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

E. Jacob Cristobal-Perez [Corresp., 1, 2, 3] , **Gilbert Barrantes** [1, 3, 4] , **Alfredo Cascante-Marín** [1, 3, 4] , **Ruth Madrigal-Brenes** [1, 3, 4] , **Paul Hanson** [1, 4] , **Eric J. Fuchs** [1, 2, 3, 4]

[1] Centro de Investigación en Biodiversidad y Ecología Tropical, Universidad de Costa Rica, San José, Costa Rica

[2] Laboratorio Nacional de Análisis y Síntesis Ecológica/ Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico

[3] Laboratorio Binacional de Análisis y Síntesis Ecológica UNAM-UCR, Universidad Nacional Autónoma de México, Universidad de Costa Rica, Morelia, Michoacán, Mexico

[4] Escuela de Biologia, Universidad de Costa Rica, San Jose, Costa Rica

Corresponding Author: E. Jacob Cristobal-Perez
Email address: ejacob@cieco.unam.mx

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.

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

2   **E. Jacob Cristóbal-Perez [1,3,4]*, Gilbert Barrantes [1,2,4], Alfredo Cascante-Marín[1,2,4] , Ruth**

3   **Madrigal-Brenes[1,2,4], Paul Hanson[1,2] and Eric J. Fuchs[1,2,4]**

5   [1] Centro de Investigación en Biodiversidad y Ecología Tropical, Universidad de Costa Rica, San

6   José, 11501-2060, Costa Rica

7   [2] Escuela de Biología, Universidad de Costa Rica, San José, 11501-2060, Costa Rica

8   [3] Laboratorio Nacional de Análisis y Síntesis Ecológica, Escuela Nacional de Estudios

9   Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán,

10   México

11   [4] Laboratorio Binacional de Análisis y Síntesis Ecológica, UNAM-UCR, México-Costa Rica.

12   *Email: ejacob@cieco.unam.mx

23 **ABSTRACT**

24 The Costa Rican Paramo is a unique ecosystem with high levels of endemism that is

25 geographically isolated from the Andean Paramos. Paramo ecosystems occur above Montane

26 Forests, below the permanent snow level, and their vegetation differs notably from that of

27 adjacent Montane Forests. We compared the composition and beta diversity of blooming plant

28 species using phenological data from functional plant groups (i.e., insect-visited, bird-visited and

29 insect+bird-visited plants) between a Paramo and a Montane Forest site in Costa Rica and

30 analyzed seasonal changes in blooming plant diversity between the rainy and dry seasons.

31 Species richness was higher in the Montane Forest for all plant categories, except for insect-

32 visited plants, which was higher in the Paramo. Beta diversity and blooming plant composition

33 differed between both ecosystems and seasons. Differences in species richness and beta diversity

34 between Paramo and the adjacent Montane Forest are likely the result of dispersal events that

35 occurred during the last glacial period and subsequent isolation, as climate turned to tropical

36 conditions after the Pleistocene, and to stressful abiotic conditions in the Paramo ecosystem that

37 limit species establishment. Differences in blooming plant composition between both ecosystems

38 and seasons are likely attributed to differential effects of climatic cues triggering the flowering

39 events in each ecosystem, but phylogenetic conservatism cannot be discarded. Analyses of

40 species composition and richness based on flowering phenology data are useful to evaluate

41 potential floral resources for floral visitors (insects and birds) and how these resources change

42 spatially and temporally in endangered ecosystems such as the Paramo.

43

44

45   **KEYWORDS:** beta diversity, endemism, floral syndromes, Paramo, plant species composition,

46   Montane Forest.

47

48   **1. INTRODUCTION**

49   A notable characteristic of tropical highland landscapes is the presence of well defined

50   ecotones between adjacent ecosystems at high elevations (Vuilleumier & Simberloff, 1980;

51   Sarmiento, 2021). This sudden change in the vegetation physiognomy is attributed mainly to

52   differences in climatic and edaphic conditions (Luteyn, 2005). The highest mountain

53   environments above the treeline are unsuitable habitats for most organisms that inhabit adjacent

54   tropical forests at lower elevations (Luteyn, 2005; Körner, 2021). It has been suggested that

55   changes in the composition of plant communities along altitudinal gradients may be determined

56   by environmental filtering, since increasing altitudes are often associated with harsh conditions

57   for life (Laiolo & Obeso, 2017). Hence, only a relatively low number of species have been

58   capable of adapting to the prevailing abiotic conditions at high altitudes, resulting in a general

59   decline in species richness but an increase in endemism (Billings, 1974; Rada et al., 2019;

60   Madriñán et al., 2013). In the Neotropics, the Paramo exemplifies a high elevation ecosystem;

61   this habitat is typically composed of low herbaceous and shrubby vegetation whose

62   physiognomy drastically contrasts with the arboreal vegetation that dominates the adjacent

63   Montane Forests (Smith & Young, 1987; Luteyn, 2005).

64   Most of the neotropical Paramos (including the Puna) are found in South America and

65   cover a large proportion of the highlands of the Andes mountain range (Madriñán et al., 2013).

66   In Central America, the Paramo vegetation is restricted to highly isolated and small natural

67   fragments on the highlands of the Talamanca mountain range that extends from Costa Rica to

68   western Panama (Kappelle & Horn, 2016). As a result, South American Paramos have been the

69   focus of research on a variety of topics, including plant physiology (Rada et al., 2019), avian

70   evolution (Vuilleumier, 1969), vegetation (Valencia et al., 2018) and butterfly distribution

71   (Pyrcz et al., 2016); whereas research in Central American Paramo ecosystem is still limited

72   (Körner, 2021). A book published by Kappelle and Horn (2005) included information on the

73   natural history of many taxa from the Costa Rican Paramo, but information on the ecology and

74   evolution of most taxonomic groups was anecdotal or based on non-systematic samplings.

75   The species diversity turnover of plants and other taxonomic groups along altitudinal

76   gradients has been studied worldwide and, in general, richness in all groups decreases with

77   elevation, but endemism increases (Wolda, 1987; Navarro, 1992; Lieberman et al., 1996; Vetaas

78   & Grytnes 2002; Khuroo et al., 2011; Steinbauer et al., 2016; Monro et al., 2017). There are also

79   changes in abiotic conditions such as a reduction in availability of surface area, atmospheric

80   pressure, air temperature, and increasing UV radiation at higher elevations (Körner, 2007). For

81   sessile organisms such as plants, these environmental gradients impose severe constraints on

82   growth, survival, flowering and fruiting phenology, which may influence the feeding behavior

83   and reproduction of associated organisms such as insects and birds. Tropical highland

84   ecosystems are also characterized by a marked seasonal variation in rainfall and daily

85   temperatures between the dry and rainy seasons (Sarmiento, 1986). Seasonality is a proximal

86   factor that can regulate plant phenology (Borchert 1983; Reich & Borchert, 1982, 1984; Cavelier

87   et al., 1992; Smith & Young, 1987), and therefore may constrain floral resource availability for

88   floral visitors.

89   In the Costa Rican highland ecosystems, plant richness also declines rapidly with

90   elevation, particularly at mountain summits (Lieberman et al., 1996; Estrada & Zamora 2004;

91   Barrantes et al., 2019; Monro et al., 2017). However, information on the dynamics of floral

92   resources availability (i.e., flowering phenology patterns) at the community level remains

93   undocumented. Patterns of plant reproductive phenology may be related to the variation in floral

94   resource availability and changes in the community composition of floral visitors throughout the

95   year.

96   Flowering plants may be classified into different pollination syndromes based on a set of

97   floral traits (e.g., morphology, color, odor, size, rewards, and anthesis time) (Faegri & Van der

98   Pijl, 1979; Rosas-Guerrero et al., 2014). Most plant species inhabiting highland tropical

99   ecosystems can be classified into insect-pollinated (bees and flies), bird-pollinated and

100 insect+bird-pollinated pollination syndromes. Evidence suggests that as elevation

101 increases, flower-visitor diversity, population abundance, and foraging activity decreases

102 (Arroyo et al., 1981; Gómez-Murillo & Cuartas-Hernández, 2016). However, there is no

103 information on the availability of floral resources in relation to the type of floral visitors in

104 Central American highland ecosystems.

105

106   This study has a twofold objective: to determine differences in floral resources

107 availability in terms of blooming plant composition and diversity between the two high-elevation

108 ecosystems in Costa Rica (Paramo and Montane Forest), and to describe their variation in

109 resource availability for insects and birds between the dry and rainy seasons. We predict

110 significant differences in community composition between the Paramo and the adjacent Montane

111 Forest, with higher species richness and beta-diversity of blooming plants in Montane Forests,

112 due to the large number of endemic species present in the Paramo and the reduction in species

113 richness as elevation increases. We also predict a higher diversity of the blooming plant

114 community in the rainy season, in both ecosystems, due to milder temperatures and higher water

115 availability compared to more severe conditions prevalent during the dry season.

116

117 **2. MATERIALS AND METHODS**

118 *2.1 Study area*

119   We selected two study sites in the highlands of the Costa Rican Talamanca mountain

120 range: the Cerro de la Muerte Biological Station (CMBS) and the Quetzales National Park

121 (QNP) (Fig. 1). The CMBS is a Montane Forest at an elevation of 3100 m asl (09° 33' N; 83°

122 44' W) and the QNP is a Paramo habitat at 3400 m asl (Fig. 1). The two sites are separated by 2

123 km. The region's average annual precipitation is 2500 mm, with a relatively dry period from

124 mid-November to April, and a mean annual temperature of 11°C for the CMBS and 7.6°C in the

125 QNP (Herrera, 2005). During the day, temperatures fluctuate dramatically, particularly in the

126 Paramo (-5 °C to 35 °C) (Herrera, 2005). Montane Forests are dominated by oaks with abundant

127 epiphytes and shrubs (e.g., Ericaceae, Asteraceae, Onagraceae) (Calderón-Sanou et al., 2019).

128 Meanwhile, the Paramo is dominated by a herbaceous stratum, with a large diversity of

129 Asteraceae and Poaceae, and scattered patches of shrubs with species mainly in the Ericaceae,

130 Asteraceae, and Hypericaceae (Vargas & Sanchez 2005).

131

132 *2.2 Sampling*

133 In each study site, we established a 2 km by 10 m transect and counted the number of individual

134 blooming plants per species per month, during a 30 month period (February 2019 to August

135 2021). We classified each plant species into insect-pollinated (bee-pollinated and fly-pollinated),

136 bird-pollinated (hummingbirds) and insect+bird-pollinated types, based on their morphology and

137 floral reward following Barrantes (2005) and Rosas-Guerrero et al., (2014). We did not include

138 wind-pollinated species, such as oaks (Fagaceae), grasses and sedges (Poaceae and Cyperaceae,

139 respectively). We defined the flowering peak for the whole community at each site and for each

140 plant category (insect-pollinated plants, insect+bird-pollinated plants, bird-pollinated plants) as

141 the month(s) fitting into the third quartile; if a sequence of months all met this requirement, we

142 chose the month with the highest number of flowering individuals.

143

144 *2.3 Statistical Analyses*

145 We compared species richness between the Montane Forest and the Paramo by means of

146 rarefaction curves with 95% confidence intervals, using the function *specaccum* in the R package

147 *vegan* (Oksanen et al., 2020). This method controls for differences in sample size by estimating

148 the expected species richness of a random subsample of individuals (Gotelli & Graves, 1996).

149   To compare the plant community composition between sites, we used a non-metric

150 multidimensional scaling (NMSD) based on a Bray-Curtis dissimilarity matrix with 1000

151 permutations. We then conducted a distance-based Permutational Multivariate Analyses of

152 Variance (PERMANOVA) as implemented in the *adonis* function in the R package *vegan*

153 (Oksanen et al., 2020). For this analysis, we included site (Montane Forest and Paramo), season

154 (Dry and rainy seasons), and their interaction as independent factors and the distance matrix as

155 the response variable.

156   Subsequently, we compared beta diversity between the two sites, measured as the mean

157 dissimilarity non-Euclidean distance of each individual observation to the mean of all

158 observations (centroid) calculated in multidimensional space, as implemented by the *betadisper*

159 function (Anderson et al., 2006; Oksanen et al., 2020). This function is used to test the

160   homogeneity of variances between sites or treatments. However, PERMANOVA is unaffected

161   by the heterogeneity of variances for balanced designs (Anderson and Walsh, 2013), as is the

162   case in this study (equal sampling at both sites). Therefore, we used the *betadisper* function to

163   test for differences in beta-diversity between sites, as has been used in other studies (Oksanen et

164   al., 2020). We used the *vegan* package (Oksanen et al., 2020) in the R statistical language for all

165   analyses (R Development Core Team, 2021).

166

167   **3. RESULTS**

168   We recorded the flowering phenology of 91 species in 41 families: 72 species in the

169   Montane Forest and 65 in the Paramo; 46 of these species were present at both sites. Based on

170   our rarefaction analysis, the species richness of blooming plants was higher in the Montane

171   Forest (Fig. 2). Similarly, the richness of plants pollinated by insects+birds and by birds only

172   was higher in the Montane Forest; however, richness of insect-visited plants was higher in the

173   Paramo site (Fig. S1a-c). This indicates that both ecosystems offer a great diversity of food

174   resources for different pollinator guilds. More resources were available for hummingbirds in the

175   Montane Forest, while insects seem to benefit more from plants in the Paramo ecosystem.

176   The number of blooming plant species varied over time (Fig. 3). All blooming plant

177   species in both ecosystems peaked during the dry season (Fig. 3), but insect-pollinated plants had

178   flowering peaks at the beginning (May) and the second half of the rainy season (September-

179   October) (Fig. S2a). Insect+bird and bird-pollinated plant categories did not show a clear

180   seasonal pattern (Fig. S2 b-c); on the contrary, floral resources in these two plant categories

181   varied little throughout the year. In the case of bird-pollinated plant species, the number of

182   blooming species was always higher in the Montane Forest than in Paramo (Fig. S2 d).

183   The multidimensional scaling distances showed that species composition differed

184 between sites (Montane Forest and Paramo), seasons (dry and rainy), and their interaction for all

185 plant categories (i.e., all blooming plant species, insect-visited plants, insect+bird-visited plants

186 and bird-visited-plants) (Table 1; Fig. S3; Table S1). In all cases, the site explained the largest

187 fraction of the variance, followed by season, and then their interaction (Table 1), though there is

188 still a large portion of the variance that is not explained by the factors included in the model.

189 This is expected since phenological cues are multifactorial, and their synergistic effect is not yet

190 fully understood (Satake et al., 2022). The changes in species composition between the rainy and

191 dry seasons are more pronounced in the Montane Forest than in the Paramo, for all blooming

192 plant species (Fig. 4). However, this pattern is reversed for bird-pollinated plant species, where

193 species composition differences between the dry and the rainy season are greater in the Paramo

194 compared to the Montane Forest (Fig. S4).

195   Beta diversity for each plant pollination type differed between the Montane Forest and

196 the Paramo for all categories of blooming plants (Table 2, Fig. 4; Fig. S4 a-d). This suggests that

197 particular factors have shaped each ecosystem, such as climatic conditions and underlying

198 historical factors (e.g. colonization-dispersal events) and influenced the beta diversity of

199 blooming plants differently.

200

201 **4. DISCUSSION**

202   Our results show differences in species composition and diversity of plants between two

203 adjacent ecosystems at tropical high elevations. Local and regional environmental traits, and

204 historical events likely act synergistically to produce the differences observed (Simpson, 1975;

205 Hooghiemstra et al., 1992; Islebe et al., 1995, 1996; Sklenář et al., 2011). In comparison to the

206   adjacent Montane Forest, the Paramo has a lower richness of flowering species. The study sites

207   are geographically adjacent and separated by 2 km; however, the relatively small change in

208   elevation (~400 m) becomes a determinant factor in shaping species composition differences.

209   Consequently, temporal turnover (beta diversity) of blooming plants also differed between

210   ecosystems and such differences are likely related to the uniqueness of the Costa Rican Paramo

211   vegetation (Cleef & Chaverri, 1992). The evolution of a unique vegetation in the Costa Rican

212   Paramo, which differs notably from the adjacent Montane Forest, could be the result of several

213   factors: a) the plant dispersal events that occurred during the late Pleistocene (Simpson & Neff,

214   1992; Sklenář et al., 2011; Londoño et al., 2014), b) the geographic isolation when climate

215   changed after the Pleistocene, and c) the prevalence of cold climatic conditions at the summit of

216   the Talamanca Mountain range. Vicariance driven by the climate shifts after the Pleistocene in

217   conjunction with topographic isolation, has shaped the evolution of several plant clades within

218   the Andean cordilleras (Simpson,1975; Luebert & Weigend, 2014). For instance, a possible

219   explanation for the rapid radiation of the common *Valeriana* and *Hypericum* species in the

220   Andean Paramo, as well as the species present in the Costa Rican Paramo, is the repeated

221   fragmentation-isolation process, as a consequence of the Pleistocene climatic fluctuations in a

222   topographically complex region (Moore & Donoghue, 2007; Nürk et al., 2014).

223   Temporal variation in floral resources imposes a constraint on plant-pollinator

224   interactions (Hegland & Boeke, 2006; Fuchs et al., 2010; Encinas-Viso et al., 2012; Bagella et

225   al., 2013). Our results showed that the flowering phenology of all groups of plants differed

226   between dry and rainy seasons. When we analyzed the entire blooming plant community as a

227   whole (i.e., insect-visited, bird-visited, and insect+bird-visited plants) flowering peaks occurred

228   in the dry season, in contrast to insect-visited plants, whose flowering peak occurred in the rainy

229 season. Such differences are often associated with the response of different groups of plants to

230 different environmental cues (Arroyo et al., 1981; Defila & Clot, 2005; Davies et al., 2013;

231 Chmura et al., 2018; Satake et al., 2022). In other seasonal ecosystems, it has been suggested that

232 water acquisition and storage strategies associated with growth form are related to different

233 temporal patterns of flowering (Cortés-Flores et al., 2017). For example, flowering of herbaceous

234 species occurs during the rainy season, while flowering in trees and shrubs can occur during both

235 rainy and dry seasons (Frankie et al., 1974; Batalha & Martins, 2004; Cortés-Flores et al., 2017).

236 The flowering phenology patterns that we observed are consistent with the assumption that in

237 seasonal tropical ecosystems, insect pollinators are more abundant during the rainy season, when

238 more floral resources are available (Southwood et al., 1979; Siemann et al., 1998; Ramírez,

239 2006; Souza et al., 2018). At least one hummingbird species is active year-round in our study

240 site, a pattern recognized in other tropical studies, which reported continuous hummingbird

241 activity across the year (Barrantes, 2005; Abrahamczyk et al., 2011). The presence of a particular

242 floral visitor functional group throughout the year can be explained by the staggered flowering

243 phenologies of plant species in tropical communities, as shown in this study (Lopezaraiza-Mikel

244 et al., 2013; Lobo et al., 2003, Abrahamczyk et al., 2011; Meléndez-Ramírez et al., 2016).

245   An important difference between the Costa Rican Paramo and Andean Paramos is that in

246 Costa Rica, this ecosystem covers only a small and isolated area at the summit of the Talamanca

247 mountain range. Such conditions make this site unique and susceptible to threats imposed by

248 climate change and human intervention. Projections on climate change indicate that temperatures

249 and the length of dry season will increase in the highlands, seriously threatening this ecosystem

250 in Central and South America (Karmalkar et al., 2008; Lyra et al., 2017; Freeman et al., 2018). In

251 Costa Rica, the Paramo ecosystem is protected within national parks, but despite this level of

252   protection, they are subject to a wide range of pressures from human activities, such as

253   anthropogenic fires, the construction of communication towers, and agricultural and urban

254   expansion around protected areas, as well as the invasion of exotic plant species (Chaverri &

255   Esquivel-Garrote, 2005) which, in addition to climate change, seriously threaten this unique

256   ecosystem.

257   **5. CONCLUSIONS**

258   We conclude that richness and beta diversity of blooming plant species differed between

259   the Paramo and the adjacent Montane Forest, and such differences are likely a consequence of

260   historical events (e.g., dispersal promoted by changes in climate), and the edaphic and climatic

261   conditions prevailing in the study region. Floral resource availability differed between the two

262   seasons (dry and rainy), due to differences in climatic conditions (Körner, 2021) that may act as

263   environmental cues that trigger the phenological patterns in different plant species; however, a

264   phylogenetic effect (e.g., related plant species flowering at the same time due to common

265   ancestry) cannot be discarded (Davies et al., 2013). Our findings also showed that the

266   composition and diversity of floral resources for insects and birds are lower in the Paramo than

267   in the Montane Forest. This supports the idea that resource depletion may limit the use of the

268   Paramo for nectar-feeding birds and insects (Janzen et al., 1976; Barrantes, 2005; Fuchs et al.,

269   2010). This study showed that analyses of species composition and richness based on flowering

270   phenology data are useful in evaluating potential floral resources for floral visitors (insects and

271   birds), and how these resources change spatially and temporarily in these endangered

272   ecosystems.

273

274 **ACKNOWLEDGEMENTS**

275 We are indebted to the late Federico Valverde for allowing us to conduct this research at the

276 Cerro de la Muerte Biological Station. We thank the personnel of Los Quetzales National Park

277 (MINAE) for granting permission for this investigation (SINAC-ACC-D- RES-1410-2020,

278 SINAC-ACLA-P-D-365-2020, SINAC-ACC-D-re-835-2021), and Zulema Carrillo-Aldape for

279 assistance in preparing the map. Map data copyrighted OpenStreetMap contributors and

280 available from https://www.openstreetmap.org/copyright.

281

282 **REFERENCES**

283 Abrahamczyk S, Kluge J, Gareca Y, Reichle S, Kessler M. 2011. The influence of climatic

284   seasonality on the diversity of different tropical pollinator groups. PLOS ONE 6(2),

285   e27115 DOI: 10.1371/journal.pone.0027115.

286 Anderson MJ, Walsh DCI. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of

287   heterogeneous dispersions: What null hypothesis are you testing? Ecological Monographs

288   83: 557–574 DOI: 10.1890/12-2010.1.

289 Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of beta

290   diversity. Ecology Letters 9: 683–693 DOI: 10.1111/j.1461-0248.2006.00926.x.

291 Arroyo MTK, Armesto JJ,Villagran C. 1981. Plant phenological patterns in the high Andean

292   Cordillera of Central Chile. Journal of Ecology 69: 205–223 DOI: 10.2307/2259826.

293 Bagella S, Satta A, Floris I, Caria MC, Rossetti I, Podani J. 2013. Effects of plant community

294   composition and flowering phenology on honeybee foraging in Mediterranean sylvo-

295   pastoral systems. Applied Vegetation Science 16 (4): 689–697 DOI: 10.1111/avsc.12023.

296   Barrantes G. 2005. Historia natural de las aves del páramo costarricense. In Kappelle M, Horn

297   S, eds. Páramos de Costa Rica. San José Costa Rica: Editorial INBio, 521-532.

298   Barrantes G. 2009. The role of historical and local factors in determining species composition of

299   the highland avifauna of Costa Rica and western Panama. Revista Biología Tropical

300   57(Suppl. 1): 323–332 DOI: 10.15517/RBT.V57I0.21360.

301   Barrantes G, Chacón E, Hanson P. 2019. Costa Rica y su Riqueza Biológica. In Godoy-Cabrera

302   C, Ramírez-Albán N, eds. Biodiversidad e inventario de la naturaleza. San José Costa

303   Rica: Editorial Universidad Estatal a Distancia, 151-202.

304   Batalha MA, Martins FR. 2004. Reproductive phenology of the cerrado plant community in

305   Emas National Park (central Brazil). Australian Journal of Botany 52(2): 149-161 DOI:

306   10.1071/BT03098.

307   Billings WD. 1974. Adaptations and origins of Alpine plants. Arctic and Alpine Research 6:

308   129-142 DOI: 10.1080/00040851.1974.12003769.

309   Borchert R. 1983. Phenology and control of flowering in tropical trees. Biotropica 15: 81-89.

310   Calderón-Sanou I, Ríos LD, Cascante-Marín A, Barrantes G, Fuchs EJ. 2019. Lack of negative

311   density-dependence regulation in a dominant oak tree from a neotropical highland forest.

312   Biotropica 51: 817–825 DOI: 10.1111/btp.12714.

313   Cavelier, J., Machado, J. L., Valencia, D., Montoya, J., Laignelet, A., Hurtado, A., Varela A,

314   Mejia C. 1992. Leaf demography and growth rates of *Espeletia barclayan* Cuatrec.

315   (Compositae), a caulescent rosette in a Colombian paramo. Biotropica. 24:52–63.

316   Chaverri A, Esquivel-Garrote O. 2005. Conservación, visitación y manejo del Parque Nacional

317   Chirripó, Costa Rica. In Kappelle M, Horn S, eds. Páramos de Costa Rica. San José Costa

318   Rica: Editorial INBio, 669-699.

319   Chmura HE, Kharouba HM, Ashander J, Ehlman SM, Rivest EB, Yang LH. 2018. The

320   mechanisms of phenology: the patterns and processes of phenological shifts. 89: e01337

321   DOI: 10.1002/ecm.1337.

322   Cleef, A. M. and A. Chaverri. 1992. Phytogeography of the páramo flora of Cordillera de

323   Talamanca, Costa Rica. In Balslev H, Luteyn JL, eds. Páramo: An Andean Ecosystem

324   Under Human Influence. London: Academic Press, 45–60.

325   Cortés-Flores J, Hernández-Esquivel KB, González-Rodríguez A, Ibarra-Manríquez G. 2017.

326   Flowering phenology, growth forms, and pollination syndromes in tropical dry forest

327   species: Influence of phylogeny and abiotic factors. American Journal of Botany. 104(1):

328   39–49 DOI: 10.3732/ajb.1600305.

329   Davies TJ, Wolkovich EM, Kraft NJB, Salamin N,   Allen JM, Ault TR, Betancourt JL,

330   Bolmgren K, Cleland EE, Cook BI, Crimmins TM, Mazer SJ, McCabe GJ, Pau S, Regetz

331   J, Schwartz MD, Travers SE. 2013. Phylogenetic conservatism in plant phenology. Journal

332   of Ecology 101: 1520–1530 DOI: 10.1111/1365-2745.12154.

333   Defila C, Clot B. 2005. Phytophenological trends in the Swiss Alps, 1951–2002.

334   Meteorologische Zeitschrift 14: 191–196 DOI: 10.1127/0941-2948/2005/0021.

335   Encinas-Viso F, Revilla TA, Etienne RS. 2012. Phenology drives mutualistic network structure

336   and diversity. Ecology Letters 15(5): 198–208 DOI: 10.1111/2041-210X.12139.

337   Estrada A, Zamora N. 2004. Riqueza, cambios y patrones florísticos en un gradiente altitudinal

338   en la cuenca hidrográfica del río Savegre, Costa Rica. Brenesia 61: 1-52.

339   Faegri K, van der Pijl L. 1979. Principles of Pollination Ecology. Oxford: Pergamon Press.

340 Frankie GW, Baker HG, Opler PA. 1974. Comparative phenological studies of trees in tropical

341   wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62(3): 881–919 DOI:

342   10.2307/2258961.

343 Freeman BG, Scholer MN, Ruiz-Gutierrez V, Fitzpatrick JW. 2018. Climate change causes

344   upslope shifts and mountaintop extirpation in a tropical bird community. Proceedings of

345   the National Academy of Sciences 115: 11982–11987 DOI: 10.1073/pnas.1804224115.

346 Fuchs EJ, Ross-Ibarra J, Barrantes G. 2010. Reproductive biology of *Macleania rupestris*

347   (Ericaceae) a pollen-limited Neotropical cloud-forest species in Costa Rica. Journal of

348   Tropical Ecology 26: 351–354 DOI: 10.1017/S0266467410000064.

349 Gotelli NJ, Graves GR. 1996. Null models in ecology. Washington DC: Smithsonian Institution

350   Press.

351 Gómez-Murillo L, Cuartas-Hernández SE. 2016. Patterns of diversity of flower-visitor

352   assemblages to the understory Araceae in a tropical mountain forest in Colombia. Journal

353   of Insect Conservation 20(6): 1069-1085 DOI:10.1007/s10841-016-9945-z.

354 Hegland SJ, Boeke L. 2006. Relationships between the density and diversity of floral resources

355   and flower visitor activity in a temperate grassland community. Ecological Entomology

356   31(5): 532–538 DOI: 10.1111/j.1365-2311.2006.00812.x.

357 Herrera W. 2005. El clima de los páramos de Costa Rica. In Kappele M, Horn S, eds. Páramos

358   de Costa Rica. San José Costa Rica: Editorial INBio, 113-128.

359 Hooghiemstra H, Cleef AM, Noldus G, Kappelle M. 1992. Upper Quaternary vegetation

360   dynamics and palaeoclimatology of the La Chonta bog area (Cordillera de Talamanca,

361   Costa Rica). Journal of Quaternary Science 7: 205-225 DOI: 10.1002/jqs.3390070303.

362   Islebe GA, Hooghiemstra H, Van der Borg G. 1995. A cooling event during the younger Dryas

363   Chron in Costa Rica. Palaeogeography, Palaeoclimatology, Paleoecology 117: 73-80

364   DOI:10.1016/0031-0182(95)00124-5.

365   Islebe GA, Hooghiemstra H, van't Veer R. 1996. Holocene vegetation and water level history in

366   two bogs of the Cordillera de Talamanca, Costa Rica. Vegetation 124: 155-171 DOI:

367   10.1007/BF00045491.

368   Janzen DH, Ataroff M, Fariñas M, Reyes S, Rincon N, Soler A, Soriano P, Vera M. 1976.

369   Changes in the arthropod community along an elevational transect in the Venezuelan

370   Andes. Biotropica 8: 193–203 DOI: 10.2307/2989685.

371   Karmalkar AV, Bradley RS, Diaz HF. 2008. Climate change scenario for Costa Rican montane

372   forests. Geophysical Research Letters 35: L11702 DOI: 10.1029/2008GL033940.

373   Kappelle M, Horn SP. 2016. The Paramo ecosystem of Costa Rica's highlands. In Kappelle M,

374   ed. Costa Rican Ecosystems. Chicago Illinois: The University of Chicago Press, 492-523.

375   Kapelle M, Horn SP. 2005. Páramos de Costa Rica. San José Costa Rica: Editorial INBio.

376   Khuroo AA, Weber E, Malik AH, Reshi ZA, Dar GH. 2011. Altitudinal distribution patterns of

377   the native and alien woody flora in Kashmir Himalaya, India. Environmental research.

378   111(7): 967-977 DOI: 10.1016/j.envres.2011.05.006.

379   Körner C. 2007. The use of 'altitude' in ecological research. Trends in Ecology and Evolution.

380   22(11): 569-574 DOI: 10.1016/j.tree.2007.09.006.

381   Körner C. 2021. Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems.

382   Berlin: Springer Verlag DOI: 10.1007/978-3-030-59538-8.

383   Laiolo P, Obeso JR. 2017. Life-history responses to the altitudinal gradient. In Catalan J, Ninot J,

384   Aniz M, eds. High mountain conservation in a changing world. Springer, Cham, 253-283

385   DOI: 10.1007/978-3-319-55982-7_11.

386   Lieberman D, Lieberman M, Peralta R, Hartshorn GS. 1996. Tropical forest structure and

387   composition on a large-scale altitudinal gradient in Costa Rica. Journal of Ecology 137-152

388   DOI: 10.2307/2261350.

389   Lobo JA, Quesada M, Stoner KE, Fuchs EJ, Herrerías-Diego Y, Rojas J, Saborío G. 2003.

390   Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa

391   Rica and Mexico. American Journal of Botany, 90(7): 1054–1063 DOI:

392   10.3732/ajb.90.7.1054.

393   Londoño C, Cleef A, Madriñán S. 2014. Angiosperm flora and biogeography of the páramo

394   region of Colombia, northern Andes. Flora 209: 81–87 DOI: 10.1016/j.flora.2013.11.006

395   Lopezaraiza-Mikel M, Quesada M, Álvarez-Añorve M, Ávila-Cabadilla LD, Martén-Rodríguez

396   S, Calvo-Alvarado J., et al. 2013. Phenological pattern of tropical dry forest along

397   latitudinal and successional gradient in the neotropics. In Sanchez-Azofeifa GA, Powers

398   JS, Fernandes GW, Quesada M, eds. Tropical dry forest in the Americas: ecology,

399   conservation, and management. Florida: CRC Press Taylor and Francis Group, 101–128.

400   Luebert F, Weigend M. 2014. Phylogenetic insights into Andean plant diversification. Frontiers

401   in Ecology and Evolution 2: 1 DOI: 10.3389/fevo.2014.00027.

402   Luteyn JL. 2005. Introducción al ecosistema de páramo. In Kappele M, Horn S. Páramos de

403   Costa Rica. San Jose Costa Rica: Editorial INBio, 37- 99.

404   Lyra A, Imbach P, Rodriguez D, Chou SC, Georgiou S, Garofolo L. 2017. Projections of

405   climate change impacts on Central America tropical rainforest. Climate Change 141: 93–

406   105 DOI: 10.1007/s10584-016-1790-2.

407   Madriñán S, Cortés AJ, Richardson JE. 2013. Páramo is the world's fastest evolving and coolest

408   biodiversity hotspot. Frontiers in Genetics 4: 192 DOI: 10.3389/fgene.2013.00192

409   Meléndez-Ramírez VM, Ayala R, González HD. 2016. Temporal Variation in Native Bee

410   Diversity in the Tropical Sub-Deciduous Forest of the Yucatan Peninsula, Mexico.

411   Tropical Conservation Science, 9, 718–734 DOI: 10.1177/194008291600900210

412   Monro AK, Bystriakova N, Gonzalez F. 2017. Are landscape attributes a useful shortcut for

413   classifying vegetation in the tropics? A case study of La Amistad International Park.

414   Biotropica, 49(6), 848-855 DOI: 10.1111/btp.12470.

415   Moore BR, Donoghue MJ. 2007. Correlates of diversification in the plant clade Dipsacales:

416   geographic movement and evolutionary innovations. American Naturalist 170: S28–S55

417   DOI: 10.1086/519460.

418   Navarro SAG. 1992. Altitudinal distribution of birds in the Sierra Madre del Sur, Guerrero,

419   Mexico. The Condor 94(1): 29-39 DOI: 10.2307/1368793.

420   Nürk NM, Scheriau C, Madriñán S. 2013. Explosive radiation in high Andean *Hypericum*-rates

421   of diversification among New World lineages. Frontiers in Genetics 175 DOI:

422   10.3389/fgene.2013.00175.

423   Oksanen J, Blanchet GF, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos

424   P, Stevens MHH, Wagner H. 2020. vegan: Community Ecology Package, R package

425   version 2.5-6. URL: http://CRAN.R-project.org/package=vegan

426   Pyrcz TW, Clavijo A, Uribe S, Marin MA, Alvarez CF, Zubek A. 2016. Páramo de Belmira

427   as an important centre of endemism in the northern Colombian Andes: new evidence from

428   Pronophilina butterflies (Lepidoptera: Nymphalidae, Satyrinae, Satyrini). Zootaxa 4179:

429   077–102 DOI: 10.11646/zootaxa.4179.1.3

430   R Development Core Team. 2021. A language and environment for statistical computing.

431   Vienna, Austria: R Foundation for Statistical Computing. URL: http://www.Rproject.org/.

432   Rada F, Azócar A, García-Núñez C. 2019. Plant functional diversity in tropical Andean páramos.

433   Plant Ecology and Diversity 12(6): 539-553 DOI: 10.1080/17550874.2019.1674396.

434   Ramírez N. 2006. Temporal variation of pollination classes in a tropical Venezuelan plain: The

435   importance of habitats and life forms. Canadian Journal of Botany 84(3) 443–452 DOI:

436   10.1139/b06-015.

437   Reich PB, Borchert R. 1982. Phenology and ecophysiology of the tropical tree, *Tabebuia*

438   *neochrysantha* (Bignoniaceae). Ecology 63(2): 294-299 DOI:10.2307/1938945.

439   Reich PB, Borchert R. 1984. Water stress and tree phenology in a tropical dry forest in the

440   lowlands of Costa Rica. The Journal of Ecology 72(1): 61-74 DOI: 10.2307/2260006.

441   Rosas-Guerrero V, Aguilar R, Martén-Rodríguez S, Ashworth L, Lopezaraiza-Mikel M, Bastida

442   JM, Quesada M. 2014. A quantitative review of pollination syndromes: do floral traits

443   predict effective pollinators? Ecology Letters 17: 388–400 DOI: 10.1111/ele.12224.

444   Sarmiento G. 1986. Ecologically crucial features of climate in high tropical mountains. In

445   Vuilleumier F, Monasterio M, eds.High Altitude Tropical Biogeography. Oxford: Oxford

446   University Press, 11-45.

447   Sarmiento FO. 2021. Dynamics of Andean treeline ecotones: between cloud forest and páramo

448   geocritical tropes. Myster AW, ed. The Andean cloud forest. Springer Cham, 25-42.

449   Satake A, Nagahama A, Sasaki E. 2022. A cross-scale approach to unravel the molecular basis

450   of plant phenology in temperate and tropical climates. New Phytologist 233: 2340–2353

451   DOI: 10.1111/nph.17897.

452   Siemann E, Tilman D, Haarstad J, Ritchie M. 1998. Experimental tests of the dependence of

453   arthropod diversity and plant diversity. American Naturalist 152: 738–750. DOI:

454   10.1086/286204.

455   Simpson BB. 1975. Pleistocene changes in the flora of the high tropical Andes. Paleobiology 1:

456   273–294 DOI: 10.1017/S0094837300002530.

457   Simpson BB, Neff J. 1992. Plants, their pollinating bees, and the great American interchange. In

458   Balsev HH, Luteyn JL, eds. Páramo: an Andean ecosystem under human influence.

459   London: Academic Press, 427-452.

460   Sklenář P, Dušková E, Balslev H. 2011. Tropical and temperate: evolutionary history of páramo

461   flora. Botanical Review 77:71–108 DOI: 10.1007/s12229-010-9061-9.

462   Smith AP Young TP. 1987. Tropical alpine plant ecology. Annual Review of Ecology and

463   Systematics 18(1): 137-158 DOI: 10.1146/annurev.es.18.110187.001033.

464   Southwood TRE, Brown VK, Reader PM. 1979. The relationship of plant and insect diversities

465   in succession. Biological Journal of the Linnean Society 12: 327–348 DOI:

466   10.1111/j.1095-8312.1979.tb00063.x.

467   Souza CS, Maruyama PK, Aoki C, Sagrist MR, Raizer J, Gross CL, de Araujo C. 2018.

468   Temporal variation in plant–pollinator networks from seasonal tropical environments:

469   Higher specialization when resources are scarce. Journal of Ecology, 106(6): 2409–2420

470   DOI: 10.1111/1365-2745.12978.

471   Steinbauer MJ, Field R, Grytnes JA, Trigas P, Ah-Peng C, Attorre F, Birks HJB, Borges

472   PAV, Cardoso P, Chou CH, de Sanctis M, de Sequeira MM, Duarte MC, Elias RB,

473   Fernández-Palacios JM, Gabriel R, R. E. Gereau RE, R. G. Gillespie RG, J. Greimler J,

474   Harter DEV, Huang TJ, Irl SDH, Jeanmonod D, Jentsch A, Jump AS, Kueffer C, Nogué

475   S, Otto R, Price J, Romeiras MM, Strasberg D, Stuessy T, Svenning JC, Vetaas OR,

476   Beierkuhnlein C. 2016. Topography-driven isolation, speciation and a global increase of

477   endemism with elevation. Global Ecology and Biogeography 25(9): 1097-1107 DOI:

478   10.1111/geb.12469.

479   Valencia BG, Bush MB, Coe AL, Orren E, Gosling WD. 2018. Polylepis woodland dynamics

480   during the last 20,000 years. Journal of Biogeography 45: 1019–1030 DOI:

481   10.1111/jbi.13209.

482   Vargas G, Sánchez JJ. 2005. Plantas con flores de los páramos de Costa Rica y Panamá: el

483   páramo ístmico. In Kappele M, Horn S, eds. Páramos de Costa Rica. San Jose Costa Rica:

484   Editorial INBio, 397-435.

485   Vetaas OR, Grytnes JA. 2002. Distribution of vascular plant species richness and endemic

486   richness along the Himalayan elevation gradient in Nepal. Global Ecology and

487   Biogeography. 11(4): 291-301 DOI: 10.1046/j.1466-822X.2002.00297.x.

488   Vuilleumier F. 1969. Pleistocene speciation in birds living in the high Andes. Nature 223: 1179–

489   1180 DOI: 10.1038/2231179a0.

490   Vuilleumier F, Simberloff D. 1980. Ecology versus history as determinants of patchy and insular

491   distributions in high Andean birds. In Hecht MK, W.C. Steere WC, eds. Evolutionary

492   Biology. New York: Plenum Publishing Corporation, 12: 235-379.

493   Wolda H. 1987. Altitude, habitat and tropical insect diversity. Biological Journal of the Linnean

494   Society. 30(4): 313-323.

495

Figure 1

Map of the region of the Costa Rican Talamanca 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).

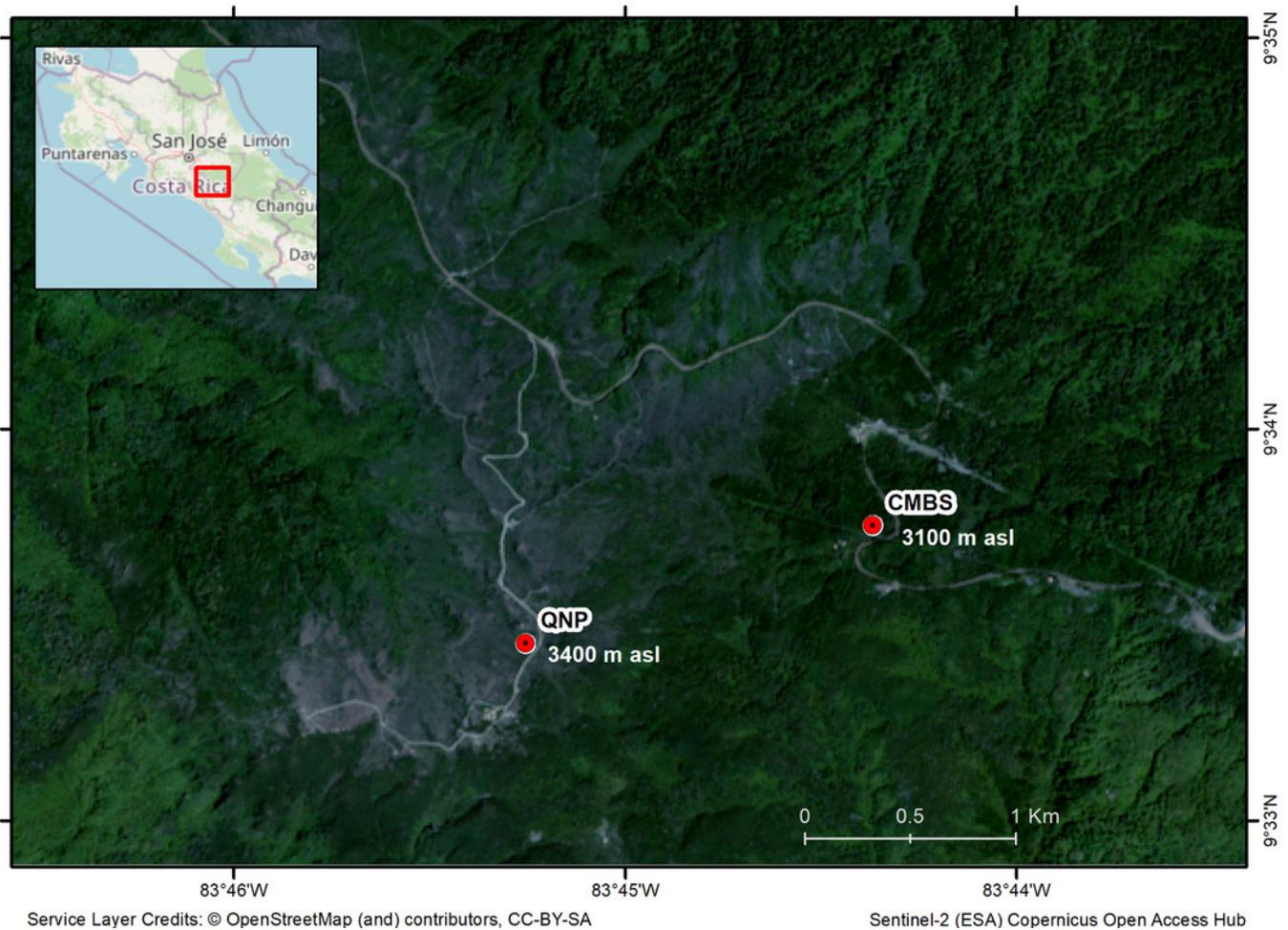



Figure 2

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 Fe

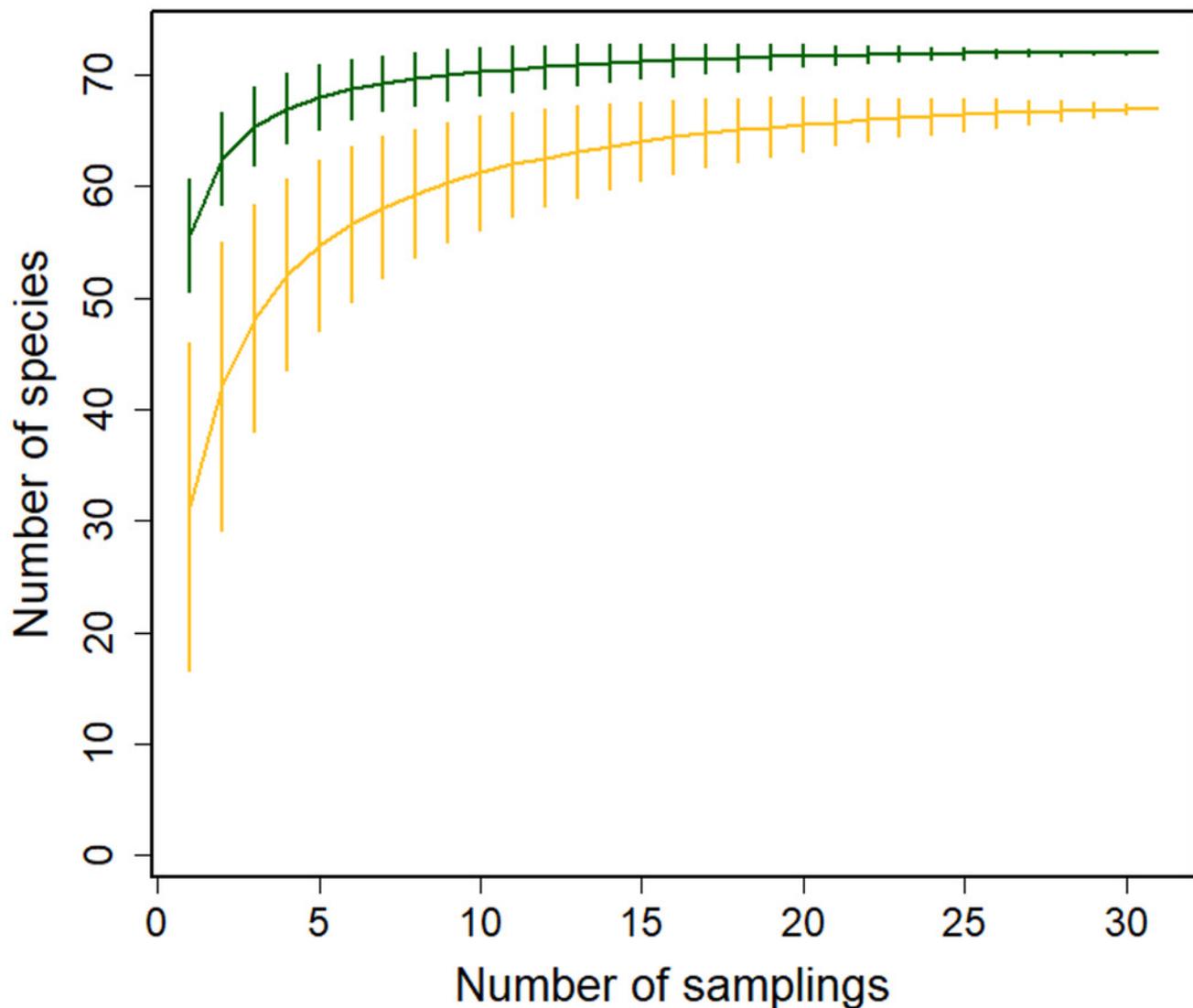



Figure 3

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

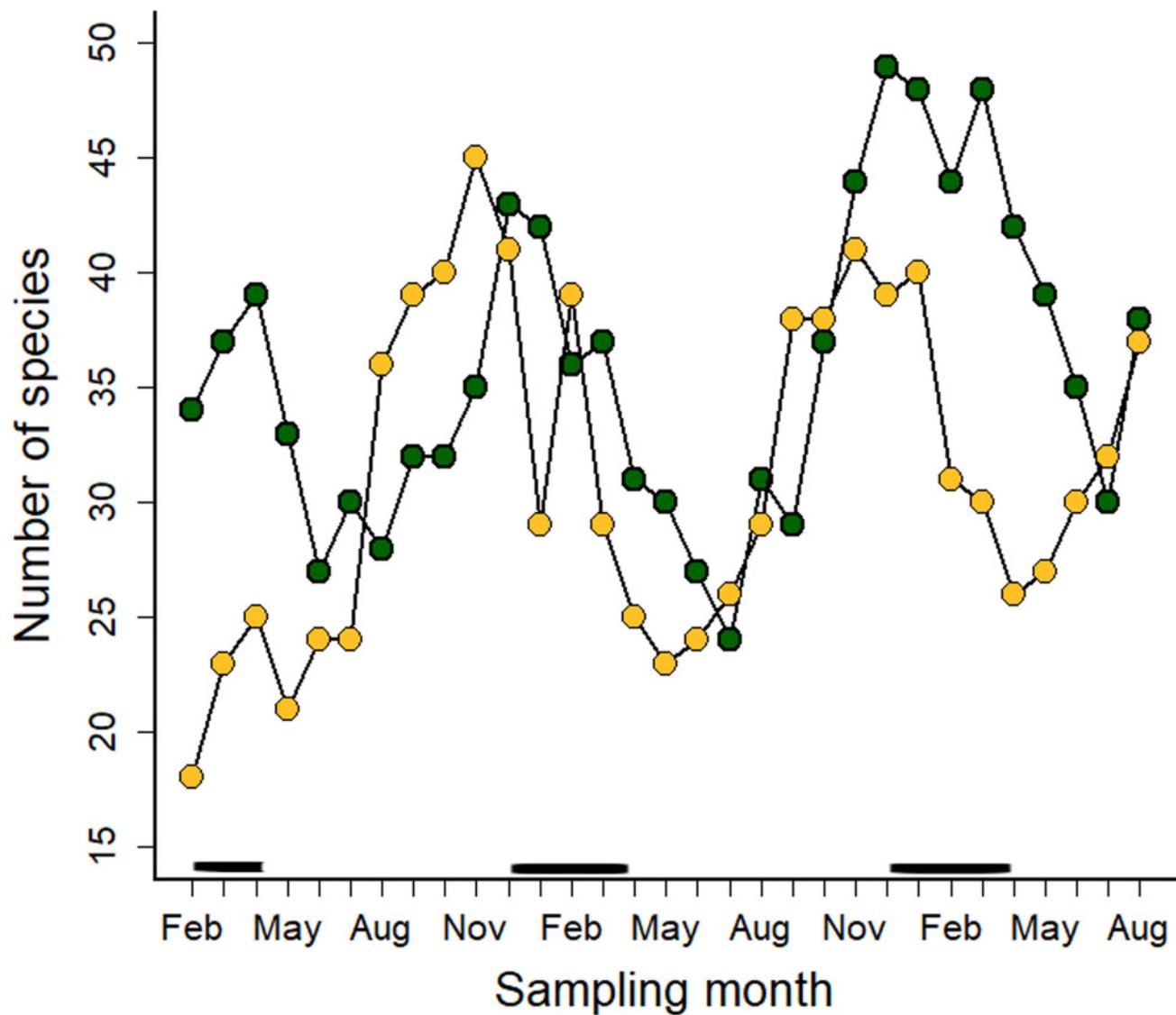
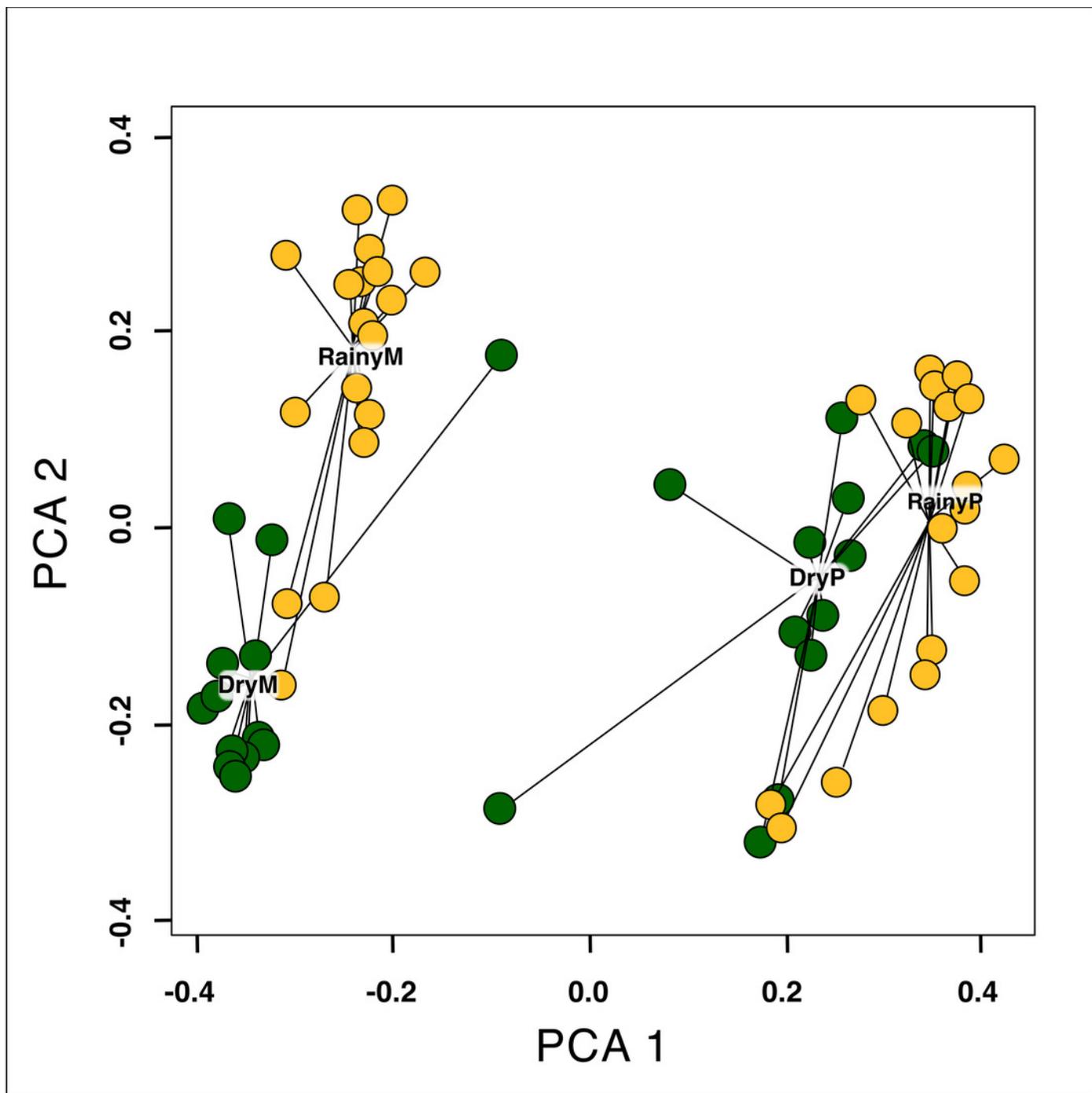



Figure 4

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.

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.
1   **Table 1**. Non-parametric PERMANOVA based on Bray–Curtis distances for all blooming plants
2   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		

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).

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

All blooming plants					
Factor	df	SS	MS	F	P
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		