbird *Chlorostilbon ricordii* (blue arrow). In contrast, the endemic gesneriad *Rhytidophyllum wrightianum* did not have holes made by robbers (e). In the Andes, plants such as *Thibaudia grandiflora* presented very high levels of robbing (f). The passerine birds of the genus *Diglossa* have a particular bill morphology that allows them to grab the flower with their hooked maxilla while introducing the sharp lower mandible into the base of the long flowers. Here *Diglossa humeralis* performing primary nectar robbing in *Passiflora mixta* (g). Arrows show the holes made by nectar robbers.

Table 1. Results of the association between the levels of nectar robbing and the morphological and nectar traits of four temperate and tropical plants communities. Given values are the percentage of variance explained by the first factors of the principal component analysis (PCA) and the results of the generalized linear model (GLM) that analyse the association of the levels of nectar robbing with each factor. The values in the GLM columns correspond to the estimates for each factor and their significance (\*\* for  $p < 0.001$ ; \* for  $p \leq 0.05$ ; NS for  $p > 0.05$ ).

Factor	Mediterranean		Alps		Antilles		Andes	
	PCA	GLM	PCA	GLM	PCA	GLM	PCA	GLM
1	36.40	0.11*	32.71	0.61**	42.00	0.16 <sup>NS</sup>	33.96	0.32**
2	20.63	0.49**	26.26	0.13 <sup>NS</sup>	32.78	1.22*	22.14	0.54**
3	15.77	-0.85**	14.21	0.72**	—	—	16.40	0.27**

Table 2. Direction and significance of the association between levels of nectar robbing and plant traits in four plant communities of temperate and tropical regions. The symbols indicate the information extracted from the contribution of each variable to the PCA factors (Supplementary material Appendix 1 Table A1–A4) and their significance in GLM models (Table 1). (+) in dark grey cells represent positive associations, (–) in grey cells represent negative associations, (x) in light grey cells represent traits that do not explain the levels of nectar robbing, and empty white cells represent cases in which only one or none of the states were present for a certain variable and therefore it was not included in the analysis for that particular community. See Methods section for a detailed description of the way we assigned symbols.

	Mediterranean	Alps	Antilles	Andes
Floral morphology				
Corolla length	+	+	+	+
Tube length	+	+	+	+
Tube diameter	+	+	+	+
Diameter/length of the tube	–	+	x	+
Orientation	+	x	x	–
Actinomorphic symmetry	x	x	x	x
Zygomorphic symmetry	x	x	x	x
Dialipetalous/sepalous flower	x	x	x	+
Gamopetalous/sepalous flower	x	x	x	–
Energy reward				
Nectar volume	+	x	x	+
Nectar concentration	x	x	x	x
No. of flowers m <sup>–2</sup>	+	x	x	+
kJ m <sup>–2</sup>	+	x	x	+
Protection against nectar robbers				
Protective structures present	–	x	x	x
Protective structures absent	+	x	x	x
High flower aggregation	–	x	x	–
Medium flower aggregation	+	x	x	x
Low flower aggregation	x	x	+	+
Thick floral tissues	x		x	+
Thin floral tissues	x		x	–
Latex present				+
Latex absent				–
Plant life form				
Epiphyte	x		x	x
Herb	x		x	+
Parasite	x			
Shrub	x		x	–
Tree			x	+
Geographic origin				
Exotic	x			x
Native	x			x

### Alpine community

Three PCA factors explained 73.2% of the variance (Table 1). The levels of robbing were significantly associated with the first and third factors of the PCA, but not with the second (Table 1). The first factor was determined mostly by positive associations with morphological variables, such as tube diameter, total corolla length, tube length and diameter / length of the tube (Supplementary material Appendix 1 Table A2). Thus, plants with long tubular flowers and a broad tube diameter presented higher levels of nectar robbing (Table 2). Flower orientation, the density of the energy reward and quantity of flowers m<sup>–2</sup> (i.e. variables highly related to the second factor of the PCA), did not explain the observed levels of robbing. Although *Aconitum napellus* represented an abundant and caloric nectar resource, we did not observe signs of nectar robbing in these flowers during the sampling.

### Antillean community

In the Antillean plants, the first two PCA factors explained 74.8% of the variance (Table 1). The first factor was mostly

determined by the energy available, nectar traits, orientation, narrowness, floral symmetry and consistency, as well as the plant's life form (Supplementary material Appendix 1 Table A3). The GLM analysis revealed that this factor was not significantly associated with the levels of nectar robbing (Table 1). Morphological traits (such as tube diameter, total flower length and tube length) and low aggregation of the flowers were relevant to determine the second PCA factor in this community, which was significantly and positively associated with the levels of robbing (Table 1). Hence, bigger and less aggregated flowers showed higher robbing frequency (Table 2). In one noteworthy case robbing did not take place despite the fact that the characteristics of the plants in the field would have indicated the presence of nectar robbing. The endemic gesneriad *Rhytidophyllum wrightianum* presents relatively long and narrow gamopetalous corollas (corolla length =  $16.3 \pm 1.3$  mm, tube length =  $14.0 \pm 1.6$  mm and tube diameter =  $7.0 \pm 0.5$  mm). It produces copious quantities of nectar ( $28.8 \pm 27.7$  µl), and was the most common nectariferous plant in the Tapaste site ( $0.08$  flowers m<sup>–2</sup>). Their flowers were legitimately visited by the hummingbird



*Chlorostilbon ricordii* during the day, sphingids at dusk and the bat *Monophyllus redmanii* during the night, providing a rich source of nectar for a broad diversity of nectarivorous animals. Although some individuals exhibited florivory by Lepidoptera larvae, we did not find signs of nectar robbing by *Xylocopa cubaecola* despite the fact that this carpenter bee robbed *Ipomoea nil* flowers nearby. The species has no bracts or a long calyx which could act as a mechanical barrier for robbers, but rather it has a thick corolla covered with sticky trichomes (Fig. 2e).

### Andes

In the Andean community three PCA factors accounted for 72.5% of the variance and were significantly and positively associated to the levels of nectar robbing (Table 1). Tube length, total corolla length, nectar volume, flower aggregation and the plant's life form contributed to the first factor (Supplementary material Appendix 1 Table A4). The density of energy rewards ( $\text{kJ m}^{-2}$ ), the quantity of flowers  $\text{m}^{-2}$ , flower consistency and orientation contributed mostly to the second factor, which was significantly associated to nectar robbing (Table 1). Hence, plants with large number of flowers that represented an abundant nectar source in the area ( $\text{kJ m}^{-2}$ ) were more robbed by birds. Tube diameter did not contribute to the second factor as for the previous communities. For the construction of the third factor the most important variables were tube diameter, width of the corolla tube, flower type (i.e. dialipetalous/sepalous or gamopetalous/sepalous), plant's life form and presence of latex. The contribution of the variables to the PCA factors and the sign of the estimate in the GLM model revealed that plants with dense and abundant nectar rewards, and long pendent dialipetalous flowers were prone to being robbed (Table 2).

Despite a non-significant relationship between the presence of protective structures and the first three factors (Supplementary material Appendix 1 Table A4), species with strong bracts and generous nectar production at the base of long and narrow corollas showed little (in the case of *Puya nitida*) or no robbing (such as all species of *Tillandsia* and *Vriesea*, Fig. 1d). Remarkably, the thickness of the corolla does not seem to represent a physical barrier to flowerpiercers. On the contrary, plant species with thick flowers, such as those present in the ericads *Thibaudia grandiflora*, *Bejaria resinosa*, *Cavendishia nitida* or *Macleania rupestris*, presented a significant association experiencing intermediate to high levels of nectar robbing (Fig. 1d). In this community few plant species produced latex when floral tissues were damaged. This trait did not totally preclude nectar robbing by birds and in some plants with latex, such as *Siphocampylus columnae* and *Centropogon ferrugineus*, nectar robbing was present with low frequency. The aggregation of the flowers was significantly associated with the first factor of the PCA and thus to the levels of robbing (Supplementary material Appendix 1 Table A4, Table 1). Plants with less-aggregated flowers presented a higher frequency of robbing (Table 2). On the other hand, highly-aggregated flowers showed low levels of robbing, suggesting that this trait constitutes a mechanical barrier that reduces nectar robbing by birds.

## Discussion

### Levels of nectar robbing in plant communities

We found that nectar robbing was present at all the sampling sites regardless of the biogeographical region, altitude and sampling effort. This reveals that nectar robbing is not only taxonomically and geographically widespread as already observed previously (Irwin and Maloof 2002, Irwin et al. 2010), but that it probably occurs in every nectariferous plant community that interacts with animals having morphological constraints impeding them from obtaining nectar legitimately and having the behavioural and physical capacity to rob.

The frequency of nectar robbing among coexisting species varied, and two different patterns of nectar robbing levels within communities were detected. These patterns are probably related to the diversity, abundance and specialization of plants, pollinators and robbers. In most plant communities nectar robbing is restricted mainly to one plant species, while other nectariferous species are less frequently or never robbed (Fig. 1). This implies that nectar robbers are not totally dependent on robbing, as they would have to feed on a series of species throughout the season. In contrast, in the Andes a higher proportion of plants in the community were robbed with different frequencies, ranging from very low to very high. At this site, ornithophily is the most important pollination mode for several groups of plants, most of which have flowers specialized for pollination by hummingbirds (Luteyn 1989). High Andean hummingbirds, in turn, present a very wide spectrum of bill morphologies, ranging from very short (7.6 mm in the case of *Ramphomicron microrhynchum*) to the longest bill in the avian world in relation to body mass (100.4 mm length in *Ensifera ensifera*) (Gutiérrez et al. 2004). In the locality studied five species of flowerpiercers (genus *Diglossa*) co-exist and compete with each other for floral nectar as well as with several species of hummingbirds. These birds are common members of the mountain Neotropical avifauna and have potential effects on the reproduction of plants (Arizmendi 2001, Rojas-Nossa 2013). Unlike insects or hummingbirds that opportunistically switch their behaviour from legitimate visitors to that of nectar robbers depending on the floral resources offered (Irwin et al. 2010, Maruyama et al. 2015), flowerpiercers rob nectar more frequently than extracting it legitimately (Rojas-Nossa 2007). Moreover, they have morphological and physiological features that make them highly specialized nectar robbers (Schondube and Martínez Del Río 2004). In tropical plant communities that have co-evolved and interact throughout the year with diverse assemblages of pollinators and robbers, competition for nectar resources might impose selective pressures between robbers producing the even pattern observed. Considering the high abundance of several flowerpiercers that coexist all year round and their specialization for robbing, the division of nectar resources is one likely mechanism to reduce the chances of a collapse of pollination interactions caused by over-exploitation.

Theoretical models also suggest that several situations might allow plant-pollinator-robber interactions to persist: when pollinators and robbers have similar level of fitness; when they show periodic dynamics of plant-robber



frequencies; when they have density-dependent mechanisms, or when plants, pollinators and robbers have intermediate efficiencies to translate the benefits of the interaction into fitness (Wang et al. 2012, Wang 2013). However, more research in this field is still needed to understand under which conditions pollination systems persist despite the high frequencies of nectar robbing recorded in certain plant species.

## Plant traits and their association with nectar robbing levels

### Floral morphology

In all the temperate and tropical plant communities studied, the levels of nectar robbing are associated with flower size. Generally, plants with long tubular flowers were more prone to high levels of robbing by both insects and birds. This result was expected considering the patterns previously observed in single species. For instance, under natural conditions Castro et al. (2009) found positive relations between flower size and robbing levels in *Polygala vayredae* by several insects, while Navarro and Medel (2009) found that the probability of nectar robbing by *Xylocopa cubaecola* increased with the length and the diameter of the flowers of *Duranta erecta*. Similarly, hummingbirds are more likely to rob longer artificial and natural flowers (Lara and Ornelas 2001, Maruyama et al. 2015). The length of the tube is, in fact, one of the most likely traits in plants to explain the causes of nectar robbing for several reasons. For animals with short proboscides a long tubular corolla with a narrow aperture is in fact a mechanical hindrance to access nectar. Also, longer flowers tend to have bigger nectaries and consequently produce more nectar (Ornelas et al. 2007, Castro et al. 2009). Besides, the length and narrowness of the tube may contribute to the storage of higher quantities of nectar because larger flowers can keep bigger volumes of nectar that evaporates at lower rates (Corbet 2003). Thus, larger flowers are a more profitable source of nectar in terms of one single visit.

Several species of *Xylocopa* and *Bombus* are common primary nectar robbers in different plant communities worldwide (Maloof and Inouye 2000, Zhang et al. 2011). Our results reveal that most of the plant species robbed by *Xylocopa violacea*, *X. cubaecola* and *Bombus terrestris*, have tubular corollas that are longer than their tongues (mean tongue length 7.7 mm for *B. terrestris* workers and 9.8 mm for *X. violacea*, Herrera 1989). However, these insects also act as nectar robbers in flowers shorter than their tongues, such as *B. terrestris* in *Fumaria officinalis*, or *X. violacea* in *Echium vulgare*, *Campanula lusitanica* and *Lathyrus latifolius*. The results reveal that in addition to the flower–tongue match other morphological constraints such as body size and the narrowness and orientation of the flower also determine the foraging strategy of these insects.

Hummingbirds are broadly recognized by their harmonious interactions with their nutritious plants. Still, a growing body of evidence reveals that some species regularly perform primary and/or secondary nectar robbing (Navarro 1999, Lara and Ornelas 2001, Maruyama et al. 2015). This evidence indicates that even very specialized nectar robbers (such as flowerpiercers) or specialized pollinators (such as hummingbirds) present a remarkable variability in foraging behaviour changing from legitimate visitors to

nectar robbers depending on their own attributes and the different morphological aspects of the flowers. In these cases, the match between the length of the tube and the length of bird's bill and tongue is important in determining the foraging strategy of birds, the frequency of nectar robbing and the consequences of this visiting behaviour for the reproductive success of tropical plants. Flowerpiercers with shorter, hooked bills rob flowers more frequently than species with longer and less hooked bills (Rojas-Nossa 2007). These birds commonly rob flowers with narrow tubes that are larger than their extended tongues, but perform 'legitimate' visits (i.e. introducing the mandible and the tongue through the entrance of the flower) in plants with shorter flowers. This explains the low levels of nectar robbing found in this study and the high frequency of pollen carryover and the probable pollination by flowerpiercers of Andean plants such as *Clusia multiflora*, *Macleania rupestris* or *Brachyotum strigosum* observed by Rojas-Nossa (2007).

Other morphological traits also explain the levels of nectar robbing, but the direction of the relationship was different for communities with insects or birds as nectar robbers (Table 2). Birds robbed predominantly fleshy and broad flowers from trees, while insects robbed mostly narrow flowers (small diameter / length of the tube) with intermediate aggregation. Trees are particularly robbed by flowerpiercers because they need branches, pedicels or inflorescences strong enough for perching while they forage for nectar, unlike hummingbirds which can rob flowers in hovering flight (Maruyama et al. 2015). In several species there is a positive relationship between the length of the flower and the diameter of the tube, meaning that longer flowers also commonly have broader tubes (Navarro and Medel 2009). However, our results suggest that length and diameter might vary separately in different communities. In the Mediterranean and the Alpine communities both traits were grouped into the same PCA factor, while in the Andean and the Antillean communities they mostly contributed to different factors (Supplementary material Appendix 1 Table A1–A4). This suggests that pollination and robbing by birds could direct selection on diameter regardless of the selection on tube length. Such differences in the patterns among insect-robbed versus bird-robbed plants are related to the idiosyncratic characteristics in foraging behaviour and morphological constraints depending on the floral visitors (including both legitimate visitors and larcenists) from each biogeographical region, and the evolutionary trends on different plant traits imposed by them.

### Energy reward

Besides the morphological constraints that operate on a single flower visit basis, our study reveals that nectar robbing is a phenomenon highly dependent on the density of resources reflecting mechanisms that operate at higher ecological scales. We found positive and significant associations between the nectar volume produced per flower, the density of flowers and the density of energy rewards with the levels of robbing only in those communities in which we examined entire blooming cycles (i.e. Mediterranean and Andes). A similar pattern was also observed in a study conducted in tropical plants, where the number of flowers per hectare was significantly related to the proportion of flowers robbed

by passerines (Rojas-Nossa 2013). The size of floral display (i.e. number of open flowers) and the density of other nectar sources commonly influence the attractiveness to floral visitors affecting the plant's reproductive success (Brys and Jacquemyn 2010, Moreira et al. 2014). For example, Goulson et al. (1998) observed that *Bombus terrestris* visited more inflorescences in plants with larger floral displays. The higher attractiveness of plants that offer concentrated resources is largely explained by the energy economy of floral visitors. Denser resources are easier to detect and the time needed to move between the flowers decreases, thus reducing both the energy investment during foraging and the risks of predation (Eckhart 1991). From the plant's point of view, large and synchronous blooming can be a useful mechanism for reducing the negative impact of nectar robbers. Plants benefit from such strategy because explosive resource abundances can satiate antagonistic larcenists and still attract enough pollinators to sustain pollination service levels. This mechanism is well known in 'masting' species that benefit from the large, synchronous production of seeds and flowers despite the high resource investment made by the plant (Silvertown 1980, Moreira et al. 2014).

We have not found evidence of robbing in any of the species that exhibit either the typical robbing syndrome (i.e. long tubes, with a high density of flowers and energy reward, high nectar production and low to median flower aggregation), or have been reported as robbed somewhere else. For instance, studies in other localities reported nectar robbing in *Hamelia patens* (Lasso and Naranjo 2003), *Aconitum napellus* (Mayer et al. 2014) or *Rhinanthus serotinus* (Kwak 1978). Similar geographical and temporal differences in the levels of robbing were observed in diverse plant species in which insects are the main robbers (Navarro 2000, Utelli and Roy 2001, Irwin and Maloof 2002, Price et al. 2005). Such variations could have different explanations: the local availability of alternative nectar resources, by changes in the abundance of floral visitors during and between seasons or by different sampling effort (Navarro 2000, Irwin et al. 2001).

### Barriers against nectar robbing

A high aggregation of flowers is associated with low nectar robbing in the Mediterranean and the Andean plant communities, which would suggest that this trait constitutes a physical barrier for both insects and birds, because they have difficulties in finding the base of the corolla to rob nectar. Moreover, the presence of long calyxes and bracts are related to low nectar robbing levels by insects in the Mediterranean community. While several authors have suggested that some plants might have mechanical barriers that ward off nectar robbing (Guerrant and Fiedler 1981, Stiles 1981, Lara and Ornelas 2001, Rojas-Nossa 2007), our findings constitute the first community-wide evidence of the association between physical barriers and low levels of primary nectar robbing by both insects and birds.

Inouye (1983) proposed that thick corollas could diminish robbing by bees. We did not find a significant association of the levels of robbing by insects with this floral feature probably because very few plants with thick corollas and profitable nectar rewards were present in the studied communities. Nevertheless, in the Andean community we found the opposite pattern to what would be expected

from Inouye's hypothesis. In this region, thick fleshy flowers (mainly ericads) presented intermediate to high levels of robbing. Therefore, this trait might therefore not be acting as a barrier, but instead might facilitate the manipulation of the flower by perching birds, particularly flowerpiercers. Additionally, considering the fact that *Diglossa lafresnayii* has been observed making scars on the bark of *Baccharis arbutifolia* to drain and drink the sap (Martin et al. 2009), it is clear that not only do these birds have the bill morphology but also a powerful mouth musculature to perforate thick corollas or flowers with long calyxes as shown in Fig. 2g. Also, the presence of latex in floral tissues did not totally reduce nectar robbing by flowerpiercers. Birds apparently have the ability to tolerate secondary compounds in nectar, but high concentrations of alkaloids reduce food preferences and disrupt physiological processes (Tadmor-Melamed et al. 2004). In a different way, consequences for insects-nectar robbers are contrasting, and some secondary compounds have negligible effects (Adler and Irwin 2012), while others reduce nectar robbing (Kessler et al. 2008).

The floral morphology, the large quantity of nectar produced and the abundance of flowers of the Antillean *Rhytidophyllum wrightianum* led us to expect robbing by *Xylocopa cubaecola*, but this was not the case. Several hypotheses might explain the absence of the typical slits made by this robber. One possibility is the presence of constitutive defences, such as the sticky trichomes observed on the corolla, or induced chemical defences in nectar and floral tissues that act as deterrents against nectar robbers. The production of these compounds could be induced by the presence of florivores commonly observed in these plants, as occur in other plant species under herbivory pressure (Adler 2000, Adler and Irwin 2005). Another hypothesis proposed by Irwin et al. (2004) is that the low concentration of sugars in nectar makes the flowers unattractive for hymenopterans without deterring the main pollinators (i.e. vertebrates in this case) adapted to feeding on nectar with lower sugar concentrations (Stiles 1981, Martínez del Río et al. 2001). Also, the flowers of *R. wrightianum* have thick corollas that might represent a mechanical hindrance to insect-robbers as suggested by Inouye (1983). The relative importance of these mechanisms in reducing nectar robbing in this and other plant species and the consequences on the evolution of the plant traits is a promising field to explore.

This study brought up new and interesting points about the global distribution of nectar robbing and its ecological implications. Our results reveal that nectar robbing is a frequent phenomenon in communities of tropical and temperate regions with species having long corollas, abundant nectar production and a high density of energy offered. The length of the tube, the quantity of nectar produced, and the low or medium aggregation of flowers are often positively related to the frequency of robbing by insects and birds. Also, the distribution and abundance of nectar resources in the environment determine the levels of nectar robbing in plants by both animal groups. Other plant traits have opposite effects when robbers are insects or birds. For instance, insects rob more frequently pendent and narrow flowers while birds rob more erect and broad flowers. This is related to differences in foraging behaviour and morphological constraints. Although morphological constraints are

important in determining the strategy of nectar extraction by nectar robbers on a single flower basis, the density of the energy reward in the environment is a relevant trait to explain the levels of nectar robbing observed.

Consequently, nectar robbers are common and relevant participants of the plant–pollinator interactions worldwide. They are potential drivers of the evolution of floral traits and blooming patterns (Irwin et al. 2001, Navarro and Medel 2009) when directly or indirectly cause changes in plant fitness (Maloof and Inouye 2000, Irwin et al. 2010). This study supports previous findings with regard to the importance of floral morphology and flower abundance to determine the frequency of nectar robbing in plants (Lara and Ornelas 2001, Castro et al. 2009, Rojas-Nossa 2013, Maruyama et al. 2015), and provide new community-wide evidences about the main traits associated to nectar robbing. Further experimental research is still necessary to understand mechanisms of compensation and resistance against nectar robbers, such as production of chemical deterrents (Adler and Irwin 2005, 2012, Kessler et al. 2008), to achieve a better knowledge of the implications of floral larceny at broad ecological and evolutionary scales.

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Supplementary material (available online as Appendix oik-02685 at <[www.oikosjournal.org/appendix/oik-02685](http://www.oikosjournal.org/appendix/oik-02685)>). Appendix 1.