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 notably differs 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 limits 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. Analyzes 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 notably differs 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 limits species establishment. Differences in blooming plant composition between both

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

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

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

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

42 change 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.

47 **1. INTRODUCTION**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

87   floral visitors.

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

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

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

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

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

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

94   year.

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

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

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

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

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

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

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

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

103 Central American highland ecosystems.

104   In this study, we used flowering phenology to describe the temporal availability of floral

105 resources for insects and birds, and compare their spatial distribution in terms of plant

106 composition and diversity between the two highest-elevation ecosystems in Costa Rica: the

107 Paramo and the Montane Forest. We predict significant differences in community composition

108 between the Paramo and the adjacent Montane Forest, with higher species richness and beta-

109 diversity of blooming plants in Montane Forests, due to the large number of endemic species

110 present in the Paramo and the reduction in species richness as elevation increases. We also

111 predict a higher diversity of the blooming plant community in the rainy season, in both

112 ecosystems, due to milder temperatures and higher water availability compared to more severe

113 conditions prevalent during the dry season.

114

2. MATERIALS AND METHODS

2.1 Study area

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

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

119 (QNP). The CMBS is a Montane Forest at an elevation of 3100 m asl (09° 33' N; 83° 44' W) and

120 the QNP is a Paramo habitat at 3400 m asl. The two sites are separated by 2 km. The region's

121 average annual precipitation is 2500 mm, with a relatively dry period from mid-November to

122 April, and a mean annual temperature of 11°C for the CMBS and 7.6°C in the QNP (Herrera,

123 2005). During the day, temperatures fluctuate dramatically, particularly in the Paramo (-5 °C to

124 35 °C) (Herrera, 2005). Montane Forests are dominated by oaks with abundant epiphytes and

125 shrubs (e.g., Ericaceae, Asteraceae, Onagraceae) (Calderón-Sanou et al., 2019). Meanwhile, the

126 Paramo is dominated by a herbaceous stratum, with a large diversity of Asteraceae and Poaceae,

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

128 Hypericaceae (Vargas & Sanchez 2005).

129

2.2 Sampling

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

132 blooming plants monthly for 30 months (February 2019 to August 2021). We classified

133 blooming plants into insect-pollinated (bee-pollinated and fly-pollinated), bird-pollinated

134 (mainly hummingbirds) and insect+bird-pollinated types, based on their morphology and floral

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

136 pollinated species, such as oaks (Fagaceae), grasses and sedges (Poaceae and Cyperaceae,

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

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

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

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

141

142 *2.3 Statistical Analyses*

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

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

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

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

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

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

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

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

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

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

153 the response variable.

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

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

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

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

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

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

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

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

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

163   analyses (R Development Core Team, 2021).

164

165   **3. RESULTS**

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

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

168   rarefaction analysis, the species richness of blooming plants was higher in the Montane Forest

169   (Fig. 1). Similarly, the richness of plants pollinated by insects+birds and by birds only was

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

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

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

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

174   The number of blooming plant species varied over time (Fig. 2). All blooming plant

175   species in both ecosystems peaked during the dry season (Fig. 2), but insect-pollinated plants had

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

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

178   seasonal pattern (Fig. S2 b-c); however, floral resources in these two plant categories were

179   constant throughout the year. In the case of bird-pollinated plant species, the number of

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

181   The multidimensional scaling distances showed that species composition differed

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

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

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

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

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

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

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

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

190   plant species (Fig. 3). However, this pattern is reversed for bird-pollinated plant species, where

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

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

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

194   the Paramo for all categories of blooming plants (Table 2, Fig. 3; Fig. S4 a-d). This suggests that

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

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

197   blooming plants differently.

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203   **4. DISCUSSION**

204   Species composition and diversity of plants at tropical high elevations have been strongly

205   influenced by local and regional environmental traits, and historical events (Simpson, 1975;

206   Hooghiemstra et al., 1992; Islebe et al., 1995, 1996; Sklenář et al., 2011). For instance, the Costa

207 Rican Paramo shares many genera with the Andean Paramo and with nearctic temperate habitats

208 (Cleef & Chaverri, 1992; Hughes and Eastwood, 2006) as a result of dispersal pulses

209 experienced by this vegetations during the last Pleistocene glacial events (Simpson & Neff,

210 1992; Sklenář et al., 2011; Londoño et al., 2014). The available habitat for those plant species

211 that established themselves in the Costa Rican highlands contracted as climate returned to

212 tropical conditions after glacial events ended. These changes isolated these species in the Costa

213 Rican highlands, promoting speciation and endemism in this region (Barrantes, 2009).

214 Additionally, the climatic conditions prevailing for the last 10 Ky at the summit of the

215 Talamanca mountain range allowed the Paramo vegetation to persist. These factors act

216 synergistically to produce the differences in diversity patterns between the Paramo and adjacent

217 Montane Forests shown in this study.

218   Our results also showed that the composition of blooming plants (based on non-metric

219 multidimensional scaling of dissimilarity measures) differed significantly between the Paramo

220 and the Montane Forest. In comparison to the adjacent Montane Forest, the Paramo has a lower

221 richness of flowering species. The study sites are geographically adjacent and separated by 2 km;

222 however, the relatively small change in elevation (~400 m) becomes a determinant factor in

223 shaping species composition differences. Consequently, temporal turnover (beta diversity) of

224 blooming plants also differed between ecosystems and such differences are likely related to the

225 uniqueness of the Costa Rican Paramo vegetation (Cleef & Chaverri, 1992). The evolution of a

226 unique vegetation in the Costa Rican Paramo, which notably differs notably from the adjacent

227 Montane Forest, can be the result of several factors: a) the plant dispersal events that occurred

228 during the late Pleistocene (Simpson & Neff, 1992; Sklenář et al., 2011; Londoño et al., 2014),

229 b) the geographic isolation when climate changed after the Pleistocene, and c) the prevalence of

230   cold climatic conditions at the summit of the Talamanca Mountain range. Vicariance driven by

231   the climate shifts after the Pleistocene in conjunction with topographic isolation, has shaped the

232   evolution of several plant clades within the Andean cordilleras (Simpson,1975; Luebert &

233   Weigend, 2014). For instance, a possible explanation for the rapid radiation of the common

234   *Valeriana* and *Hypericum* species in the Andean Paramo, as well as the species present in the

235   Costa Rican Paramo, is the repeated fragmentation-isolation process, as a consequence of the

236   Pleistocene climatic fluctuations in a topographically complex region (Moore & Donoghue,

237   2007; Nürk et al., 2014).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

254   2006; Souza et al., 2018). At least one hummingbird species is active year-round in our study

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

271   ecosystem.

272   In conclusion, we found that richness and beta diversity differed between the Paramo and

273   an adjacent Montane Forest, and such differences are likely a consequence of historical events

274   (e.g., dispersal promoted changes in climate), and the edaphic and climatic conditions prevailing

275   in the study region. The blooming species composition and flowering phenology differed

276   between the two ecosystems and seasons (dry and rainy). Paramo ecosystems are more exposed

277   to strong wind gusts, direct sun radiation, and lower temperatures when compared with Montane

278   Forests (Körner, 2021). These factors may act as climatic cues that trigger the phenological

279   patterns in different plant species, but a phylogenetic effect (e.g., related plant species flowering

280   at the same time due to common ancestry) cannot be discarded (Davies et al., 2013). Our

281   findings also showed that the composition and diversity of floral resources for insects and birds

282   are lower in the Paramo than in the Montane Forest. This supports the idea that resource

283   depletion may limit the use of the Paramo for nectar-feeding birds and insects (Janzen et al.,

284   1976; Barrantes, 2005; Fuchs et al., 2010). However, this abrupt reduction in insect and bird

285   diversity is more likely explained by the synergetic effect of vegetation structure, severe climatic

286   conditions, and the availability of food resources than by a single factor. This study showed that

287   analyses of species composition and richness based on flowering phenology data are useful in

288   evaluating potential floral resources for floral visitors (insects and birds), and how these

289   resources change spatially and temporarily in these endangered ecosystems.

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291   **ACKNOWLEDGEMENTS**

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516

Figure 1

FIG 1. 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
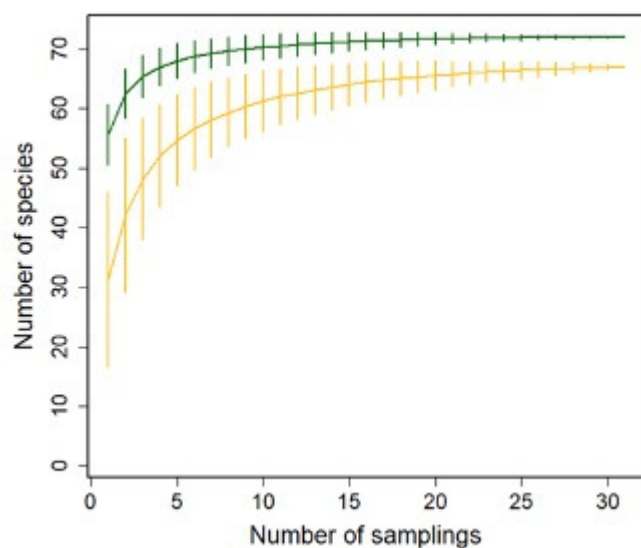
Figure 2

FIG 2. 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 in
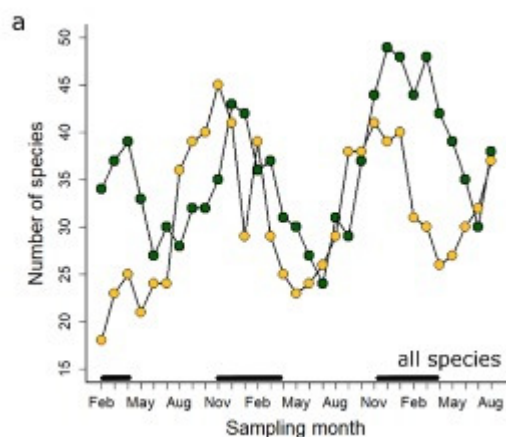
Figure 3

FIG 3. Effect of site and season (WetM: Montane Forest - rainy season; DryM: Montane Forest - dry season; WetP: Paramo - rainy season; DryP: Paramo - dry season) on the beta diversity of blooming plant species, in the Costa Rican Talamanca mountain range.

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.
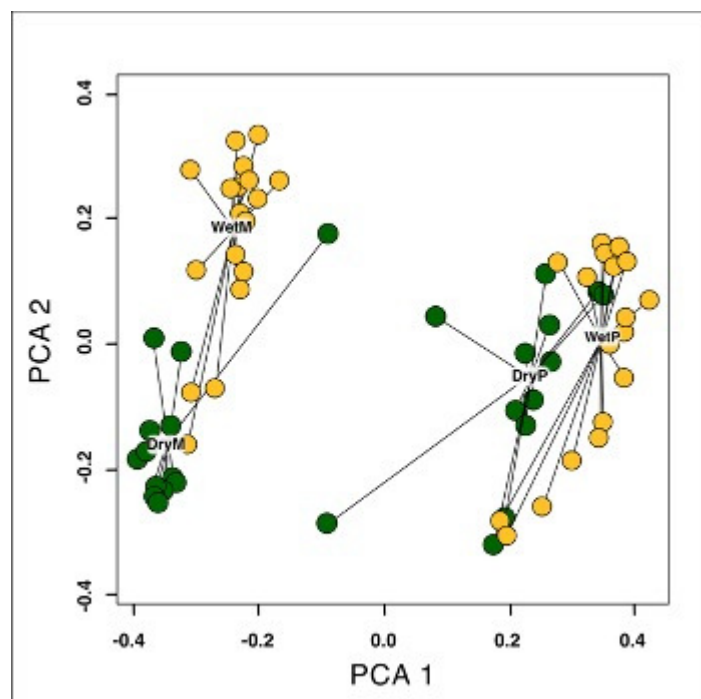
Table 1(on next page)

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.

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

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).

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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