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Phenological patterns and pollination network structure in a Venezuelan páramo: a community-scale perspective on plant-animal interactions

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ABSTRACT

Background: Little information is available about life history of páramo plants such as phenology and plant-animal interactions.

Aims: We analysed phenological patterns of flowering and characterised the structure of a plant-pollinator network in a Venezuelan páramo in order to identify key species in this ecosystem.

Methods: We counted the number of individuals with flowers of 76 native plant species and recorded their pollinators in 16 permanent plots between 3000 and 4200 m monthly for three years. We used this dataset to develop a plant-pollinator network, on which nine different metrics related to structural properties were calculated.

Results: The flowering of most species concentrated during the rainy season (between May and November), however some species have continuous flowering. The guild of floral visitors included hummingbirds, flower piercers, bumblebees, Diptera and Lepidoptera. The plant – flower visitor interaction network did not exhibit nestedness, but showed a significant specialization index (H2) and high values of functional complementarity.

Conclusions: Páramo plants have the capacity of maintaining a resident nectarivorous fauna (bumblebees and hummingbirds) because of continuous flower offer during the year. However, the plant – pollinator network identified could be very sensitive to the loss component species, owing to high levels of specialisation and functional complementarity.

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Introduction

The páramos are tropical alpine ecosystems, dominated by grassland and shrublands, distributed between 3000 and 4800 m along the Northern Andes (Monasterio 1980). These ecosystems can be considered as ‘islands’ in the highest reaches of the humid tropical Andes (North of Peru, Ecuador, Colombia and Venezuela), together constituting a continental archipelago, surrounded by montane forests (Luteyn 1999). During its relatively short evolutionary history (less than 4 million years), the páramo biota had to adapt to the unique environmental conditions of the cold tropics including high daily thermal variability, highly variable cloud cover, high solar radiation loads and low partial pressures of O₂ and CO₂ (Altshuler and Dudley 2006; Azócar and Rada 2006; Dillon et al. 2006). This coupled with their insular distribution and the influence of glacial and periglacial processes during the Quaternary, has resulted in remarkable evolutionary dynamics, such as high speciation rates

and evolutionary convergence, particularly well documented for the flora (Hedberg and Hedberg 1979; Monasterio and Sarmiento 1991; Madriñán et al. 2013; Llambí et al. 2013).

From a conservation perspective, facing the challenges that climate and land use changes impose, requires detailed knowledge of the ecological functions that species play within communities (McConkey and O’Farrill 2015; Valiente-Banuet et al. 2015). Even though most studies on the biodiversity of ecosystems have focused on species richness, Valiente-Banuet et al. (2015) have emphasised the relevance of considering species interactions as critical indicators of ecosystem health as well as to understand ecosystem functioning. Knowledge on the interactions between species from an ecological and evolutionary perspective is a key aspect in both the management and conservation of protected areas. The loss of ecological interactions may have pervasive effects, accelerating local species extinctions and the decay of ecosystem functions, which could ultimately induce a collapse in ecosystem services provided to human populations (Díaz et al. 2013; Valiente-Banuet et al. 2015).

Published research on plant-animal interactions in the páramos of South America is scarce and geographically biased (37 studies, Table S1). Most studies (46%) cover the páramos of Venezuela, while 38% correspond to Colombia and 16% to Ecuador. These studies include analyses of herbivory, seed dispersal and pollination. They involve 211 species of plants belonging to 47 families, while the animals include 30 vertebrates (Aves: Fringillidae, Thraupidae, Trochilidae, Turdidae; Mammalia: Cervidae, Leporidae, Rodentia, Tapiridae, Ursidae), four bumblebees and an indeterminate number of other insects including Lepidoptera, Diptera and Coleoptera in both adult and larval stages (Table S2).

Studies on herbivory by native fauna in the páramos, although few, include a broad spectrum of taxa ranging from vertebrates (*Tremarctos ornatus*, *Tapirus pinchaque*, *Sylvilagus brasiliensis*, *Odocoileus virginianus*, hummingbirds and flower piercers). Insect herbivory includes several species of Coleoptera and Lepidoptera (Table S2). Most of this research has focused on describing the diet of the animal, and all refer to leaf herbivory. In all cases, the effect described on the plants is negative. The studies describing foliar herbivory by insects have mainly focused on the emblematic giant rosettes (*Espeletia* spp.) of the Asteraceae (Lamotte et al. 1989; Sturm 1990; Fagua and Bonilla 2005).

Regarding seed dispersal, Melcher et al. (2000) have predicted that, based on the morphological characteristics of seeds, a high number of páramo species must be dispersed by animals. Posada (2014) and Velasco-Linares and Vargas (2007) have described *Turdus fuscater* (Turdidae) dispersing seeds of fleshy-fruited shrubs such as *Vaccinium floribundum*, *Gaultheria myrsinoides* and *Cestrum buxifolium*. Molinillo and Brener (1993) have found that cattle (*Bos taurus*) disperse seeds of *Acaena elongata* in a Venezuelan páramo. Based on dispersal syndromes, van der Pijl (1982) and Posada (2014) have reported that species that are poor colonisers of disturbed areas in the páramo have predominantly zoochorous dispersal. The shortage of perches for frugivorous birds has been argued as a possible cause for the lack of endozoochorous dispersal (Posada 2014; see also Bueno and Llambí 2015). Finally, although seeds have been found in the diet of some mammals (Lizcano and Cavelier 2004), their impact on the dynamics of regeneration of these plants has not been evaluated yet.

Regarding pollination, the available research indicates that among the diurnal pollinators of

páramo plants, hummingbirds are the most abundant taxonomic group, with 16 species described as floral visitors. Bumblebees, with four species, lead the group of Hymenoptera identified, although a number of Lepidoptera, Diptera and Coleoptera have also been observed (Table S2). It is noteworthy that some species of flower piercers (*Diglossa* spp.) have been observed among the Thraupidae. Fagua and González (2007) have found that the contribution of nocturnal pollination to seed production in *Espeletia grandiflora*, albeit low, was significant. However, to our knowledge, there are no previous studies of pollination interactions and the dynamics of flower production (plant phenology) at the community level in the páramos.

The study of ecological interactions through complex networks, allows analysing ecological properties such as the interdependence of the components of the network (e.g. plants and pollinators or seed dispersers). Thus, by calculating metrics such as connectance, the degree of association between species can be assessed; other metrics such as nesting, allow to evaluate the robustness of the system to the loss of species, while the indices of specialisation and complementarity provide a measure of the degree of interdependence of the species that make up the network (Jordano 1987; Bascompte et al. 2006; Blüthgen et al. 2006, 2007; Burgos et al. 2007; Tylianakis et al. 2007; Almeida-Neto and Ulrich 2011; Devoto et al. 2012; Dormann and Strauss 2014).

Analysing the patterns of annual flowering of the plants of the páramos as well as the interactions they establish with their pollinators thus forming networks, allows identifying keystone species and at the same time assess their sensitivity to global changes. Here we analyse the phenological patterns of flowering and characterised the structure of the plant-pollinator network in a Venezuelan páramo. Based on the results of this study, we formulated some general hypotheses that could be tested as more detailed and less geographically restricted data become available.

Materials and methods

Study area

We selected an elevation gradient in a páramo in the upper watersheds of the Chama, Motatán and Santo Domingo rivers in the Sierra Nevada and the Sierra de La Culata mountain ranges of the Cordillera de Mérida, Venezuela. The study area is within the largest páramo complex in the country and extends

62,868 ha. Our study gradient ranged from 3000 to 4200 m a.s.l. (Figure 1), in which the alpine belt (locally known as the Andean páramo) extends between 3000 and 3900 and the subnival belt (locally known as high Andean páramo or superpáramo) extends between 3900–4200 m. In a typical Andean páramo site at 3550 m (Mucubají weather station) annual average temperature is 5.4°C, and minimum temperature can drop below freezing at night, particularly during the dry season. Within this belt, precipitation can range between 800 mm in the Chama and Motatán watersheds and 1800 mm in the Santo Domingo watershed. The relief is characterised by glacier modelling (moraines and U-shaped valleys) and vegetation varies from pure shrublands towards lower elevations, through rosette-shrublands and giant rosette dominated communities depending on elevation, drainage and other environmental factors (Monasterio 1980). In the high Andean páramo, annual average temperature ranges between 2.5 and –2°C and annual precipitations range between 800 and 1200 mm. There are recurrent daily cycles of freezing and thawing, which affect the superficial soil layers and induce soil instability. Within this belt two types of vegetation can be distinguished: (a) the

desert páramo, dominated by scattered giant rosettes (genus *Espeletia*) together with a lower stratum dominated by cushion plants, acaulescent rosettes, low shrubs, tussock grasses and herbs; and (b) the periglacial desert, where plant cover is normally less than 10%, and where cushion plants, and small grasses and herbs are dominant (Monasterio 1980).

Flowering phenology

We established 16 permanent plots of 50 m² (5 m x 10 m), eight in the Andean páramo belt and eight in the high Andean páramo belt. The vegetation physiognomy and the dominant species of flowering plants in each plot are indicated in Table 1. In each plot we counted the number of individuals with flowers of all native plant species every month for three years (2013 to 2015). We did not consider graminoid or alien plant species. To analyse the monthly patterns in the dynamics of flowering we accumulated the monthly relative frequency of the number of flowering individuals per species of plant during the three years of sampling. With the data on flowering phenology we calculated a phenological overlap index among species, to analyse the degree of synchrony of flowering for

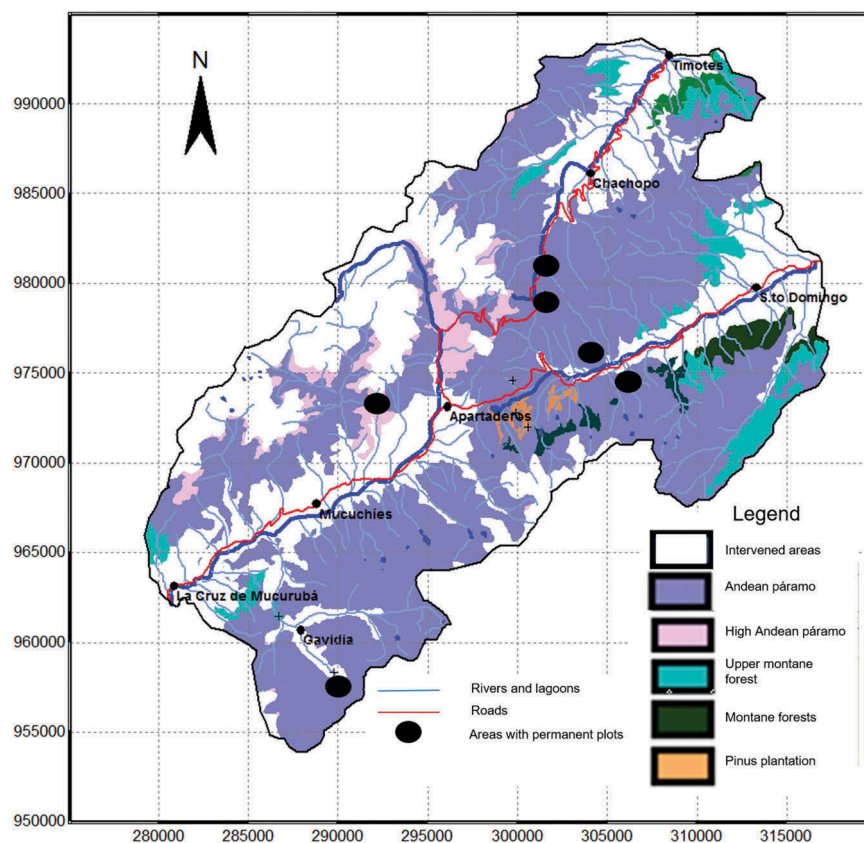


Figure 1. Location of the study area in the upper sections of the Chama, Motatán and Santo Domingo Watersheds, Mérida State, Venezuela. Sampling areas are indicated by ovals. Vegetation types are after Josse et al. (2009). UTM coordinate system.

Table 1. Characteristics of the vegetation in the 16 plots used for sampling flowering phenology in the páramo, Merida, Venezuelan Andes.

Ecosystem	Elevation (m)	Dominant plant species observed with flowers
Andean páramo	3025	<i>Espeletia schultzii</i> , <i>Sisyrinchium tinctorium</i> , <i>Lupinus meridanus</i> , <i>Hypericum laricifolium</i> , <i>Orthrosanthus chimboracensis</i> , <i>Oenothera epilobiifolia</i> , <i>Castilleja fissifolia</i> , <i>Geranium chamaense</i> and <i>Bidens triplernervia</i>
	3025	<i>Espeletia schultzii</i> , <i>Sisyrinchium tinctorium</i> , <i>Lupinus meridanus</i> , <i>Hypericum laricifolium</i> , <i>Orthrosanthus chimboracensis</i> , <i>Oenothera epilobiifolia</i> , <i>Castilleja fissifolia</i> , <i>Geranium chamaense</i> , <i>Bidens triplernervia</i> and <i>Hesperomeles obtusifolia</i>
	3255	<i>Stevia elatior</i> , <i>Orthrosanthus chimboracensis</i> , <i>Espeletia schultzii</i> , <i>Hieracium erianthum</i> , <i>Oenothera epilobiifolia</i> , <i>Sisyrinchium tinctorium</i> and <i>Gaultheria myrsinoides</i>
	3255	<i>Stevia elatior</i> , <i>Orthrosanthus chimboracensis</i> , <i>Espeletia schultzii</i> , <i>Hieracium erianthum</i> , <i>Oenothera epilobiifolia</i> , <i>Sisyrinchium tinctorium</i> and <i>Gaultheria myrsinoides</i>
	3605	<i>Eleutherine bulbosa</i> , <i>Sisyrinchium tinctorium</i> , <i>Lachemilla orbiculata</i> , <i>Hypericum juniperinum</i> , <i>Epilobium denticulatum</i> , <i>Noticastrum marginatum</i> , <i>Bartsia laniflora</i> , <i>Erodium cicutarium</i> , <i>Acaena elongata</i> and <i>Veronica serpyllifolia</i>
	3605	<i>Noticastrum marginatum</i> , <i>Stevia elatior</i> , <i>Eleutherine bulbosa</i> , <i>Oenothera epilobiifolia</i> , <i>Oenothera epilobiifolia</i> , <i>Veronica serpyllifolia</i> , <i>Stevia lucida</i> , <i>Sisyrinchium tinctorium</i> , <i>Oxalis spiralis</i> , <i>Acaulmalva acaulis</i> , <i>Lachemilla ophanoides</i> , <i>Geranium multiceps</i> and <i>Myosmodes brevis</i>
	3630	<i>Hypericum laricifolium</i> , <i>Espeletia schultzii</i> , <i>Stevia elatior</i> , <i>Lupinus meridanus</i> , <i>Chaetolepis lindeniana</i> , <i>Baccharis prunifolia</i> , <i>Bidens triplernervia</i> , <i>Gaultheria myrsinoides</i> and <i>Oenothera epilobiifolia</i>
	3630	<i>Hypericum laricifolium</i> , <i>Espeletia schultzii</i> , <i>Stevia elatior</i> , <i>Lupinus meridanus</i> , <i>Chaetolepis lindeniana</i> , <i>Baccharis prunifolia</i> , <i>Bidens triplernervia</i> , <i>Gaultheria myrsinoides</i> , <i>Bartsia laniflora</i> and <i>Echeveria bicolor</i>
	3905	<i>Pentacalia andicola</i> , <i>Bidens triplernervia</i> , <i>Geranium chamaense</i> , <i>Hypericum laricifolium</i> , <i>Espeletia schultzii</i> , <i>Stevia lucida</i> , <i>Acaena cylindristachya</i> and <i>Sisyrinchium tinctorium</i>
	3905	<i>Geranium chamaense</i> , <i>Hypericum laricifolium</i> , <i>Castilleja fissifolia</i> , <i>Bidens triplernervia</i> , <i>Espeletia schultzii</i> , <i>Vaccinium floribundum</i> , <i>Centranthus calceitrapa</i> and <i>Hinterhubera columbica</i>
High Andean páramo	3980	<i>Hypericum laricifolium</i> , <i>Castilleja fissifolia</i> , <i>Centranthus calceitrapa</i> , <i>Geranium chamaense</i> , <i>Draba pulvinata</i> , <i>Arcytophyllum nitidum</i> , <i>Lachemilla polyplepis</i> and <i>Lasiocephalus longipencilatus</i>
	3980	<i>Geranium chamaense</i> , <i>Hypericum laricifolium</i> , <i>Castilleja fissifolia</i> , <i>Bidens triplernervia</i> , <i>Espeletia schultzii</i> , <i>Vaccinium floribundum</i> , <i>Centranthus calceitrapa</i> and <i>Hinterhubera columbica</i> , <i>Lachemilla polyplepis</i> , <i>Centranthus calceitrapa</i> , <i>Draba pulvinata</i> , <i>Lobelia tenera</i>
	4170	<i>Castilleja fissifolia</i> , <i>Hypochaeris setosa</i> , <i>Hypericum laricifolium</i> , <i>Lasiocephalus longipencilatus</i> , <i>Oenothera epilobiifolia</i> , <i>Senecio wedgicalis</i> , <i>Arenaria musciformis</i> , <i>Pluchea bifloris</i> , <i>Espeletia schultzii</i> and <i>Sisyrinchium tinctorium</i>
	4170	<i>Castilleja fissifolia</i> , <i>Hypochaeris setosa</i> , <i>Hypericum laricifolium</i> , <i>Oenothera epilobiifolia</i> , <i>Senecio wedgicalis</i> and <i>Espeletia schultzii</i>
	4212	<i>Coespeletia timotensis</i> , <i>Castilleja fissifolia</i> , <i>Pluchea bifloris</i> , <i>Echeveria bicolor</i> , <i>Hypericum laricifolium</i> , <i>Senecio wedgicalis</i> and <i>Oenothera epilobiifolia</i>
	4212	<i>Coespeletia timotensis</i> , <i>Castilleja fissifolia</i> , <i>Pluchea bifloris</i> , <i>Hypericum laricifolium</i> , <i>Oxylobus glanduliferus</i> , <i>Pentacalia apiculata</i> , <i>Senecio wedgicalis</i> and <i>Sisyrinchium tinctorium</i>

the different species in the community (Primack 1985; Arroyo 1988). We analysed the flowering phenology of each species without discriminating by elevation belt, because most of the species have a wide elevation range of distribution (Briceño and Morillo 2002). Plant names used follow accepted names in the Plant List (<http://www.theplantlist.org>). Botanical voucher specimens were deposited in the MER Herbarium, Universidad de Los Andes, Mérida, Venezuela.

Plant-pollinator network in the páramo of venezuela

We carried out focal observations for periods of 10 minutes in each plot, for a total effort to 360 min/plot, in order to record pollinators, considering only those floral visitors that contacted reproductive structures on flowers. The censuses were conducted on sunny days, between 06:00am and 06:00pm. Flower visitors were identified to the species level for birds and bumblebees and to the level of order for other invertebrates (distinguishing the different morphospecies in this case). Birds were identified by visual comparison with the guide of birds of Venezuela (Hilty 2003), while insects were compared with the reference collection of Pelayo et al. (2015). The range of their geographic and elevation distribution was characterised by searches in the GBIF database. Based on this information, species were classified as endemic of páramo eco-systems or not (Table S3).

Rarefaction curves and the Chao 2 richness index were calculated for plants, pollinators and plant-pollinator interactions using EstimateS 9.1.0 (Colwell 2013), with the purpose of evaluating if the sampling was complete. Because the number of pollinators registered in the plots was too low to allow an independent analysis at each plot, and because the plants visited presented a wide elevational distribution (Briceño and Morillo 2002), we summarised the interactions across the whole elevation gradient sampled as a single bipartite matrix (, where each cell was filled with the frequency of the pair-wise interaction between a plant and a pollinator. Based on this matrix, we developed a plant-pollinator network for the whole elevation gradient, and calculated its structural properties by means of the following metrics: degree of a species (Bascompte et al. 2006), connectance (Jordano 1987), weighted connectance (Tylianakis et al. 2007), weighted nestedness metric based on overlap and decreasing fill (NODF; Almeida-Neto and Ulrich 2011), interaction strength asymmetry

(dependence Bascompte et al. 2006; Blüthgen et al. 2007), specialisation complementarity index (H2; Blüthgen et al. 2006), robustness (Burgos et al. 2007), functional complementarity (Devoto et al. 2012) and modularity (Dormann and Strauss 2014). Calculations of network metrics were conducted with the bipartite package (Dormann et al. 2008) in R (R Development Core Team 2016). Significance of weighted connectance, weighted NODF, H2, and robustness were tested by comparing empirical values vs. a null model (10,000 repetitions of similar dimension network) in R.

Results

Flowering phenology

We collected information on the phenology of flowering of 76 species, belonging to 30 families. The most species-rich families were the Asteraceae (23 species) and the Rosaceae (9), followed by the Apiaceae, Caryophyllaceae, Geraniaceae and Iridaceae, with three species each (Figure 2).

Most species flowered in the wet season; some of them with periods of explosive blooming limited to a single month per year (Figure 2), without overlapping with each other during their flowering periods. Other species, such as *Castilleja fissifolia* and *Eleutherine bulbosa* showed continuous flowering. There were also species of plants that flowered in the dry season, including *Pluchea biformis* and *Lachemilla ramosissima*. The rest of the species showed a long bloom period, except in the dry months, or peaks of bloom at the beginning and at the end of the rainy season. The phenological overlap index between plant species was 0.25, showing, in general, little synchrony in flowering among species.

Plant – pollinator network

Of the 76 species recorded in our study plots which produced flowers, 29 were included in the pollination network (Figure 3); the rest were excluded because they were not visited during our observations. The number of plants included in the pollination network was within the 95% confidence interval of the Chao 2 richness index, suggesting that the sampling was complete; in the case of pollinators, no saturation was reached (Figure 4). The 96 h of observations carried out during 3 years yielded a total of 145 visits (77 interactions), an estimated 20.4% of the total possible interactions

(Total number of plants multiplied by total number of animals in the network; Figure 4). However, to perform this calculation, forbidden interactions were not considered for morphological mismatch, phenological or behavioural incompatibility (Olesen et al. 2010).

The guild of floral visitors observed covered taxa as diverse as hummingbirds (six species), flower piercers (1), bumblebees (2), Diptera (2) or Lepidoptera (2). Hummingbirds, with 43.5% of the interactions, were the most frequent morphotype of floral visitors. Two bumblebees (*Bombus rohweri* and *B. rubicundus*) accounted for 36.5% of the visits, whereas the flower piercer *Diglossa gloriosa* contributed 9%, the rest being distributed between two morphospecies of Diptera and two Lepidoptera (4.1 and 6.9%, respectively) (Table S3). By species, the greatest number of records corresponded, in order of importance, to *Bombus rohweri* (Apidae, 23.5%), *Oxygogon lindenii* (Trochilidae, 15.9%), *Bombus rubicundus* (13%), *Metallura tyrianthina* (Trochilidae, 11.7%) and *Colibri coruscans* (Trochilidae, 11.0%). Among the rest, the flower piercer *Diglossa gloriosa* (Thraupidae), carried out 9% of the visits recorded. The rest of the morphospecies together contributed to less than 16% of the visits (Figure 3).

The interaction network was dominated by the bumblebees *B. rohweri* and *B. rubicundus* with 20 and 13 connections, respectively; whereas the hummingbirds *Oxygogon lindenii* and *Metallura tyrianthina* had values of 11 and 12, respectively. Among plants, *Vaccinium floribundum* and *Castilleja fissifolia*, with 8 and 6 connections each, were most connected. The plant-flower visitor interaction network showed a significant specialisation (H2), although the value was relatively low (Table 2). This network exhibited low values of connectance, asymmetry and nestedness, and high values of functional complementarity, with the robustness being non-significant.

Of the 76 species of plants, 36 (48%) were endemic to the páramo and of the 29 plant species with pollinator records, 11 species (38%) were endemic. Finally, we found that five species of pollinators were páramo endemics (Table S3).

Discussion

We found a high number of species with a marked flowering peak in the dry season, as well as few with a continuous flowering, guaranteeing permanent offer of resources for the resident nectarivorous fauna. The main pollinators are hummingbirds and bumblebees,

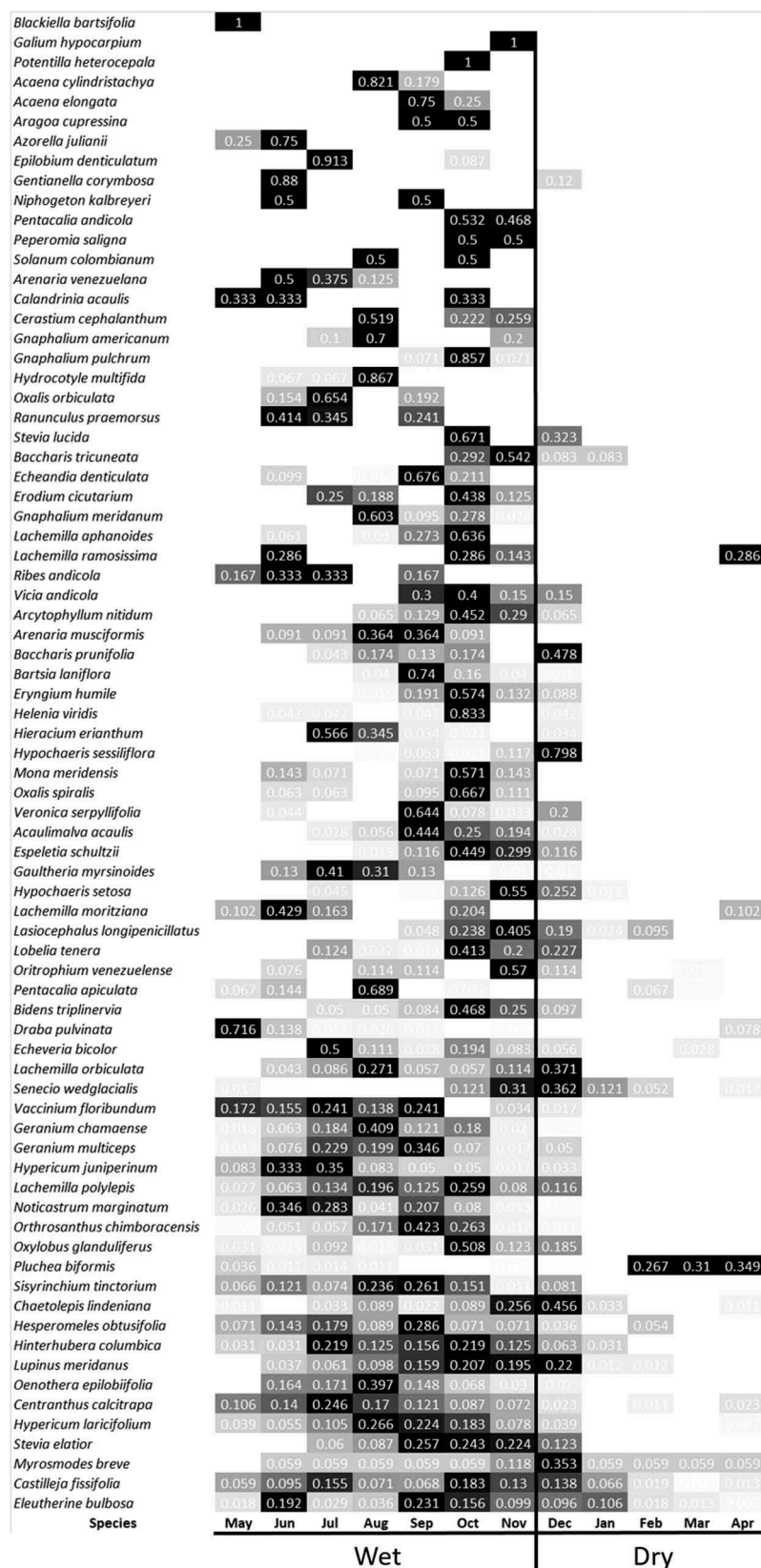


Figure 2. Relative monthly frequency of the number of individuals with flowers per species of plant accumulated during the three years of sampling in a Venezuelan páramo, Chama, Motatán and Santo Domingo Watersheds, Mérida State, Venezuela. The wet and dry season months are indicated. The shading scale represents the intensity of the bloom from white (no flowers) to black (high frequency of flowering plants).

being the most frequent floral visitors and interacting with a large number of plant species.

Seasonality in the flowering of páramo plants, with abundant flowering in the wet season, agrees with

patterns reported for some individual species in other páramos (Velez et al. 1998; Gutiérrez-Z et al. 2004; Fagua and Bonilla 2005). However, the low value of the phenological overlap index across all species

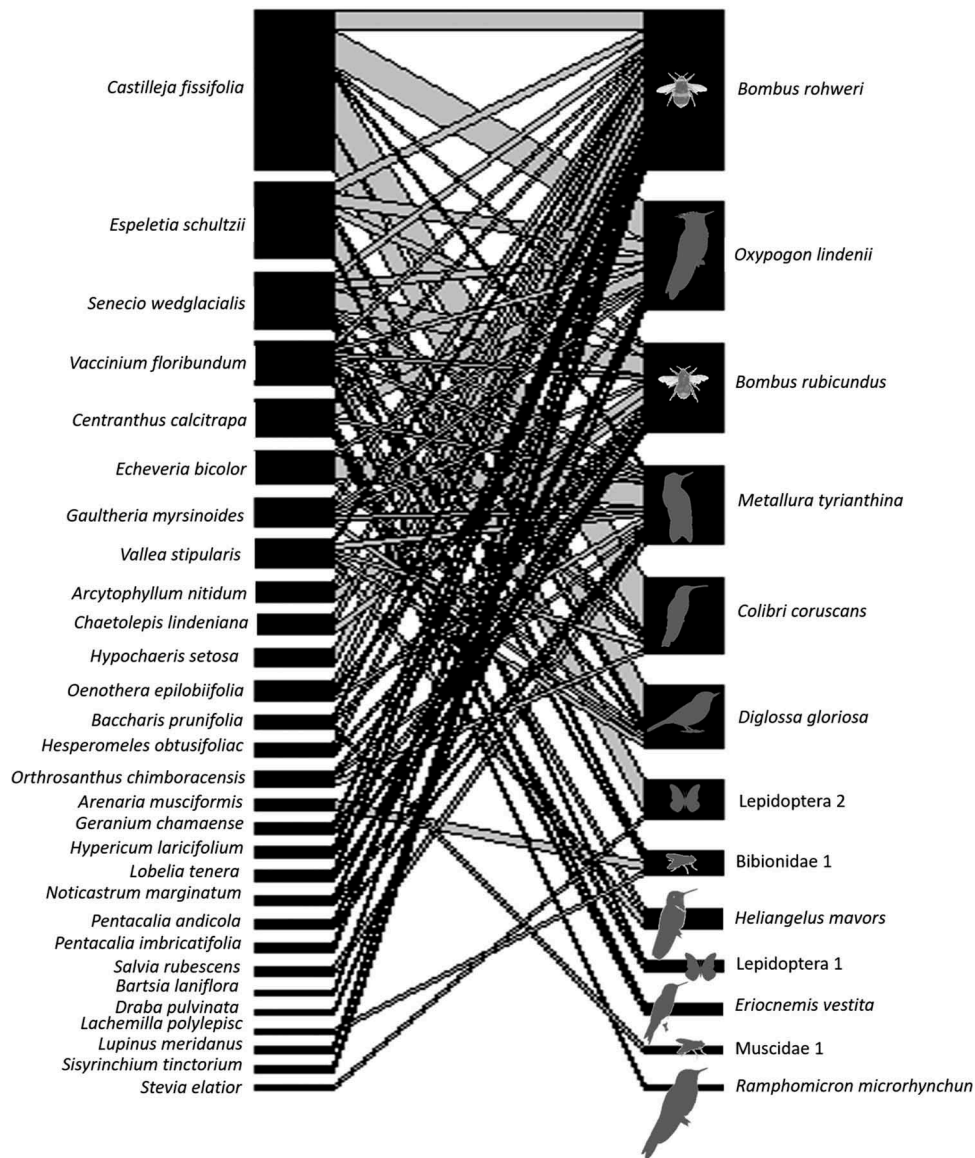


Figure 3. Pollination network of animals and plants in a Venezuelan páramo, Chama, Motatán and Santo Domingo Watersheds, Mérida State, Venezuela. The thickness of the links represent the intensity of the interaction (visitation frequency). The size of the rectangles represents the relative importance of the species in the network (in terms of the number and intensity of its interactions with other species).

could be interpreted as a mechanism to minimise competition between plant species in conditions of low availability of pollinators and low visitation frequencies (Waser 1983), as was the case in our study area. Bawa (1983) has suggested that the main selective pressure affecting the length and synchrony of the flowering period was pollinator availability. Synchronic flowering over a short period may reflect competition for pollinators: the resources are used to attract opportunist pollinators that show density-dependent foraging (Janzen 1967; Augspurger 1983; Handel 1983; Schmitt 1983). This does not seem to be the case in our study region. The native species that produce floral rewards distribute their flowering throughout the year. This could promote the stable presence and maintenance of floral visitors

throughout the year and probably reduces competition for pollinators. Moreover, the analysis of the flowering phenology in these páramos, suggest that *Castilleja fissifolia* and *Eleutherine bulbosa*, which showed continuous flowering throughout the year, act as keystone species for the maintenance of the guild of pollinators under seasonal drought conditions, such as those prevalent in the Venezuelan páramos.

Although a high proportion of plants in the páramo require animal pollination (Berry 1986; Sobrevila 1986, 1989; Ricardi et al. 1987; Berry and Calvo 1989; Fagua and Bonilla 2005), our knowledge on this mutualistic interaction is, in general, poor. The whole taxonomic diversity of pollinators observed is generally low when compared with that

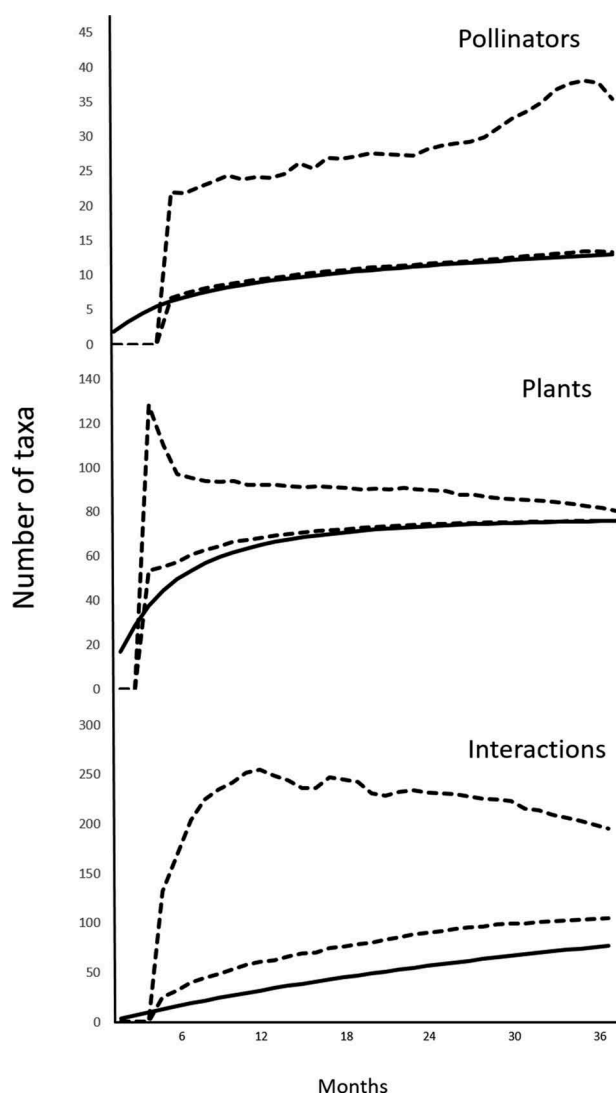


Figure 4. Rarefaction curves (Cole index, black line) and confidence intervals (95%) of the Chao 2 richness index (dotted line) for plants, pollinator and plant-pollinator interactions in a Venezuelan páramo, Chama, Motatán and Santo Domingo Watersheds, Mérida State, Venezuela. The sampling effort along the x axis corresponds to the number of months of observation.

Table 2. Structural properties of a pollination network in a Venezuelan páramo, Chama, Motatán and Santo Domingo Watersheds, Mérida State, Venezuela. Statistical significance compared to null model: ** $P < 0.001$; * $P \leq 0.05$; ns (not significant) $P > 0.05$.

Network Index	Value
Grade plants	1 and 8
Grade pollinators	1 and 20
Connectance	21,49
Weighted connectance	0.15 NS
Weighted NODF	13.82 NS
Web asymmetry	0,381
Interaction strength asymmetry (Dependence Bascompte et al. 2006)	-0,0638
H2	0.30 **
Robustness	0.91 NS
Robustness to pollinator extinction	0,76
Robustness to plant extinction	0,68
Functional complementarity of plants	83,66
Functional complementarity of pollinators	68,65
Modularity	0,42
Number of modules	5

observed in lowland Neotropical communities (see Ramirez and Brito 1992 for an example in the lowlands of Venezuela). This low taxonomic diversity among pollinators in our study region could be explained, at least partially, by the difficult conditions for animal life in these high mountain ecosystems (Totland 2001). Not all organisms are able to forage at these elevations. The environmental characteristics of high mountain environments greatly limit the spectrum of floral visitors to few organisms physiologically adapted for life in these unique cold tropical habitats (Wolf et al. 1976; Schondube and Martínez Del 2004). In fact, Gómez-Murillo and Cuartas-Hernández (2016) found that flower-visitor diversity decreased with elevation in a tropical mountain forest in Colombia.

Given the harsh climatic conditions of high mountain ecosystems, it is expected that pollinator assembly could be drastically different from those of nearby lowlands (Totland 2001). Although preliminary, our results do not coincide with predictions for other alpine communities (Arroyo et al. 1982), which indicate a predominance of low energy demanding species like Diptera as the main flower visitors. Animals with high metabolic rates, such as hummingbirds, are the main floral visitors in our study area and other páramos studied; they are followed by bumblebees, which also have higher energy requirements than Diptera. However, unlike temperate alpine ecosystems, the occurrence of a permanent set of floral resources throughout the year in our páramo studied could favour the permanent presence of this assemblage of visitors with a high-energy demand. This is an aspect that will require more detailed study in the future. Published studies indicate that generalist pollination systems prevail in the páramos (Berry 1986; Fagua and Bonilla 2005; Pelayo et al. 2015). However, future studies should address aspects related to the efficiency of different floral visitors (Schemske and Horvitz 1984; Rodríguez-Rodríguez et al. 2013).

In spite of the hummingbirds being the main pollinators in our study area and in most of the studied plant species in the páramos, many other taxa participate in pollination interactions. For example, the pollinator guild of some widespread and abundant species in the South American páramos such as *Bejaria resinosa* (Kraemer 2001), *Espeletia corymbosa*

(Sturm 1990), *E. grandiflora* (Fagua and Bonilla 2005; Fagua and González 2007) or *E. schultzei* (Berry 1986; Sobrevila 1988; Pelayo et al. 2015), include not only hummingbirds but a considerable number of Hymenoptera, Diptera, Lepidoptera or Coleoptera, all of them with large differences from a functional perspective (Table S3).

The network of plants and pollinators studied by us in the northern páramos of Mérida is the first one studied for these ecosystems. Only three out of the 21 pollination networks (from temperate ecosystems in Europe and North America) analysed by Blüthgen et al. (2007) had a degree of specialisation H_2 as low as that found in the network analysed in this study. Even so, our network exhibited values of connectance and asymmetry similar to those found for alpine and temperate pollination networks (Olesen and Jordano 2002; Santamaría et al. 2014). However, the studies in temperate alpine systems have also reported a high degree of nestedness (Dupont et al. 2003), which was not the case in our study system. Our data match the lack of nestedness found by Ramos-Jiliberto et al. (2010) in the Chilean Andes. This may be due to the relatively few species of plants and animals that make up the network (Bascompte et al. 2003) and the decrease in pollinator/plant ratio along elevation (Medan et al. 2002; Ramos-Jiliberto et al. 2010; Trøjsgaard and Olesen 2013). It is probable that the non-significance of robustness in our network is due to the lack of nestedness, as the two metrics are positively correlated (Santamaría et al. 2014).

Considering the low availability of pollinators and of visits typically received at high elevations (e.g., Arroyo et al. 1985; Totland 2001), both a high degree of generalisation and high niche overlap are expected for harsh and variable alpine environments (MacArthur 1955; Fagua and González 2007). However, our results suggest the coexistence of some species of generalist plants and pollinators, with an important component of specialists, as in other plant/pollinator networks in the Peruvian Andes (Watts et al. 2016). For these reasons and because of the high degree of endemism, the plant – pollinator system in the páramos could be very vulnerable to the loss of some of its components (Valiente-Banuet et al. 2015). Specialised systems have been considered to be sensitive to global change (Gilman et al. 2010). Moreover, the species of *Bombus* found in our study area, which are typically adapted to cold conditions, could be particularly susceptible to climate change, and, in turn, disrupting their interactions with plants (Miller-Struttmann et al. 2015).

Conclusions and future research avenues

Páramo plants have the capacity of maintaining a resident nectarivorous fauna, because of their continuous offer of flowers throughout the year. This vegetation supports a network of interdependent relationships with animals that use them as food resources. In this way, many of these organisms are involved in key ecological processes such as pollination and seed dispersal.

Bumblebees and hummingbirds are essential for pollination in the studied páramos. The of plant – pollinator networks in these páramos could be very sensitive to the loss of component species because of their high levels of specialisation and functional complementarity.

However, there are still large information gaps that need to be explored both in terms of scope (e.g. at the community level) and detail. To further our mechanistic understanding of the ecological role played by plant-animal interactions include establishing if: (1) páramo plants show generalised and self-independent syndromes or reproductive mechanisms, (2) there is pollen or seed dispersal limitations in the páramos and if they translate into an overall lower plant genetic diversity and higher genetic differentiation, (3) animals that participate in interactions with plants in the páramos show different metabolic adaptations from those that inhabit lower elevation ecosystems, (4) the diversity of mutualists visiting a particular plant species generally lower in the páramo than in lowland ecosystems where the species is found?, (5) páramo mutualists are more generalists than their lowland counterparts, and if (6) the effects of landscape changes on mutualist diversity and abundance, and subsequently on plant reproductive success, higher in the páramos than in lowland ecosystems. Is this linked to a lower functional redundancy in the páramos?

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Disclosure statement

No potential conflict of interest was reported by the authors.

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