



Blooming plant species diversity patterns in two adjacent Costa Rican highland ecosystems

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ABSTRACT

The Costa Rican Paramo is a unique ecosystem with high levels of endemism that is geographically isolated from the Andean Paramos. Paramo ecosystems occur above Montane Forests, below the permanent snow level, and their vegetation differs notably from that of adjacent Montane Forests. We compared the composition and beta diversity of blooming plant species using phenological data from functional plant groups (*i.e.*, insect-visited, bird-visited and insect + bird-visited plants) between a Paramo and a Montane Forest site in Costa Rica and analyzed seasonal changes in blooming plant diversity between the rainy and dry seasons. Species richness was higher in the Montane Forest for all plant categories, except for insect-visited plants, which was higher in the Paramo. Beta diversity and blooming plant composition differed between both ecosystems and seasons. Differences in species richness and beta diversity between Paramo and the adjacent Montane Forest are likely the result of dispersal events that occurred during the last glacial period and subsequent isolation, as climate turned to tropical conditions after the Pleistocene, and to stressful abiotic conditions in the Paramo ecosystem that limit species establishment. Differences in blooming plant composition between both ecosystems and seasons are likely attributed to differential effects of climatic cues triggering the flowering events in each ecosystem, but phylogenetic conservatism cannot be discarded. Analyses of species composition and richness based on flowering phenology data are useful to evaluate potential floral resources for floral visitors (insects and birds) and how these resources change spatially and temporarily in endangered ecosystems such as the Paramo.

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page 10

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INTRODUCTION

A notable characteristic of tropical highland landscapes is the presence of well defined ecotones between adjacent ecosystems at high elevations (*Vuilleumier & Simberloff, 1980*;

Sarmiento, 2021). This sudden change in the vegetation physiognomy is attributed mainly to differences in climatic and edaphic conditions (*Luteyn, 2005*). The highest mountain environments above the treeline are unsuitable habitats for most organisms that inhabit adjacent tropical forests at lower elevations (*Luteyn, 2005; Körner, 2021*). It has been suggested that changes in the composition of plant communities along altitudinal gradients may be determined by environmental filtering, since increasing altitudes are often associated with harsh conditions for life (*Laiolo & Obeso, 2017*). Hence, only a relatively low number of species have been capable of adapting to the prevailing abiotic conditions at high altitudes, resulting in a general decline in species richness but an increase in endemism (*Billings, 1974; Rada, Azócar & García-Núñez, 2019; Madriñán, Cortés & Richardson, 2013*). In the Neotropics, the Paramo exemplifies a high elevation ecosystem; this habitat is typically composed of low herbaceous and shrubby vegetation whose physiognomy drastically contrasts with the arboreal vegetation that dominates the adjacent Montane Forests (*Smith & Young, 1987; Luteyn, 2005*).

Most of the neotropical Paramos (including the Puna) are found in South America and cover a large proportion of the highlands of the Andes mountain range (*Madriñán, Cortés & Richardson, 2013*). In Central America, the Paramo vegetation is restricted to highly isolated and small natural fragments on the highlands of the Talamanca mountain range that extends from Costa Rica to western Panama (*Kappelle & Horn, 2016*). As a result, South American Paramos have been the focus of research on a variety of topics, including plant physiology (*Rada, Azócar & García-Núñez, 2019*), avian evolution (*Vuilleumier, 1969*), vegetation (*Valencia et al., 2018*) and butterfly distribution (*Pyrz et al., 2016*); whereas research in Central American Paramo ecosystem is still limited (*Körner, 2021*). A book published by *Kappelle & Horn (2005)* included information on the natural history of many taxa from the Costa Rican Paramo, but information on the ecology and evolution of most taxonomic groups was anecdotal or based on non-systematic samplings.

The species diversity turnover of plants and other taxonomic groups along altitudinal gradients has been studied worldwide and, in general, richness in all groups decreases with elevation, but endemism increases (*Wolda, 1987; Navarro, 1992; Lieberman et al., 1996; Vetaas & Grytnes, 2002; Khuroo et al., 2011; Steinbauer et al., 2016; Monro, Bystrikova & Gonzalez, 2017*). There are also changes in abiotic conditions such as a reduction in availability of surface area, atmospheric pressure, air temperature, and increasing UV radiation at higher elevations (*Körner, 2007*). For sessile organisms such as plants, these environmental gradients impose severe constraints on growth, survival, flowering and fruiting phenology, which may influence the feeding behavior and reproduction of associated organisms such as insects and birds. Tropical highland ecosystems are also characterized by a marked seasonal variation in rainfall and daily temperatures between the dry and rainy seasons (*Sarmiento, 1986*). Seasonality is a proximal factor that can regulate plant phenology (*Borchert, 1983; Reich & Borchert, 1982; Reich & Borchert, 1984; Cavelier et al., 1992; Smith & Young, 1987*), and therefore may constrain floral resource availability for floral visitors.

In the Costa Rican highland ecosystems, plant richness also declines rapidly with elevation, particularly at mountain summits (*Lieberman et al., 1996; Estrada & Zamora,*

2004; Barrantes, Chacón & Hanson, 2019; Monro, Bystriakova & Gonzalez, 2017). However, information on the dynamics of floral resources availability (*i.e.*, flowering phenology patterns) at the community level remains undocumented. Patterns of plant reproductive phenology may be related to the variation in floral resource availability and changes in the community composition of floral visitors throughout the year.

Flowering plants may be classified into different pollination syndromes based on a set of floral traits (*e.g.*, morphology, color, odor, size, rewards, and anthesis time) (Faegri & Van der Pijl, 1979; Rosas-Guerrero *et al.*, 2014). Most plant species inhabiting highland tropical ecosystems can be classified into insect-pollinated (bees and flies), bird-pollinated and insect + bird-pollinated pollination syndromes. Evidence suggests that as elevation increases, flower-visitor diversity, population abundance, and foraging activity decreases (Arroyo, Armesto & Villagran, 1981; Gómez-Murillo & Cuartas-Hernández, 2016). However, there is no information on the availability of floral resources in relation to the type of floral visitors in Central American highland ecosystems.

This study has a twofold objective: to determine differences in floral resources availability in terms of blooming plant composition and diversity between the two high-elevation ecosystems in Costa Rica (Paramo and Montane Forest), and to describe their variation in resource availability for insects and birds between the dry and rainy seasons. We predict significant differences in community composition between the Paramo and the adjacent Montane Forest, with higher species richness and beta-diversity of blooming plants in Montane Forests, due to the large number of endemic species present in the Paramo and the reduction in species richness as elevation increases. We also predict a higher diversity of the blooming plant community in the rainy season, in both ecosystems, due to milder temperatures and higher water availability compared to more severe conditions prevalent during the dry season.

MATERIALS AND METHODS

Study area

We selected two study sites in the highlands of the Costa Rican Talamanca mountain range: the Cerro de la Muerte Biological Station (CMBS) and the Quetzales National Park (QNP) (Fig. 1). The CMBS is a Montane Forest at an elevation of 3100 m asl (09°33'N; 83°44'W) and the QNP is a Paramo habitat at 3400 m asl (Fig. 1). The two sites are separated by 2 km. The region's average annual precipitation is 2500 mm, with a relatively dry period from mid-November to April, and a mean annual temperature of 11 °C for the CMBS and 7.6 °C in the QNP (Herrera, 2005). During the day, temperatures fluctuate dramatically, particularly in the Paramo (−5 °C to 35 °C) (Herrera, 2005). Montane Forests are dominated by oaks with abundant epiphytes and shrubs (*e.g.*, Ericaceae, Asteraceae, Onagraceae) (Calderón-Sanou *et al.*, 2019). Meanwhile, the Paramo is dominated by a herbaceous stratum, with a large diversity of Asteraceae and Poaceae, and scattered patches of shrubs with species mainly in the Ericaceae, Asteraceae, and Hypericaceae (Vargas & Sánchez, 2005).

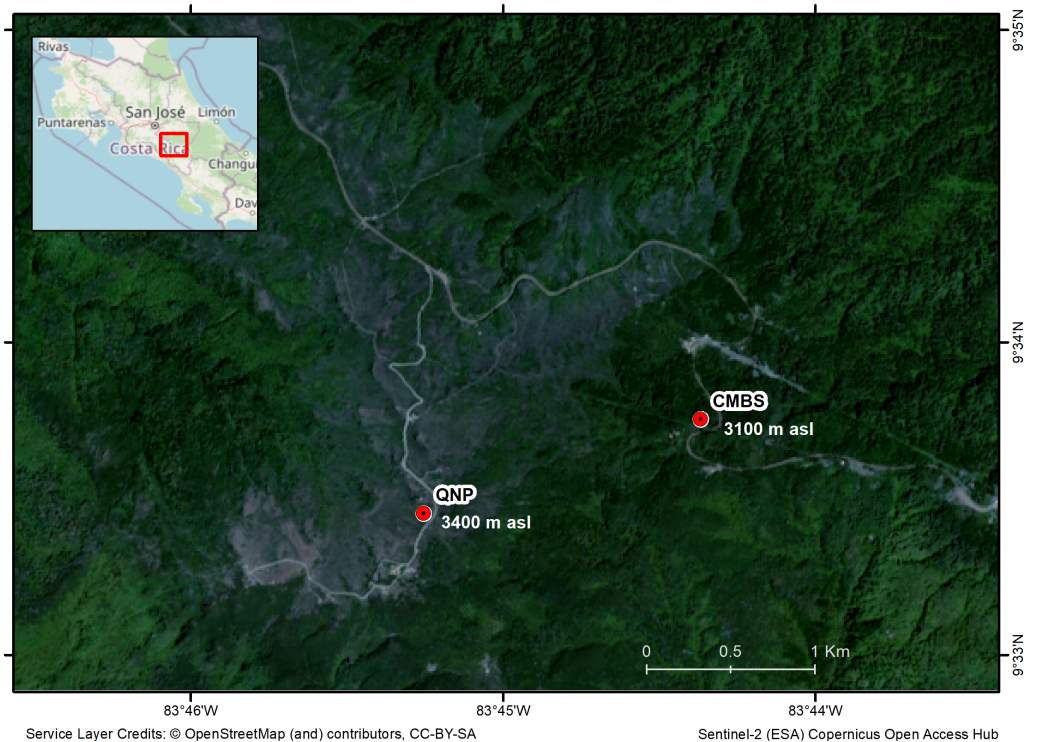


Figure 1 Map of the region of the Costa Rican Talamancan mountain region, showing the study sites and the elevation above sea level (asl): the Cerro de la Muerte Biological Station (CMBS) and the Quetzales National Park (QNP).

Full-size DOI: [10.7717/peerj.14445/fig-1](https://doi.org/10.7717/peerj.14445/fig-1)

Sampling

In each study site, we established a 2 km by 10 m transect and counted the number of individual blooming plants per species per month, during a 30 month period (February 2019 to August 2021). We classified each plant species into insect-pollinated (bee-pollinated and fly-pollinated), bird-pollinated (hummingbirds) and insect + bird-pollinated types, based on their morphology and floral reward following *Barrantes (2005)* and *Rosas-Guerrero et al. (2014)*. We did not include wind-pollinated species, such as oaks (Fagaceae), grasses and sedges (Poaceae and Cyperaceae, respectively). We defined the flowering peak for the whole community at each site and for each plant category (insect-pollinated plants, insect + bird-pollinated plants, bird-pollinated plants) as the month(s) fitting into the third quartile; if a sequence of months all met this requirement, we chose the month with the highest number of flowering individuals.

Statistical analyses

We compared species richness between the Montane Forest and the Paramo by means of rarefaction curves with 95% confidence intervals, using the function *specaccum* in the R package *vegan* (*Oksanen et al., 2020*). This method controls for differences in sample size by estimating the expected species richness of a random subsample of individuals (*Gotelli & Graves, 1996*).

To compare the plant community composition between sites, we used a non-metric multidimensional scaling (NMDS) based on a Bray-Curtis dissimilarity matrix with 1000 permutations. We then conducted a distance-based Permutational Multivariate Analyses of Variance (PERMANOVA) as implemented in the *adonis* function in the R package *vegan* (Oksanen et al., 2020). For this analysis, we included site (Montane Forest and Paramo), season (Dry and rainy seasons), and their interaction as independent factors and the distance matrix as the response variable.

Subsequently, we compared beta diversity between the two sites, measured as the mean dissimilarity non-Euclidean distance of each individual observation to the mean of all observations (centroid) calculated in multidimensional space, as implemented by the *betadisper* function (Anderson, Ellingsen & McArdle, 2006; Oksanen et al., 2020). This function is used to test the homogeneity of variances between sites or treatments. However, PERMANOVA is unaffected by the heterogeneity of variances for balanced designs (Anderson & Walsh, 2013), as is the case in this study (equal sampling at both sites). Therefore, we used the *betadisper* function to test for differences in beta-diversity between sites, as has been used in other studies (Oksanen et al., 2020). We used the *vegan* package (Oksanen et al., 2020) in the R statistical language for all analyses (R Development Core Team, 2021).

RESULTS

We recorded the flowering phenology of 91 species in 41 families: 72 species in the Montane Forest and 65 in the Paramo; 46 of these species were present at both sites. Based on our rarefaction analysis, the species richness of blooming plants was higher in the Montane Forest (Fig. 2). Similarly, the richness of plants pollinated by insects + birds and by birds only was higher in the Montane Forest; however, richness of insect-visited plants was higher in the Paramo site (Figs. S1a–S1c). This indicates that both ecosystems offer a great diversity of food resources for different pollinator guilds. More resources were available for hummingbirds in the Montane Forest, while insects seem to benefit more from plants in the Paramo ecosystem.

The number of blooming plant species varied over time (Fig. 3). All blooming plant species in both ecosystems peaked during the dry season (Fig. 3), but insect-pollinated plants had flowering peaks at the beginning (May) and the second half of the rainy season (September–October) (Fig. S2a). Insect + bird and bird-pollinated plant categories did not show a clear seasonal pattern (Figs. S2b–S2c); on the contrary, floral resources in these two plant categories varied little throughout the year. In the case of bird-pollinated plant species, the number of blooming species was always higher in the Montane Forest than in Paramo (Fig. S2d).

The multidimensional scaling distances showed that species composition differed between sites (Montane Forest and Paramo), seasons (dry and rainy), and their interaction for all plant categories (*i.e.*, all blooming plant species, insect-visited plants, insect + bird-visited plants and bird-visited-plants) (Table 1; Fig. S3; Table S1). In all cases, the site explained the largest fraction of the variance, followed by season, and then their

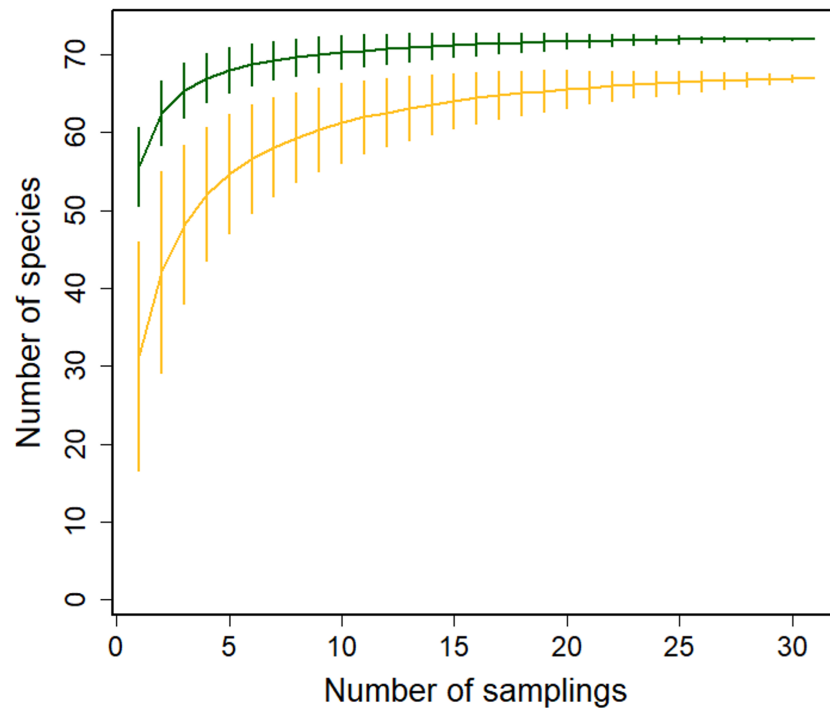


Figure 2 Sample-based rarefaction curves with 95% confidence intervals for flowering plant richness in the Montane Forest (green lines) and the Paramo (golden lines) ecosystems from the Costa Rican Talamanca mountain range. Data are from flowering censuses from February 2019 to August 2021.

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Table 1 Non-parametric PERMANOVA based on Bray–Curtis distances for all blooming plants at two sites (Montane Forest and the Paramo), two seasons (dry and rainy), and their interaction.

All blooming plants (MSD/Bray – Stress = 0.98)					
Factor	df	SS	R2	F	P
Site	1	5.03	0.38	48.55	0.001
Season	1	1.46	0.11	14.11	0.001
Site*season	1	0.87	0.06	8.37	0.001
Residual	58	5.99	0.45		
Total	61	13.36	1.00		

interaction (Table 1), though there is still a large portion of the variance that is not explained by the factors included in the model. This is expected since phenological cues are multifactorial, and their synergistic effect is not yet fully understood (Satake, Nagahama & Sasaki, 2022). The changes in species composition between the rainy and dry seasons are more pronounced in the Montane Forest than in the Paramo, for all blooming plant species (Fig. 4). However, this pattern is reversed for bird-pollinated plant species, where species composition differences between the dry and the rainy season are greater in the Paramo compared to the Montane Forest (Fig. S4).

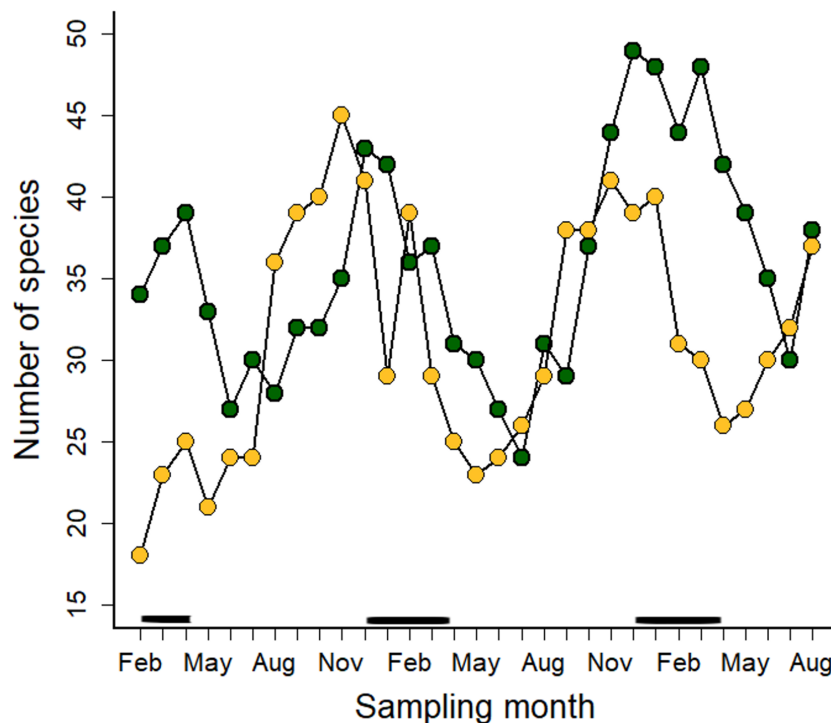


Figure 3 Number of blooming plant species in the Montane Forest (green dots) and the Paramo (golden dots) recorded during the study period of February 2019 to August 2021 in the Costa Rican Talamanca mountain range. The solid black lines above the x-axis indicate the dry season months.

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Beta diversity for each plant pollination type differed between the Montane Forest and the Paramo for all categories of blooming plants (Table 2, Fig. 4; Figs. S4a–S4d). This suggests that particular factors have shaped each ecosystem, such as climatic conditions and underlying historical factors (e.g., colonization-dispersal events) and influenced the beta diversity of blooming plants differently.

DISCUSSION

Our results show differences in species composition and diversity of plants between two adjacent ecosystems at tropical high elevations. Local and regional environmental traits, and historical events likely act synergistically to produce the differences observed (Simpson, 1975; Hooghiemstra et al., 1992; Islebe, Hooghiemstra & Van der Borg, 1995; Islebe, Hooghiemstra & Van't Veer, 1996; Sklenář, Dušková & Balslev, 2011; Barrantes, 2009). In comparison to the adjacent Montane Forest, the Paramo has a lower richness of flowering species. The study sites are geographically adjacent and separated by 2 km; however, the relatively small change in elevation (~400 m) becomes a determinant factor in shaping species composition differences. Consequently, temporal turnover (beta diversity) of blooming plants also differed between ecosystems and such differences are likely related to the uniqueness of the Costa Rican Paramo vegetation (Cleef & Chaverri, 1992). The evolution of a unique vegetation in the Costa Rican Paramo, which differs notably from

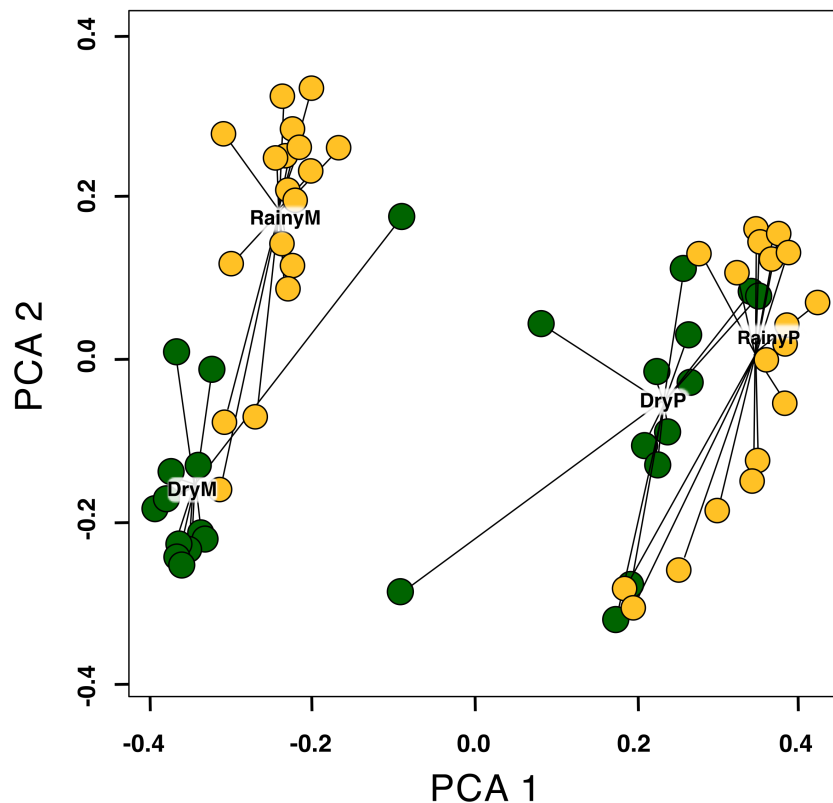


Figure 4 Effect of site and season (RainyM, Montane Forest—rainy season; DryM, Montane Forest—dry season; RainyP, Paramo—rainy season; DryP, Paramo—dry season) on the beta diversity of blooming plant species, in the Costa Rican Talamanca mountain range. The analysis was performed using the *betadisper* function in R. Each dot represents the mean non-Euclidean distance of blooming plants at a particular sampling date relative to the centroid of all samplings on the two first PCA components.

Full-size DOI: 10.7717/peerj.14445/fig-4

the adjacent Montane Forest, could be the result of several factors: (a) the plant dispersal events that occurred during the late Pleistocene (*Simpson & Neff, 1992; Sklenář, Dušková & Balslev, 2011; Londoño, Cleef & Madriñán, 2014*), (b) the geographic isolation when climate changed after the Pleistocene, and (c) the prevalence of cold climatic conditions at the summit of the Talamanca Mountain range. Vicariance driven by the climate shifts after the Pleistocene in conjunction with topographic isolation, has shaped the evolution of several plant clades within the Andean cordilleras (*Simpson, 1975; Luebert & Weigend, 2014*). For instance, a possible explanation for the rapid radiation of the common *Valeriana* and *Hypericum* species in the Andean Paramo, as well as the species present in the Costa Rican Paramo, is the repeated fragmentation-isolation process, as a consequence of the Pleistocene climatic fluctuations in a topographically complex region (*Moore & Donoghue, 2007; Nürk, Scheriau & Madriñán, 2013*).

Temporal variation in floral resources imposes a constraint on plant–pollinator interactions (*Hegland & Boeke, 2006; Fuchs, Ross-Ibarra & Barrantes, 2010; Encinas-Viso, Revilla & Etienne, 2012; Bagella et al., 2013*). Our results showed that the flowering

Table 2 Comparison of beta diversity for blooming plants between Montane Forest and Paramo forest in Costa Rica, based on the “betadisper” function (Oksanen et al., 2020).

Factor	df	SS	MS	F	P
All blooming plants					
Site	1	0.03	0.03	9.48	0.003
Residual	60	0.21	0.00		
Insect + bird-visited plants					
Site	1	0.03	0.03	9.26	0.002
Residual	60	0.22	0.00		
Insect-visited plants					
Site	1	0.05	0.05	11.96	0.002
Residual	60	0.27	0.00		
Bird-visited plants					
Site	1	0.05	0.05	3.83	0.057
Residual	60	0.76	0.01		

phenology of all groups of plants differed between dry and rainy seasons. When we analyzed the entire blooming plant community as a whole (*i.e.*, insect-visited, bird-visited, and insect + bird-visited plants) flowering peaks occurred in the dry season, in contrast to insect-visited plants, whose flowering peak occurred in the rainy season. Such differences are often associated with the response of different groups of plants to different environmental cues (Arroyo, Armesto & Villagran, 1981; Defila & Clot, 2005; Davies et al., 2013; Chmura et al., 2018; Satake, Nagahama & Sasaki, 2022). In other seasonal ecosystems, it has been suggested that water acquisition and storage strategies associated with growth form are related to different temporal patterns of flowering (Cortés-Flores et al., 2017). For example, flowering of herbaceous species occurs during the rainy season, while flowering in trees and shrubs can occur during both rainy and dry seasons (Frankie, Baker & Opler, 1974; Batalha & Martins, 2004; Cortés-Flores et al., 2017). The flowering phenology patterns that we observed are consistent with the assumption that in seasonal tropical ecosystems, insect pollinators are more abundant during the rainy season, when more floral resources are available (Southwood, Brown & Reader, 1979; Siemann et al., 1998; Ramírez, 2006; Souza et al., 2018). At least one hummingbird species is active year-round in our study site, a pattern recognized in other tropical studies, which reported continuous hummingbird activity across the year (Barrantes, 2005; Abrahamczyk et al., 2011). The presence of a particular floral visitor functional group throughout the year can be explained by the staggered flowering phenologies of plant species in tropical communities, as shown in this study (Lopezaraiza-Mikel et al., 2013; Lobo et al., 2003; Abrahamczyk et al., 2011; Meléndez-Ramírez, Ayala & González, 2016).

An important difference between the Costa Rican Paramo and Andean Paramos is that in Costa Rica, this ecosystem covers only a small and isolated area at the summit of the Talamanca mountain range. Such conditions make this site unique and susceptible to threats imposed by climate change and human intervention. Projections on climate change indicate that temperatures and the length of dry season will increase in the highlands,

seriously threatening this ecosystem in Central and South America (*Karmalkar, Bradley & Diaz, 2008; Lyra et al., 2017; Freeman et al., 2018*). In Costa Rica, the Paramo ecosystem is protected within national parks, but despite this level of protection, they are subject to a wide range of pressures from human activities, such as anthropogenic fires, the construction of communication towers, and agricultural and urban expansion around protected areas, as well as the invasion of exotic plant species (*Chaverri & Esquivel-Garrote, 2005*) which, in addition to climate change, seriously threaten this unique ecosystem.

CONCLUSIONS

We conclude that richness and beta diversity of blooming plant species differed between the Paramo and the adjacent Montane Forest, and such differences are likely a consequence of historical events (*e.g.*, dispersal promoted by changes in climate), and the edaphic and climatic conditions prevailing in the study region. Floral resource availability differed between the two seasons (dry and rainy), due to differences in climatic conditions (*Körner, 2021*) that may act as environmental cues that trigger the phenological patterns in different plant species; however, a phylogenetic effect (*e.g.*, related plant species flowering at the same time due to common ancestry) cannot be discarded (*Davies et al., 2013*). Our findings also showed that the composition and diversity of floral resources for insects and birds are lower in the Paramo than in the Montane Forest. This supports the idea that resource depletion may limit the use of the Paramo for nectar-feeding birds and insects (*Janzen et al., 1976; Barrantes, 2005; Fuchs, Ross-Ibarra & Barrantes, 2010*). This study showed that analyses of species composition and richness based on flowering phenology data are useful in evaluating potential floral resources for floral visitors (insects and birds), and how these resources change spatially and temporarily in these endangered ecosystems.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- E. Jacob Cristóbal-Pérez conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Gilbert Barrantes conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Alfredo Cascante-Marín conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Ruth Madrigal-Brenes conceived and designed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Paul Hanson conceived and designed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Eric J. Fuchs conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.

Field Study Permissions

The following information was supplied relating to field study approvals (*i.e.*, approving body and any reference numbers):

The Los Quetzales National Park (MINAE) for granted permission for this investigation (SINAC-ACC-D-RES-1410-2020, SINAC-ACLA-P-D-365-2020, SINAC-ACC-D-re-835-2021).

Data Availability

The following information was supplied regarding data availability:

Raw data of phenology of 30 months of blooming plant species from Costa Rican montane forest and paramo are available in the [Supplemental Files](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.14445#supplemental-information>.

REFERENCES

- Abrahamczyk S, Kluge J, Gareca Y, Reichle S, Kessler M. 2011. The influence of climatic seasonality on the diversity of different tropical pollinator groups. *PLOS ONE* 6(2):e27115 DOI 10.1371/journal.pone.0027115.
- Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683–693 DOI 10.1111/j.1461-0248.2006.00926.x.

- Anderson MJ, Walsh DCI. 2013.** PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs* **83**:557–574 DOI [10.1890/12-2010.1](https://doi.org/10.1890/12-2010.1).
- Arroyo MTK, Armesto JJ, Villagran C. 1981.** Plant phenological patterns in the high Andean Cordillera of Central Chile. *Journal of Ecology* **69**:205–223 DOI [10.2307/2259826](https://doi.org/10.2307/2259826).
- Bagella S, Satta A, Floris I, Caria MC, Rossetti I, Podani J. 2013.** Effects of plant community composition and flowering phenology on honeybee foraging in Mediterranean sylvo-pastoral systems. *Applied Vegetation Science* **16**(4):689–697 DOI [10.1111/avsc.12023](https://doi.org/10.1111/avsc.12023).
- Barrantes G. 2005.** Historia natural de las aves del páramo costarricense. In: Kappelle M, Horn S, eds. *Páramos de Costa Rica*. San José Costa Rica: Editorial INBio, 521–532.
- Barrantes G. 2009.** The role of historical and local factors in determining species composition of the highland avifauna of Costa Rica and western Panama. *Revista Biología Tropical* **57**(Suppl. 1):323–332 DOI [10.15517/RBT.V57I0.21360](https://doi.org/10.15517/RBT.V57I0.21360).
- Barrantes G, Chacón E, Hanson P. 2019.** Costa Rica y su Riqueza Biológica. In: Godoy-Cabrera C, Ramírez-Albán N, eds. *Biodiversidad e inventario de la naturaleza*. San José Costa Rica: Editorial Universidad Estatal a Distancia, 151–202.
- Batalha MA, Martins FR. 2004.** Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). *Australian Journal of Botany* **52**(2):149–161 DOI [10.1071/BT03098](https://doi.org/10.1071/BT03098).
- Billings WD. 1974.** Adaptations and origins of Alpine plants. *Arctic and Alpine Research* **6**:129–142 DOI [10.1080/00040851.1974.12003769](https://doi.org/10.1080/00040851.1974.12003769).
- Borchert R. 1983.** Phenology and control of flowering in tropical trees. *Biotropica* **15**:81–89 DOI [10.2307/2387949](https://doi.org/10.2307/2387949).
- Calderón-Sanou I, Ríos LD, Cascante-Marín A, Barrantes G, Fuchs EJ. 2019.** Lack of negative density-dependence regulation in a dominant oak tree from a neotropical highland forest. *Biotropica* **51**:817–825 DOI [10.1111/btp.12714](https://doi.org/10.1111/btp.12714).
- Cavelier J, Machado JL, Valencia D, Montoya J, Laignelet A, Hurtado A, Varela A, Mejia C. 1992.** Leaf demography and growth rates of *Espeletia barclayan* Cuatrec. (Compositae), a caulescent rosette in a Colombian paramo. *Biotropica* **24**:52–63 DOI [10.2307/2388473](https://doi.org/10.2307/2388473).
- Chaverri A, Esquivel-Garrote O. 2005.** Conservación, visitación y manejo del Parque Nacional Chirripó, Costa Rica. In: Kappelle M, Horn S, eds. *Páramos de Costa Rica*. San José Costa Rica: Editorial INBio, 669–699.
- Chmura HE, Kharouba HM, Ashander J, Ehlman SM, Rivest EB, Yang LH. 2018.** The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecological Monographs* **89**:e01337 DOI [10.1002/ecm.1337](https://doi.org/10.1002/ecm.1337).
- Cleef AM, Chaverri A. 1992.** Phytogeography of the páramo flora of Cordillera de Talamanca, Costa Rica. In: Balslev H, Luteyn JL, eds. *Páramo: an Andean ecosystem under human influence*. London: Academic Press, 45–60.
- Cortés-Flores J, Hernández-Esquivel KB, González-Rodríguez A, Ibarra-Manríquez G. 2017.** Flowering phenology, growth forms, and pollination syndromes in tropical dry

- forest species: influence of phylogeny and abiotic factors. *American Journal of Botany* **104**(1):39–49 DOI [10.3732/ajb.1600305](https://doi.org/10.3732/ajb.1600305).
- Davies TJ, Wolkovich EM, Kraft NJB, Salamin N, Allen JM, Ault TR, Betancourt JL, Bolmgren K, Cleland EE, Cook BI, Crimmins TM, Mazer SJ, McCabe GJ, Pau S, Regetz J, Schwartz MD, Travers SE. 2013.** Phylogenetic conservatism in plant phenology. *Journal of Ecology* **101**:1520–1530 DOI [10.1111/1365-2745.12154](https://doi.org/10.1111/1365-2745.12154).
- Defila C, Clot B. 2005.** Phytophenological trends in the Swiss Alps, 1951–2002. *Meteorologische Zeitschrift* **14**:191–196 DOI [10.1127/0941-2948/2005/0021](https://doi.org/10.1127/0941-2948/2005/0021).
- Encinas-Viso F, Revilla TA, Etienne RS. 2012.** Phenology drives mutualistic network structure and diversity. *Ecology Letters* **15**(5):198–208 DOI [10.1111/2041-210X.12139](https://doi.org/10.1111/2041-210X.12139).
- Estrada A, Zamora N. 2004.** Riqueza, cambios y patrones florísticos en un gradiente altitudinal en la cuenca hidrográfica del río Savegre, Costa Rica. *Brenesia* **61**:1–52.
- Faegri K, Van der Pijl L. 1979.** *Principles of pollination ecology*. Oxford: Pergamon Press.
- Frankie GW, Baker HG, Opler PA. 1974.** Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* **62**(3):881–919 DOI [10.2307/2258961](https://doi.org/10.2307/2258961).
- Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW. 2018.** Climate change causes upslope shifts and mountaintop extirpation in a tropical bird community. *Proceedings of the National Academy of Sciences of the United States of America* **115**:11982–11987 DOI [10.1073/pnas.1804224115](https://doi.org/10.1073/pnas.1804224115).
- Fuchs EJ, Ross-Ibarra J, Barrantes G. 2010.** Reproductive biology of *Macleania rupestris* (Ericaceae) a pollen-limited Neotropical cloud-forest species in Costa Rica. *Journal of Tropical Ecology* **26**:351–354 DOI [10.1017/S0266467410000064](https://doi.org/10.1017/S0266467410000064).
- Gómez-Murillo L, Cuartas-Hernández SE. 2016.** Patterns of diversity of flower-visitor assemblages to the understory Araceae in a tropical mountain forest in Colombia. *Journal of Insect Conservation* **20**(6):1069–1085 DOI [10.1007/s10841-016-9945-z](https://doi.org/10.1007/s10841-016-9945-z).
- Gotelli NJ, Graves GR. 1996.** *Null models in ecology*. Washington: Smithsonian Institution Press.
- Hegland SJ, Boeke L. 2006.** Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology* **31**(5):532–538 DOI [10.1111/j.1365-2311.2006.00812.x](https://doi.org/10.1111/j.1365-2311.2006.00812.x).
- Herrera W. 2005.** El clima de los páramos de Costa Rica. In: Kappelle M, Horn S, eds. *Páramos de Costa Rica*. San José Costa Rica: Editorial INBio, 113–128.
- Hooghiemstra H, Cleef AM, Noldus G, Kappelle M. 1992.** Upper Quaternary vegetation dynamics and palaeoclimatology of the La Chonta bog area (Cordillera de Talamanca, Costa Rica). *Journal of Quaternary Science* **7**:205–225 DOI [10.1002/jqs.3390070303](https://doi.org/10.1002/jqs.3390070303).
- Islebe GA, Hooghiemstra H, Van der Borg G. 1995.** A cooling event during the younger Dryas Chron in Costa Rica. *Palaeogeography, Palaeoclimatology, Paleoecology* **117**:73–80 DOI [10.1016/0031-0182\(95\)00124-5](https://doi.org/10.1016/0031-0182(95)00124-5).

- Islebe GA, Hooghiemstra H, Van't Veer R. 1996.** Holocene vegetation and water level history in two bogs of the Cordillera de Talamanca, Costa Rica. *Vegetation* 124:155–171 DOI 10.1007/BF00045491.
- Janzen DH, Ataroff M, Fariñas M, Reyes S, Rincon N, Soler A, Soriano P, Vera M. 1976.** Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8:193–203 DOI 10.2307/2989685.
- Kappelle M, Horn SP. 2005.** *Páramos de Costa Rica*. San José Costa Rica: Editorial INBio.
- Kappelle M, Horn SP. 2016.** The Paramo ecosystem of Costa Rica's highlands. In: Kappelle M, ed. *Costa Rican ecosystems*. Chicago: The University of Chicago Press, 492–523.
- Karmalkar AV, Bradley RS, Diaz HF. 2008.** Climate change scenario for Costa Rican montane forests. *Geophysical Research Letters* 35:L11702 DOI 10.1029/2008GL033940.
- Khuroo AA, Weber E, Malik AH, Reshi ZA, Dar GH. 2011.** Altitudinal distribution patterns of the native and alien woody flora in Kashmir Himalaya, India. *Environmental Research* 111(7):967–977 DOI 10.1016/j.envres.2011.05.006.
- Körner C. 2007.** The use of 'altitude' in ecological research. *Trends in Ecology and Evolution* 22(11):569–574 DOI 10.1016/j.tree.2007.09.006.
- Körner C. 2021.** Alpine plant life. In: *Functional plant ecology of high mountain ecosystems*. Berlin: Springer Verlag DOI 10.1007/978-3-030-59538-8.
- Laiolo P, Obeso JR. 2017.** Life-history responses to the altitudinal gradient. In: Catalan J, Ninot J, Aniz M, eds. *High mountain conservation in a changing world*. Cham: Springer, 253–283 DOI 10.1007/978-3-319-55982-7_11.
- Lieberman D, Lieberman M, Peralta R, Hartshorn GS. 1996.** Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84(2):137–152 DOI 10.2307/2261350.
- Lobo JA, Quesada M, Stoner KE, Fuchs EJ, Herrerías-Diego Y, Rojas J, Saborío G. 2003.** Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. *American Journal of Botany* 90(7):1054–1063 DOI 10.3732/ajb.90.7.1054.
- Londoño C, Cleef A, Madriñán S. 2014.** Angiosperm flora and biogeography of the páramo region of Colombia, northern Andes. *Flora* 209:81–87 DOI 10.1016/j.flora.2013.11.006.
- Lopezaraiza-Mikel M, Quesada M, Álvarez Añorve M, Ávila Cabadilla LD, Martín-Rodríguez S, Calvo-Alvarado J, Espirito-Santo MMD, Fernandes GW, Sanchez-Azofeifa A, Aguilar MDJA, Balvino-Olvera F, Brandao D, Contreras-Sanchez JM, Correa-Santos J, Cristobal-Perez J, Fernandez P, Hilje B, Jacobi C, Pezzini FF, Rosas F, Rosas-Guerrero V, Sanchez-Montoya G, Sayago R, Vazquez-Ramirez A. 2013.** Phenological pattern of tropical dry forest along latitudinal and successional gradient in the neotropics. In: Sanchez-Azofeifa GA, Powers JS, Fernandes GW, Quesada M, eds. *Tropical dry forest in the Americas: ecology, conservation, and management*. Florida: CRC Press Taylor and Francis Group, 101–128.

- Luebert F, Weigend M. 2014. Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution* 2:1 DOI 10.3389/fevo.2014.00027.
- Luteyn JL. 2005. Introducción al ecosistema de páramo. In: Kappele M, Horn S, eds. *Páramos de Costa Rica*. San Jose Costa Rica: Editorial INBio, 37–99.
- Lyra A, Imbach P, Rodriguez D, Chou SC, Georgiou S, Garofolo L. 2017. Projections of climate change impacts on Central America tropical rainforest. *Climate Change* 141:93–105 DOI 10.1007/s10584-016-1790-2.
- Madriñán S, Cortés AJ, Richardson JE. 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers in Genetics* 4:192 DOI 10.3389/fgene.2013.00192.
- Meléndez-Ramírez VM, Ayala R, González HD. 2016. Temporal variation in native bee diversity in the tropical sub-deciduous forest of the Yucatan Peninsula, Mexico. *Tropical Conservation Science* 9:718–734 DOI 10.1177/194008291600900210.
- Monro AK, Bystriakova N, Gonzalez F. 2017. Are landscape attributes a useful shortcut for classifying vegetation in the tropics? A case study of La Amistad International Park. *Biotropica* 49(6):848–855 DOI 10.1111/btp.12470.
- Moore BR, Donoghue MJ. 2007. Correlates of diversification in the plant clade Dipsacales: geographic movement and evolutionary innovations. *American Naturalist* 170:S28–S55 DOI 10.1086/519460.
- Navarro SAG. 1992. Altitudinal distribution of birds in the Sierra Madre del Sur, Guerrero, Mexico. *The Condor* 94(1):29–39 DOI 10.2307/1368793.
- Nürk NM, Scheriau C, Madriñán S. 2013. Explosive radiation in high Andean *Hypericum*-rates of diversification among New World lineages. *Frontiers in Genetics* 4:175 DOI 10.3389/fgene.2013.00175.
- Oksanen J, Blanchet GF, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2020. vegan: community ecology package. R package version 2.5-6.
- Pyrz TW, Clavijo A, Uribe S, Marin MA, Alvarez CF, Zubek A. 2016. Páramo de Belmira as an important centre of endemism in the northern Colombian Andes: new evidence from Pronophilina butterflies (Lepidoptera: Nymphalidae, Satyrinae, Satyrini). *Zootaxa* 4179:077–102 DOI 10.11646/zootaxa.4179.1.3.
- R Development Core Team. 2021. *A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing Available at <http://www.Rproject.org/>.
- Rada F, Azócar A, García-Núñez C. 2019. Plant functional diversity in tropical Andean páramos. *Plant Ecology and Diversity* 12(6):539–553 DOI 10.1080/17550874.2019.1674396.
- Ramírez N. 2006. Temporal variation of pollination classes in a tropical Venezuelan plain: the importance of habitats and life forms. *Canadian Journal of Botany* 84(3):443–452 DOI 10.1139/b06-015.
- Reich PB, Borchert R. 1982. Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology* 63(2):294–299 DOI 10.2307/1938945.

- Reich PB, Borchert R. 1984.** Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *The Journal of Ecology* 72(1):61–74 DOI 10.2307/2260006.
- Rosas-Guerrero V, Aguilar R, Martín-Rodríguez S, Ashworth L, Lopezaraiza-Mikel M, Bastida JM, Quesada M. 2014.** A quantitative review of pollination syndromes: do floral traits predict effective pollinators? *Ecology Letters* 17:388–400 DOI 10.1111/ele.12224.
- Sarmiento G. 1986.** Ecologically crucial features of climate in high tropical mountains. In: Vuilleumier F, Monasterio M, eds. *High altitude tropical biogeography*. Oxford: Oxford University Press, 11–45.
- Sarmiento FO. 2021.** Dynamics of Andean treeline ecotones: between cloud forest and páramo geocritical tropes. In: Myster AW, ed. *The Andean cloud forest*. Cham: Springer, 25–42.
- Satake A, Nagahama A, Sasaki E. 2022.** A cross-scale approach to unravel the molecular basis of plant phenology in temperate and tropical climates. *New Phytologist* 233:2340–2353 DOI 10.1111/nph.17897.
- Siemann E, Tilman D, Haarstad J, Ritchie M. 1998.** Experimental tests of the dependence of arthropod diversity and plant diversity. *American Naturalist* 152:738–750 DOI 10.1086/286204.
- Simpson BB. 1975.** Pleistocene changes in the flora of the high tropical Andes. *Paleobiology* 1:273–294 DOI 10.1017/S0094837300002530.
- Simpson BB, Neff J. 1992.** Plants, their pollinating bees, and the great American interchange. In: Balsev HH, Luteyn JL, eds. *Páramo: an Andean ecosystem under human influence*. London: Academic Press, 427–452.
- Sklenář P, Dušková E, Balslev H. 2011.** Tropical and temperate: evolutionary history of páramo flora. *Botanical Review* 77:71–108 DOI 10.1007/s12229-010-9061-9.
- Smith AP, Young TP. 1987.** Tropical alpine plant ecology. *Annual Review of Ecology and Systematics* 18(1):137–158 DOI 10.1146/annurev.es.18.110187.001033.
- Southwood TRE, Brown VK, Reader PM. 1979.** The relationship of plant and insect diversities in succession. *Biological Journal of the Linnean Society* 12:327–348 DOI 10.1111/j.1095-8312.1979.tb00063.x.
- Souza CS, Maruyama PK, Aoki C, Sagrist MR, Raizer J, Gross CL, De Araujo C. 2018.** Temporal variation in plant–pollinator networks from seasonal tropical environments: Higher specialization when resources are scarce. *Journal of Ecology* 106(6):2409–2420 DOI 10.1111/1365-2745.12978.
- Steinbauer MJ, Field R, Grytnes JA, Trigas P, Ah-Peng C, Attorre F, Birks HJB, Borges PAV, Cardoso P, Chou CH, De Sanctis M, De Sequeira MM, Duarte MC, Elias RB, Fernández-Palacios JM, Gabriel R, Gereau RE, Gillespie RG, Greimler J, Harter DEV, Huang TJ, Irl SDH, Jeanmonod D, Jentsch A, Jump AS, Kueffer C, Nogué S, Otto R, Price J, Romeiras MM, Strasberg D, Stuessy T, Svenning JC, Vetaas OR, Beierkuhnlein C. 2016.** Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography* 25(9):1097–1107 DOI 10.1111/geb.12469.

- Valencia BG, Bush MB, Coe AL, Orren E, Gosling WD. 2018.** Polylepis woodland dynamics during the last 20,000 years. *Journal of Biogeography* **45**:1019–1030 DOI [10.1111/jbi.13209](https://doi.org/10.1111/jbi.13209).
- Vargas G, Sánchez JJ. 2005.** Plantas con flores de los páramos de Costa Rica y Panamá: el páramo ístmico. In: Kappelle M, Horn S, eds. *Páramos de Costa Rica*. San Jose Costa Rica: Editorial INBio, 397–435.
- Vetaas OR, Grytnes JA. 2002.** Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography* **11**(4):291–301 DOI [10.1046/j.1466-822X.2002.00297.x](https://doi.org/10.1046/j.1466-822X.2002.00297.x).
- Vuilleumier F. 1969.** Pleistocene speciation in birds living in the high Andes. *Nature* **223**:1179–1180 DOI [10.1038/2231179a0](https://doi.org/10.1038/2231179a0).
- Vuilleumier F, Simberloff D. 1980.** Ecology versus history as determinants of patchy and insular distributions in high Andean birds. In: Hecht MK, Steere WC, eds. *Evolutionary biology*. 12. New York: Plenum Publishing Corporation, 235–379.
- Wolda H. 1987.** Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society* **30**(4):313–323 DOI [10.1111/j.1095-8312.1987.tb00305.x](https://doi.org/10.1111/j.1095-8312.1987.tb00305.x).