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

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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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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 temporarily in endangered ecosystems such as the Paramo.

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

46   Montane Forest.

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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.

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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).
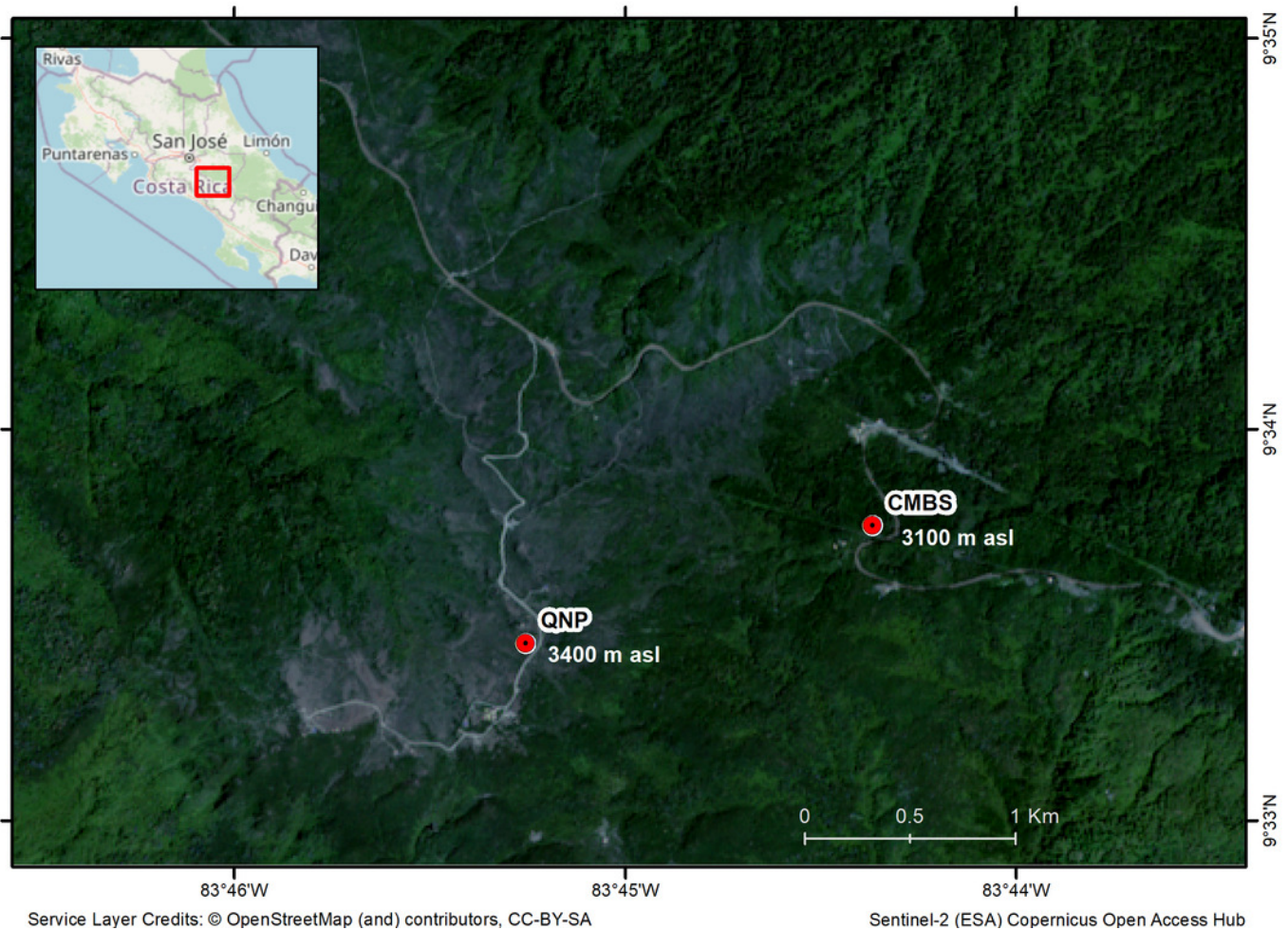
Figure 2

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
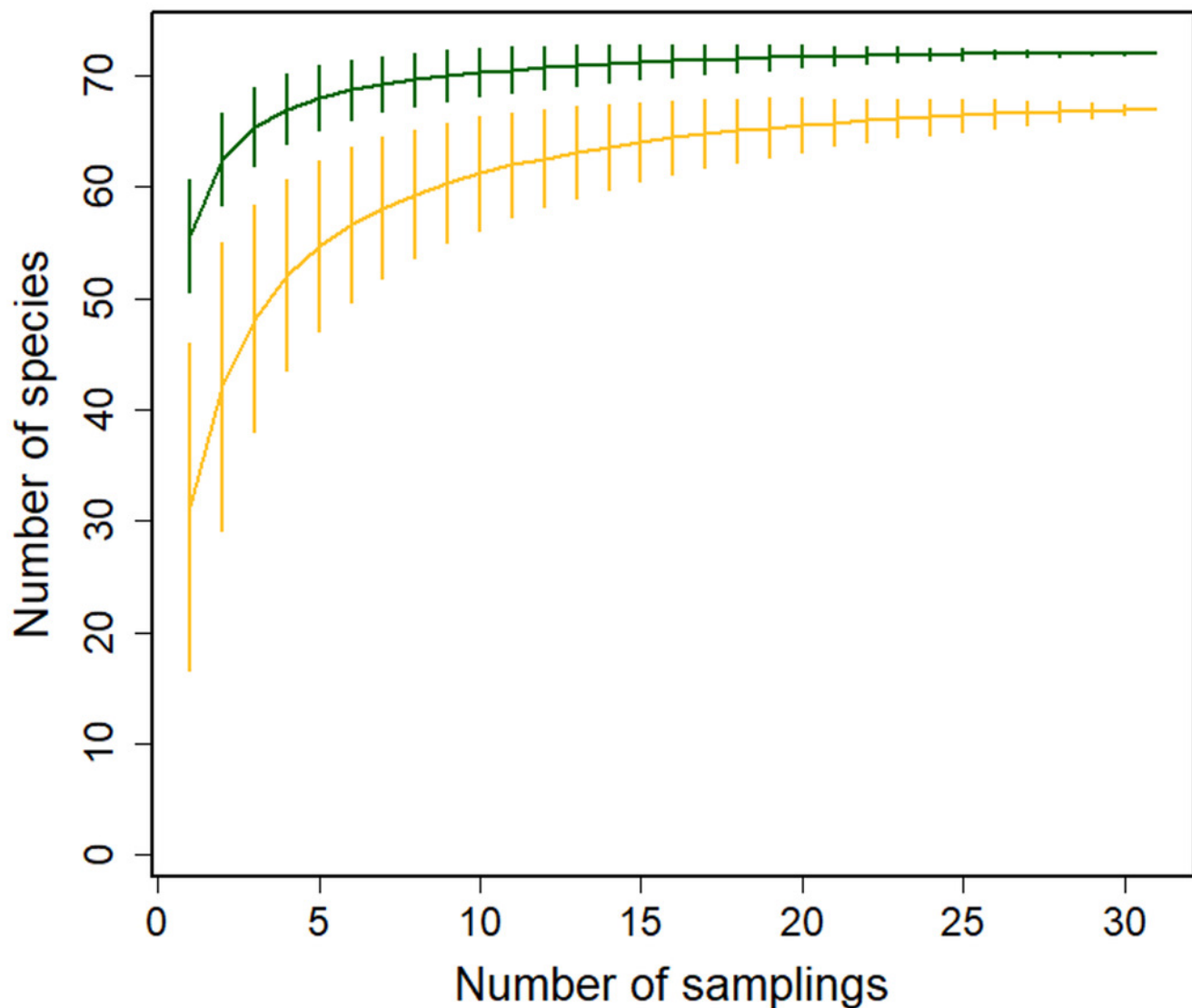
Figure 3

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
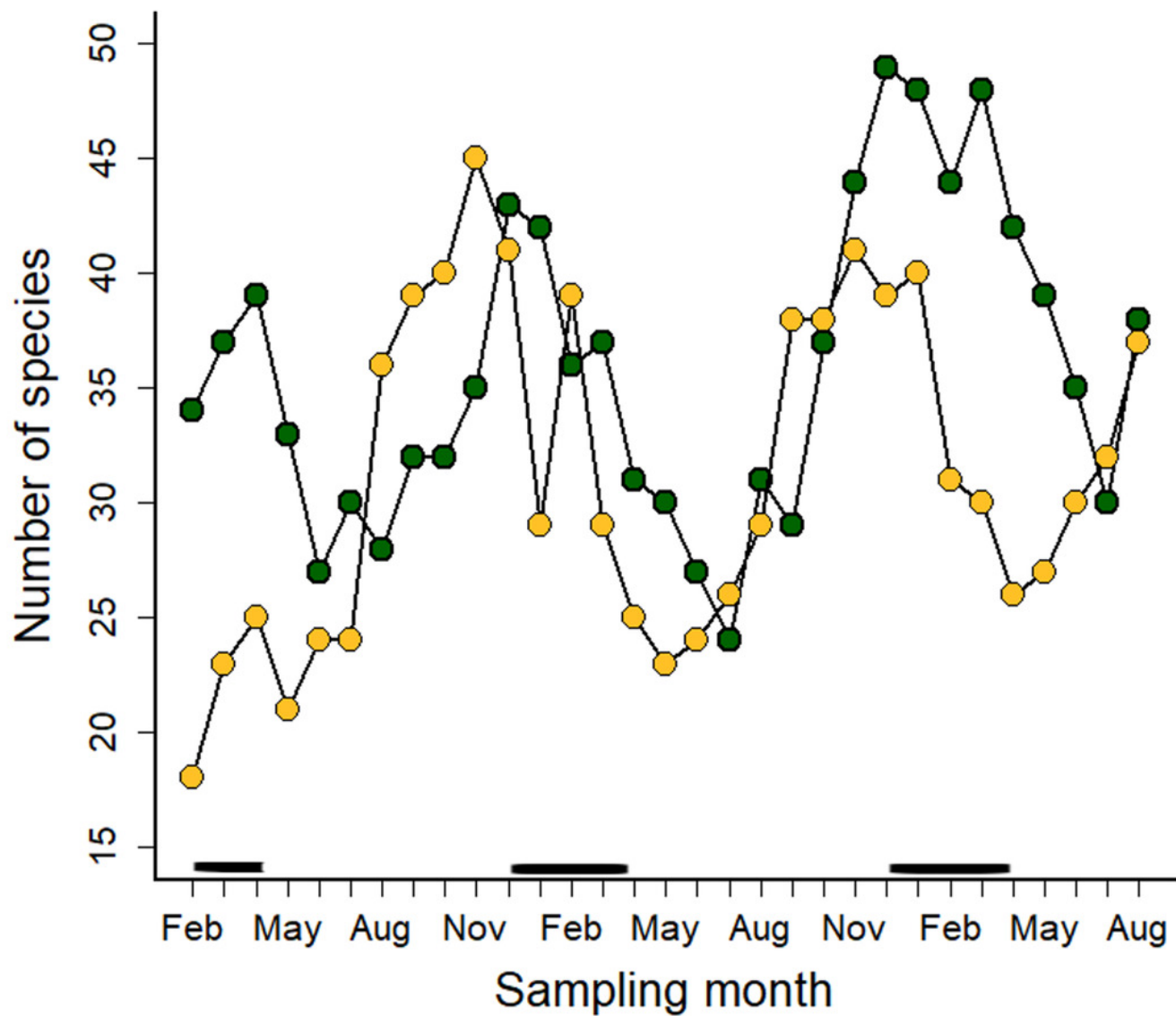
Table 1(on next page)

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.

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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.
3

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		

4

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.
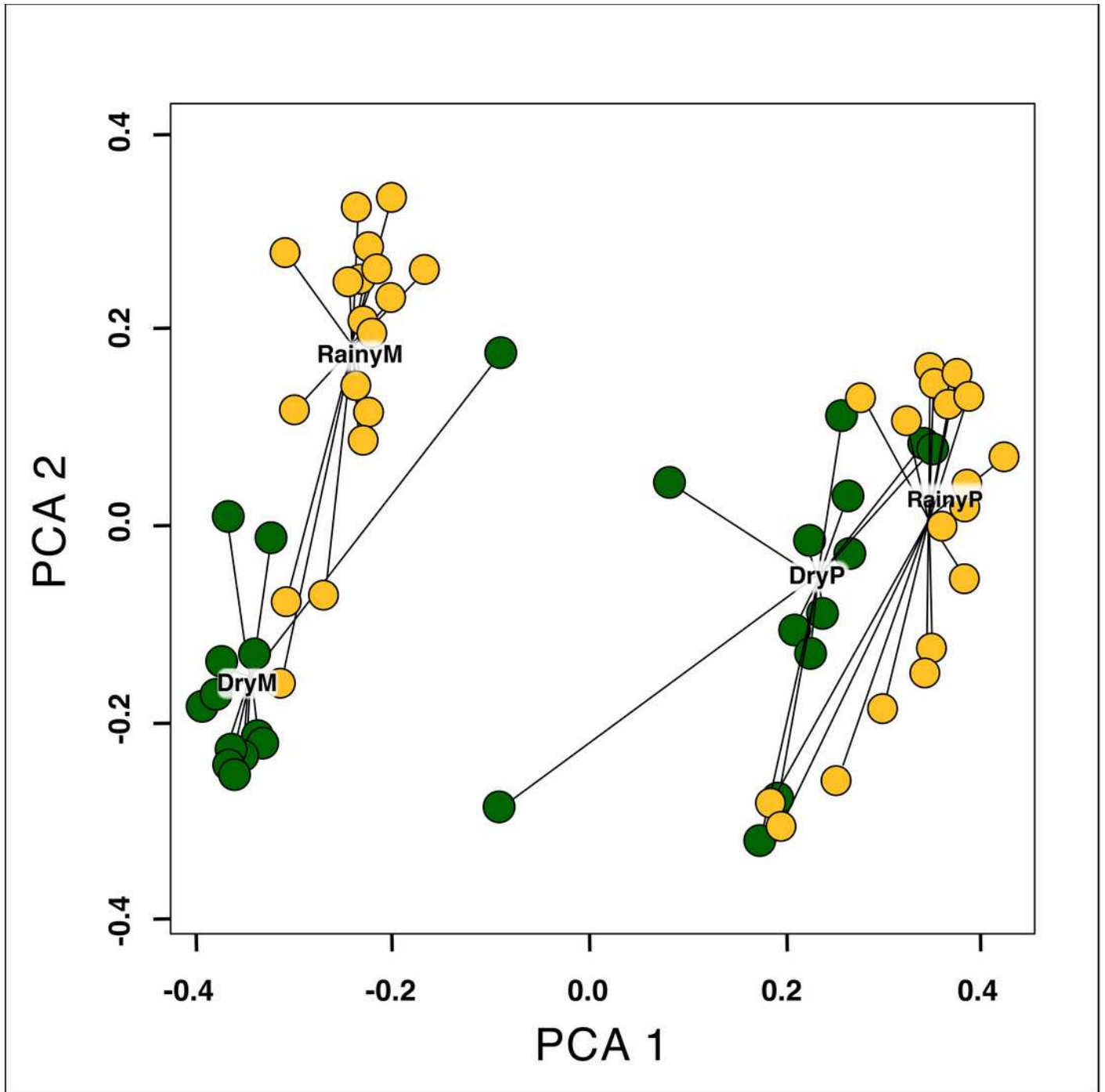
Table 2(on next page)

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).

1

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).
4

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		

5

6