Flower diversity and bee reproduction in an arid ecosystem

Jimena Dorado, Diego P. Vázquez

Background. Diverse flower communities are more stable in floral resource production along the flowering season, but the question about how the diversity and stability of resources affect pollinator reproduction remains open. High plant diversity could favor short foraging trips, which in turn would enhance bee fitness. In addition to plant diversity, greater temporal stability of floral resources in diverse communities could favor pollinator fitness because such communities are likely to occupy the phenological space more broadly, increasing floral availability for pollinators throughout the season. In addition, this potential effect of flower diversity on bee reproduction could be stronger for generalist pollinators because they can use a broader floral spectrum. Based on above arguments we predicted that pollinator reproduction would be positively correlated to flower diversity, and to temporal stability in flower production, and that this relationship would be stronger for the most generalized pollinator species. **Materials & Methods.** Using structural equation models, we evaluated the effect of these variables and other ecological factors on three estimates of bee reproduction, and whether such effects were modulated by bee generalization on floral resources. **Results.** Contrary to our expectations, flower diversity had no effect on bee reproduction, stability in flower production had a weakly negative effect on one of the bee reproductive variables, and the strength of the fitness-diversity relationship was unrelated to bee generalization. In contrast, elevation had a weak, non significant negative effect on bee reproduction, despite the narrow elevation range encompassed by our sites. **Discussion.** Flower diversity did not affect the reproduction of the solitary bees studied here. Although high temporal stability in flower production is expected to enhance pollinator reproduction, in our study it had a weakly negative---instead of positive---effect on the average number of brood cells per nest. Other environmental factors that vary with elevation could influence bee reproduction. Our study focused on a small group of closely-related bee species, which cautions against generalization of our findings to other groups of pollinators. More studies are clearly needed to assess the extent to which pollinator demography is influenced by the diversity of floral resources.

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Abstract

Background. Diverse flower communities are more stable in floral resource production along the flowering season, but the question about how the diversity and stability of resources affect pollinator reproduction remains open. High plant diversity could favor short foraging trips, which in turn would enhance bee fitness. In addition to plant diversity, greater temporal stability of floral resources in diverse communities could favor pollinator fitness because such communities are likely to occupy the phenological space more broadly, increasing floral availability for pollinators throughout the season. In addition, this potential effect of flower diversity on bee reproduction could be stronger for generalist pollinators because they can use a broader floral spectrum. Based on above arguments we predicted that pollinator reproduction would be positively correlated to flower diversity, and to temporal stability in flower production, and that this relationship would be stronger for the most generalized pollinator species.

Materials & Methods. Using structural equation models, we evaluated the effect of these variables and other ecological factors on three estimates of bee reproduction, and whether such effects were modulated by bee generalization on floral resources. **Results.** Contrary to our expectations, flower diversity had no effect on bee reproduction, stability in flower production had a weakly negative effect on one of the bee reproductive variables, and the strength of the fitness-diversity relationship was unrelated to bee generalization. In contrast, elevation had a weak, non significant negative effect on bee reproduction, despite the narrow elevation range encompassed by our sites. **Discussion.** Flower diversity did not affect the reproduction of the solitary bees studied here. Although high temporal stability in flower production is expected to enhance pollinator reproduction, in our study it had a weakly negative---instead of positive--- effect on the average number of brood cells per nest. Other environmental factors that vary with

elevation could influence bee reproduction. Our study focused on a small group of closely-related bee species, which cautions against generalization of our findings to other groups of pollinators. More studies are clearly needed to assess the extent to which pollinator demography is influenced by the diversity of floral resources.

Key words: pollination, flower diversity, bee fitness

Introduction

There is a consensus that diversity enhances ecosystem functioning (Cardinale et al. 2012). Species diversity provides redundancy in function, so that ecological processes are more stable in more diverse communities (MacArthur 1955, Elton 1958). Stability has multiple definitions, resulting in a variety of diversity–stability relationships (Ives & Carpenter 2007). In plant communities, the diversity–stability relationship has been well studied for biomass production (Caldeira et al. 2005, Tilman, Reich & Knops 2006, Isbell et al. 2009, Hector et al. 2010), and we have recently reported that diverse flower communities are also more temporally stable in terms of floral resource production (Dorado & Vázquez 2014). But the question about how the diversity and stability of resources affect reproduction of pollinators remains open. Wild bees are gaining increasing attention as they are known to enhance fruit set of crops regardless of honey bee abundance (Garibaldi et al. 2013). Thus, generating knowledge that contributes to understand the determinants of the demography and population dynamics of pollinators is becoming a priority, as it can contribute to their conservation.

There is a general positive association between plant and pollinator diversity (e.g., Steffan-Dewenter & Tscharntke 2001, Potts et al. 2003a, Ebeling et al. 2008, Fründ, Linsenmair & Blüthgen 2010), but little is known about the mechanisms behind this relationship. A positive relationship would be expected if the diversity in one group enhanced the populations in the other group, so that greater flower diversity enhanced the demography of pollinator populations, and greater pollinator diversity enhanced the demography of plant populations. For example, blueberries planted next to wild flowers that support rich pollinator assemblages produced higher fruit set, berry weight, and number of mature seeds per berry (Blaauw & Isaacs 2014). Similarly,

a generalist cavity nesting bee species (*Osmia rufa*) reduces its foraging trip duration as the number of plant species increases (Gathmann & Tscharntke 2002), which can result in higher energy available for reproduction. Another bee (*Dieunomia triangulifera*) increased its mean reproductive success when collecting high amount of pollen in shorter foraging trips (Minckley et al. 1994), whereas other bees (*Hoplitis adunca* and *Chelostoma rapunculi*) decreased the proportion of brood cells provisioned per time unit with long foraging trips (Zurbuchen et al. 2010). In another species (*Osmia lignaria*), fitness depends on the closeness to natural patches (Williams & Kremen 2007), which usually harbor greater plant diversity; this bee species also feeds its larvae using pollen from different plant species despite higher foraging costs (Williams & Tepedino 2003). Thus, if high plant diversity tends to shorten foraging trips, and short foraging trips enhance bee fitness, plant diversity could indirectly enhance bee fitness. This effect should be stronger for polylectic than oligolectic pollinators, given that the latter are more restricted in their diet.

In addition to plant diversity, greater temporal stability of floral resources in diverse communities (Dorado & Vázquez 2014) could favor pollinator fitness because such communities are likely to occupy the phenological space more broadly than their species-poor counterparts, increasing floral availability for pollinators throughout the season. For example, in multi-species assemblages of herbaceous plants of the genus *Clarkia*, diverse communities provide more resources along the flowering season, sustaining a higher number of pollinator individuals per plant (Moeller 2004). Furthermore, a bumblebee study found that even if floral resources are abundant, high stability of floral resources throughout the flowering season is needed to enhance bumblebee fitness (Wesphal et al. 2009). Thus, both high flower abundance and high temporal

stability of floral resources are likely to enhance pollinator reproduction (Müller et al. 2006, Westphal, Steffan-Dewenter, & Tscharntke 2009).

To evaluate whether there is an effect of flower diversity on pollinator reproduction it is necessary to disentangle the effect of flower abundance, as it could be positively correlated with flower richness, as it happens with biomass in plant communities (Tilman 1999); if so, there could be a spurious positive correlation between flower richness and pollinator fitness. Other local environmental factors, such as elevation or disturbance history, should also be accounted for, as they are known to influence species diversity (Potts et al. 2003b, Grytnes and McCain 2007, Dorado & Vázquez 2014). Structural equation modeling (SEM) represents an excellent tool to assess causal relationships among multiple variables simultaneously (Grace 2006).

Our aim is to study the effect of flower diversity and temporal stability of floral resources on the reproduction of seven species of cavity nesting bees from the Monte desert in Argentina. Based on the above arguments, we expected to find that flower diversity and temporal stability of floral resources correlates positively to three estimates of bee reproduction: average number of brood cells per nest per site, total number of brood cells per site, and total number of nests per site. We also expected to find a positive correlation between the strength of the fitness-diversity correlation and the degree of generalization of each bee species.

Methods

Study area and sampling

This study was conducted in the Monte desert in Villavicencio Nature Reserve, located ca. 40

106 km north of Mendoza city, Argentina, during the 2008 flowering season (15 October – 8
107 December 2008; authorized by Dirección de Recursos Naturales Renovables de la Provincia de
108 Mendoza, approval numbers 1130 and 646). We worked in fourteen 100 m × 200 m rectangular
109 study sites (minimum and maximum distance between them were 1.11 km and 14.13 km
110 respectively). These sites lie at 1100-1500 m above sea level, at the ecotone between the Monte
111 desert and the Prepuna biomes (Ambrosetti et al. 1986). The plant community is a 2 m tall
112 shrubland dominated by *Larrea divaricata* (Zygophyllaceae), *Zuccagnia punctata* (Fabaceae),
113 *Prosopis flexuosa* (Fabaceae), *Condalia microphylla* (Rhamnaceae), *Acantholippia seriphioides*
114 (Verbenaceae), and *Opuntia sulphurea* (Cactaceae). We selected sites with contrasting flower
115 abundance, composition and diversity. The region suffers from recurrent fires, which are mostly
116 human-caused and are in fact the most common human disturbance (E. L. Stevani, pers. comm.);
117 the time elapsed since the last fire varied substantially among our study sites (Table S1).
118
119 Trap nest sampling
120 We placed trap nests in 6 points per plot as shown in Fig. S1. Each point had two groups of 24
121 trap nests consisting of a wood piece with a longitudinal cavity of 5 mm, 8 mm or 11 mm in
122 diameter, and 15 cm of length for the smallest two diameters and 28 cm of length for the largest
123 diameter; wood pieces were arranged as shown in Fig. S2. Trap nests were checked weekly;
124 occupied traps were taken to the laboratory and replaced by empty ones. Each trap nest
125 constitutes one bee nest. Once in the laboratory, nests were opened to record the number of cells;
126 whenever the nest had more than one brood cell, one of them was extracted for pollen
127 identification, and the rest was kept until adult emergence. Pollen identification was done by
128 comparison with a reference collection, prepared including all plant species that flowered at each

129 study plot (Dorado et. al 2011, Vázquez et. al 2012). The number of emerged adults and their
130 taxonomic identity were recorded in all nests. Although adult number may be a good estimator
131 of female fitness in the absence of larval mortality, because of the high rate of nest parasitism
132 recorded in our study we used instead the number of brood cells per nest as an estimate of female
133 fitness. One species, *Trichothurgus laticeps* Friese, lacks brood cells, as females lay eggs bare
134 amidst a pollen mass; thus, for this species we used the length of the trap cavity occupied by
135 pollen as an estimate of the number of brood cells. For the analysis, we used only the seven bee
136 species that occupied at least 30 trap nests, as we judged smaller sample sizes unreliable for
137 statistical analyses.
138
139 Plant sampling
140 Floral resource availability was studied using flower density. Although he have estimates of the
141 amount of pollen per flower for each species, we decided to use flower density as a measure of
142 resource abundance, as flowers represent the resources packages encountered by pollinators as
143 they forage (see also Vázquez et al. 2009). Flower density was measured weekly at four 8 m ×
144 20 m plots and two 2 m × 50 m transects per site, as described in Fig. S1. We considered weekly
145 sampling intervals adequate, as flowers in our system usually last less than a week. Flower
146 density was estimated multiplying the mean number of flowers per individual by the total
147 number of flowering individuals in the transect or plot when individuals could be distinguished
148 (shrubs and some herbs); we estimated the number of flowers per individual in at least ten
149 individuals of the site. When it was not possible to identify flowering individuals (some
150 herbaceous species), all flowers in a plot or transect were counted. We included in the study all
151 flowering plant species that were assumed to be animal pollinated (we excluded only grass

152 species).

153

154 Statistical analysis

155 To evaluate the effects of flower diversity and temporal stability of floral resources on bee
156 fitness and to assess the influence of other ecological factors on this relationship, we used
157 structural equation models (hereafter SEM). We built a general initial model to explore the
158 effects of flower richness, flower abundance, time elapsed since the last fire, elevation, and
159 temporal stability in flower production on three bee reproductive parameters (average number of
160 brood cells per nest, total number of brood cells per site and total number of nests per site). To
161 estimate the average number of brood cells per nest we used only data of sites where species
162 were present; for the total number of brood cells per site and the total number of nests per site we
163 used data of all sites, as the absence of a species in a site represented zero abundance. Flower
164 richness was used as a proxy of flower diversity; it was rarefied to remove the effect of flower
165 abundance. Flower abundance was estimated as flower density per site. Time elapsed since the
166 last fire was provided by park rangers (E. L. Stevani, personal communication). Temporal
167 stability in flower production along the season was calculated as the inverse of its coefficient of
168 variation (see Dorado & Vázquez 2014). All variables were standardized subtracting each value
169 by the mean and dividing by the standard deviation. For each bee species, from the initial model
170 we generated more parsimonious nested models by removing variables with small non-
171 significant path coefficients (see models in Fig. S3; see also Maestre et al. 2010).

172

173 We evaluated alternative SEM models using a d-separation test (Shipley 2000, 2013) described
174 in S1 section. This analysis allowed us to select the best fitting model based on Akaike's

175 information criterion (AIC) using a small sampling size. To discriminate among competing
176 models we used the AIC difference, ΔAIC, between a given model and the best-fitting one, i.e.,
177 that with the lowest value of AIC. When $\Delta AIC < 3$, models are generally considered to have
178 substantial support; for $3 > \Delta AIC < 7$. models are considered to have considerably less support,
179 while for $\Delta AIC > 10$, models have essentially no support relative to the best model of the set
180 (Richards 2005, Burnham & Anderson 2010). To evaluate whether the studied effects were
181 general for all bee species, we used meta-analytical methods (S2).
182
183 To evaluate whether the effect of flower diversity becomes stronger with increasing pollinator
184 generalization, we performed Spearman's rank correlations between the path coefficient
185 representing the effect of flower richness on each of the three bee reproductive parameters
186 mentioned above, and two measures of the corresponding species degree of generalization. We
187 estimated the degree of diet generalization of each bee species using the species degree and
188 Simpson's diversity index; degree is simply the number of food species consumed from all sites
189 polled, whereas Simpson's index is a function of the number of food items and the proportion in
190 which they were consumed. We used rarefaction to estimate both measures of generalization to
191 make them comparable among bee species, as the number of brood cells was highly variable
192 among nests. A positive correlation between the path coefficient of flower richness on bee
193 reproduction and generalization would support our hypothesis that the reproduction of generalist
194 pollinators is enhanced by flower richness.
195
196 All analyses were performed using R statistical software (R Core Team 2013). Rarefaction of
197 flower richness was performed using the rarefy function of the vegan package (Oksanen et al.

198 2013). Pearson's partial correlations were performed using the pcor.test function of the ppcor
199 package to obtain independence probabilities and the path coefficients (Kim and Yi 2007, Kim &
200 Yi 2006, Johnson & Dean 2002).
201
202 **Results**
203 We recorded 598 occupied trap nests by 11 solitary bee species (Table 1).
204
205 The complete model assessing the influence of multiple ecological factors on the potential
206 relationship between flower diversity and bee fitness (Model 1, Fig. S3a) showed no effect of
207 flower abundance or time elapsed since the last fire on the bee reproductive variables studied.
208 Although the only significant effect was that of temporal stability on the average number of
209 brood cells per nest, we kept flower richness and elevation in the simplified model because they
210 showed suggestive, albeit non significant, trends. There was a weak positive effect of flower
211 richness on average number of brood cells per nest and a weak negative effect of elevation on
212 the three reproductive variables (Fig S4); however, none of these effects were statistically
213 significant. The simplified model (model 2, Fig. S3b) fitted best according to ΔAIC (8.43) for all
214 species (see S1 and Fig S3); this model fits the data well according to the d-separation test (p =
215 0.84, df = 2, C = 3.69). In this simplified model, the negative effect of temporal stability in
216 flower production on the average number of cells per nest was weaker than in the complete
217 model (Fig 1 blue error bars; confidence limits of path coefficient for model 1: -0.467, -0.101;
218 confidence limits of path coefficient of model 2: -0.264, -0.004). Also, the simplified model
219 shows a negative trend in the effect of elevation on the total number of cells and nests per site,
220 but this trend is statistically non significant (confidence limits of path coefficients for the total

221 number of cells and nests per site respectively: -0.465, 0.031, and -0.472, 0.027).

222

223 The effect of flower diversity on pollinator reproduction was unrelated to pollinator
224 generalization for any of the bee reproductive variables and generalization indices used (Table
225 2).

226

227 **Discussion**

228 Contrary to our expectations, we found no effects of flower diversity and flower abundance on
229 bee reproduction. Thus, flower diversity did not matter for the reproduction of the solitary bees
230 studied here. Although high temporal stability in flower production is expected to enhance
231 pollinator reproduction (Wesphal et al. 2009, Dorado & Vázquez 2014), in our study it had a
232 weakly negative---instead of positive---effect on the average number of brood cells per nest. In
233 contrast, elevation had a non significant negative effect on bee reproduction, despite the narrow
234 elevational range encompassed by our sites (1100–1500 m), which suggests that the intrinsic
235 characteristics of the study sites could have influenced the relationship between floral diversity
236 and bee reproduction.

237

238 An explanation of the negative effect of temporal stability on brood cell production concerns a
239 compensatory behavior of females to avoid parasitism. In sites with high temporal stability in
240 flower production, females might lay fewer eggs per nest while building more nests, so as to
241 maximize larval survival per site. This reasoning makes two implicit assumptions. First, that the
242 bee species are parasitized , which we indeed observed for many of the bee species studied here
243 (data not shown). Second, that nesting sites are not limited for the population. In fact, the trap

244 nest sampling with replacement highly increased the nest availability in our study sites. If this
245 mechanism were responsible for the observed negative effect of temporal stability in flower
246 production on the average number of brood cells per nest, we would expect the number of cells
247 per site to be either unrelated to temporal stability or to be higher in the more temporally stable
248 sites, and the number of nests to be higher in the more temporally stable sites, as females would
249 be laying eggs at their maximum capacity but distributing them in more nests. Matching these
250 expectations, the total number of brood cells per site was unrelated to temporal stability (Fig. 1,
251 flower stability), while the number of nests per site tends to increase with temporal stability for
252 most species, although the effect was statistically non-significant.
253
254 An alternative explanation of the negative effect of temporal stability on brood cell production
255 per nest could be that elevation might be weakening the effects of other variables on pollinator
256 reproduction. This is particularly likely considering the positive direct effect of elevation on
257 flower diversity, the positive indirect effect of elevation on stability, and the (nonsignificant)
258 negative effect of elevation on bee reproduction (Fig. 1); these effects could be neutralizing the
259 effect of the flower diversity and temporal stability in flower production on bee reproduction.
260 The upper sites are located in ravines, which are probably wetter and cooler than the lower sites,
261 located in open land. Thus, changes in humidity and temperature associated to elevation could be
262 influencing bee reproduction more strongly than the other ecological factors studied here.
263
264 We found no support for the idea that generalist bees are more favored in their reproduction by
265 flower diversity than specialized ones, despite bee species of this study having contrasting
266 degrees of feeding specialization. This result is reasonable given our finding of no general effect

of flower diversity on bee reproduction.

Our study focused on a small group of closely-related bee species, representing less than 5% of the pollinator assemblage in our study area (Chacoff et. al 2012). Our study is in this sense limited, and our finding of no effects of floral diversity on pollinator demography cannot be generalized. More studies are clearly needed to assess the extent to which pollinator demography is influenced by the diversity of floral resources. Furthermore, although we have considered environmental factors, such as elevation or time post-fire, which appeared a priori good candidates to influence bee demography, other environmental factors may also be important. These include humidity and temperature, which should covary with elevation, and other biotic factors such as competition, predation and parasitism.

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Figure 1. Box-plot summarizing the path coefficients of model 2 (see Fig. S3) for the seven bee species studied here. Model 2 describes the effect of flower diversity (estimated using flower richness), temporal stability of flower production along the flowering season (estimated as the inverse of the coefficient of variation of the weekly flower abundance mean), and elevation (m above sea level). The ordinates represents the path coefficients; the abscissa represent the effect of the above ecological variables on three bee reproductive variables: A, average brood cell number per nest per site; B, total number of brood cells per site; C, total number of nests per site. Black error bars are the maximum and minimum values, and blue error bars are the ninety-five percent confidence limits of path coefficients obtained from bootstrap sampling of the distribution of path coefficients, and black.

Table 1(on next page)

Table 1

Number of nests per species. We used in this study the species that had more than 30 nests.

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Bee species	Occupied trap nests
Anthidium andinum Jörgensen	6
Anthidium decaspilum Moure	54
Anthidium rubripes Friese	31
Anthidium vigintipunctatum Friese	39
Megachile sp. A	222
Megachile sp. C	17
Megachile ctenophora Holmberg	74
Mourecotelles triciliatus Toro y Cabezas	3
Trichothurgus laticeps Friese	59
Xylocopa ordinaria Smith	88
Xylocopa splendidula Lepertier	5

Table 2(on next page)

Table 2

Correlation coefficients between effect of flower diversity on pollinator reproduction and bee generalization.

Table 2. Correlation coefficients between effect of flower diversity on pollinator reproduction and bee generalization.

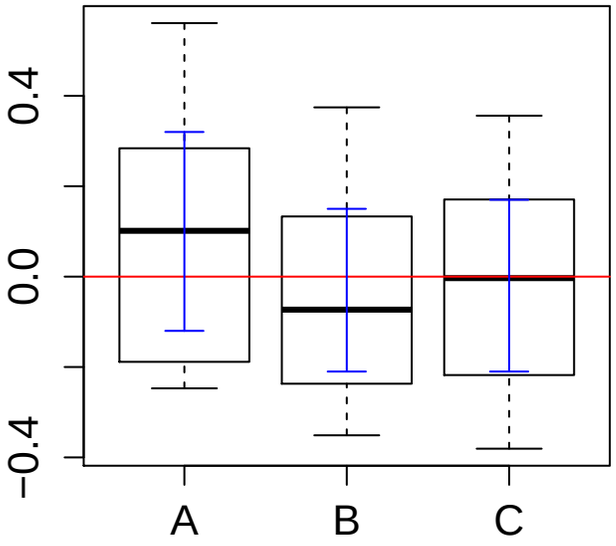
Generalization index	Reproductive variable	Correlation coeficient (*r*)	*p*-value	*N*
degree	Average number of cells per nest	- 0.21	0.66	7
degree	Total number of cells per site	0.42	0.35	7
degree	Total number of nests per site	0.39	0.39	7
Simpson's diversity index	Average number of cells per nest	0.14	0.78	7
Simpson's diversity index	Total number of cells per site	0.46	0.30	7
Simpson's diversity index	Total number of nests per site	0.28	0.55	7

Figure 1(on next page)

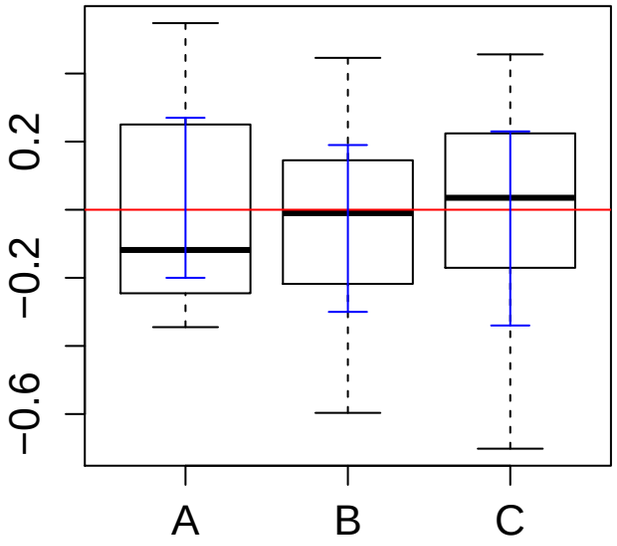
Figure 1

Figure 1. Box-plot summarizing the path coefficients of model 2 (see Fig. S3) for the seven bee species studied here. Model 2 describes the effect of flower diversity (estimated using flower richness), temporal stability of flower production along the flowering season (estimated as the inverse of the coefficient of variation of the weekly flower abundance mean), and elevation (m above sea level). The ordinates represents the path coefficients; the abscissa represent the effect of the above ecological variables on three bee reproductive variables: A, average brood cell number per nest per site; B, total number of brood cells per site; C, total number of nests per site. Black error bars are the maximum and minimum values, and blue error bars are the ninety-five percent confidence limits of path coefficients obtained from bootstrap sampling of the distribution of path coefficients, and black.

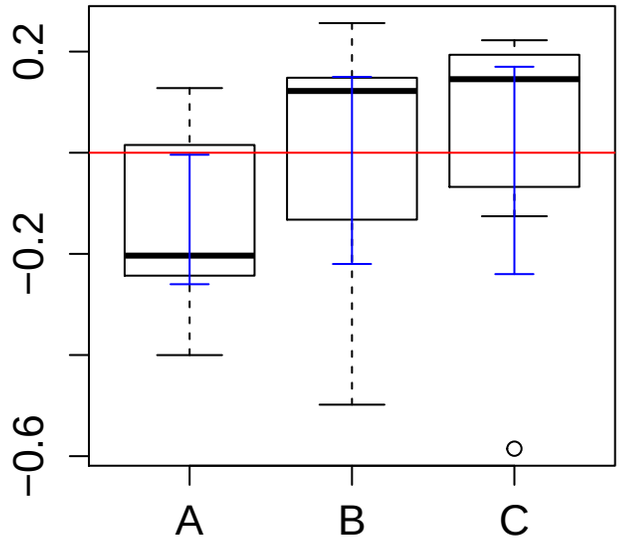
Flower diversity



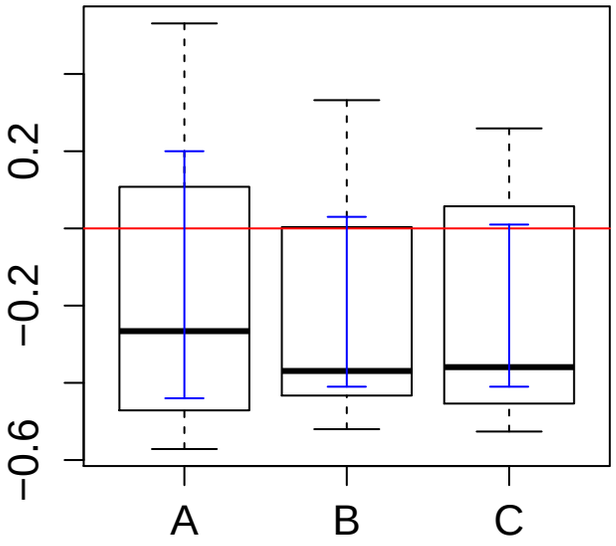
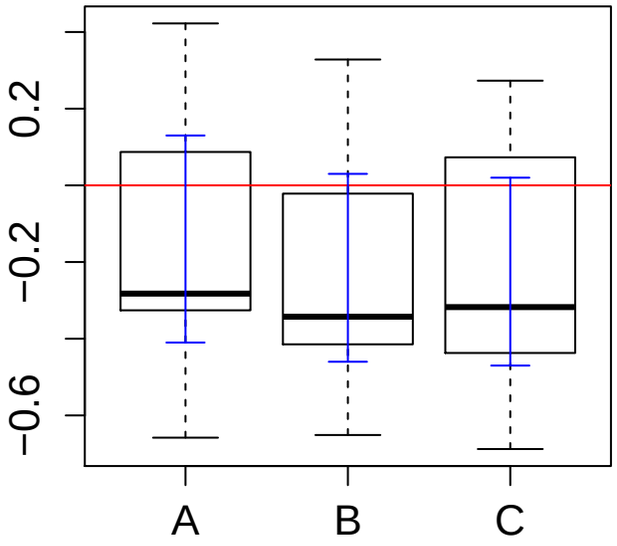
Flower diversity total effect



Flower stability



Elevation



Elevation total effect