

support, while for $\Delta\text{AIC} > 10$, models have essentially no support relative to the best model of the set (Richards, 2005; Burnham & Anderson, 2010). We used meta-analytical methods to evaluate whether the studied effects were general for all bee species. To apply the meta-analytical methods, the path coefficients from the SEM models for each bee species were normalized by applying Fisher's z transform, $z = 0.5 \ln [(1 + r)/(1 - r)]$ (Zar, 1999) to make them comparable. To weigh the correlation coefficients, we divided them by the inverse of the sampling variance, $w = 1/\text{var}(r) = N - 3$ (Rosenthal, 1991; Zar, 1999; Gurevitch, Curtis & Jones, 2001). We used a bootstrap resampling procedure written in R (R Core Team, 2013), with a sample size of 1,00,000, with which we calculated the mean and 95% percentile confidence limits of z_w (Manly, 1997).

To evaluate whether the effect of flower diversity becomes stronger with increasing pollinator generalization, we performed Spearman's rank correlations between the path coefficient representing the effect of flower richness on each of the three bee reproductive parameters mentioned above, and two measures of the corresponding species degree of generalization. We estimated the degree of diet generalization of each bee species using the species degree and Simpson's diversity index; degree is simply the number of food species consumed from all sites polled, whereas Simpson's index is a function of the number of food items and the proportion in which they were consumed. We used rarefaction to estimate both measures of generalization to make them comparable among bee species, as the number of brood cells was highly variable among nests. A positive correlation between the path coefficient of flower richness on bee reproduction and generalization would support our hypothesis that the reproduction of generalist pollinators is enhanced by flower richness.

All analyses were performed using R statistical software (R Core Team, 2013). Rarefaction of flower richness was performed using the `rarefy` function of the `vegan` package (Oksanen et al., 2013). Pearson's partial correlations were performed using the `pcor.test` function of the `ppcor` package to obtain independence probabilities and the path coefficients (Kim & Yi, 2007; Kim & Yi, 2006; Johnson & Dean, 2002).

RESULTS

We recorded 598 occupied trap nests by 11 solitary bee species (Table 1).

The complete model assessing the influence of multiple ecological factors on the potential relationship between flower diversity and bee reproduction at a community level (Model 1, Fig. 1A) showed a negative effect of elevation on bee reproductive variables, and no effect of the other evaluated factors on bee reproduction (Table 2).

The complete model assessing the influence of multiple ecological factors on the potential relationship between flower diversity and each bee species fitness (Model 1, Fig. 1A) showed no effect of flower abundance or time elapsed since the last fire on the bee reproductive variables studied. Although the only significant effect was that of temporal stability on the average number of brood cells per nest, we kept flower richness and elevation in the simplified model because they showed suggestive, albeit non-significant, trends. There was a weak positive effect of flower richness on average number of brood cells per nest and a weak negative effect of elevation on the three reproductive variables (Fig. S3);

Table 1 Number of nests per species. We used in this study the species that had more than 30 nests.

Bee species	Occupied trap nests
<i>Anthidium andinum</i> Jörgensen	6
<i>Anthidium decaspilum</i> Moure	54
<i>Anthidium rubripes</i> Friese	31
<i>Anthidium vigintipunctatum</i> Friese	39
<i>Megachile leucographa</i> Friese	222
<i>Megachile</i> sp. C	17
<i>Megachile ctenophora</i> Holmberg	74
<i>Mourecotelles triciliatus</i> Toro & Cabezas	3
<i>Trichothurgus laticeps</i> Friese	59
<i>Xylocopa atamisquensis</i> Lucia & Abrahamovich	88
<i>Xylocopa splendidula</i> Lepertier	5

Table 2 Path coefficients of Models 1 for community bee reproduction.

Model	Variables	Path coefficients	p-value
1	Elevation → Flower richness	0.39	0.15
	Elevation → Flower abundance	-0.51	0.06
	Flower richness → Stability	-0.54	0.04
	Elevation → Total brood cells	-0.59	0.03
	Elevation → Total nests	-0.57	0.04
	Flower abundance → Total brood cells	0.26	0.43
	Flower abundance → Total nests	0.24	0.48
	Flower richness → Total brood cells	0.27	0.80
	Flower richness → Total nests	0.38	0.23
	Stability → Total brood cells	0.35	0.35
	Stability → Total nests	0.30	0.35
	Time elapsed since last fire → Total brood cells	0.35	0.28
	Time elapsed since last fire → Total nests	0.45	0.14

however, none of these effects were statistically significant. The simplified model (Model 2, Fig. 1B) fitted best according to ΔAIC (8.43) for all species (see Figs. S1 and 1); this model fits the data well according to the d-separation test ($p = 0.84$, $df = 2$, $C = 3.69$). In this simplified model, the negative effect of temporal stability in flower production on the average number of cells per nest was weaker than in the complete model (Fig. 2 blue error bars; confidence limits of path coefficient for Model 1: -0.467, -0.101; confidence limits of path coefficient of Model 2: -0.264, -0.004). Also, the simplified model shows a negative trend in the effect of elevation on the total number of cells and nests per site, but this trend is statistically non-significant (confidence limits of path coefficients for the total number of cells and nests per site respectively: -0.465, 0.031, and -0.472, 0.027).

The effect of flower diversity on pollinator reproduction was unrelated to pollinator generalization for any of the bee reproductive variables and generalization indexes used (Table 3).

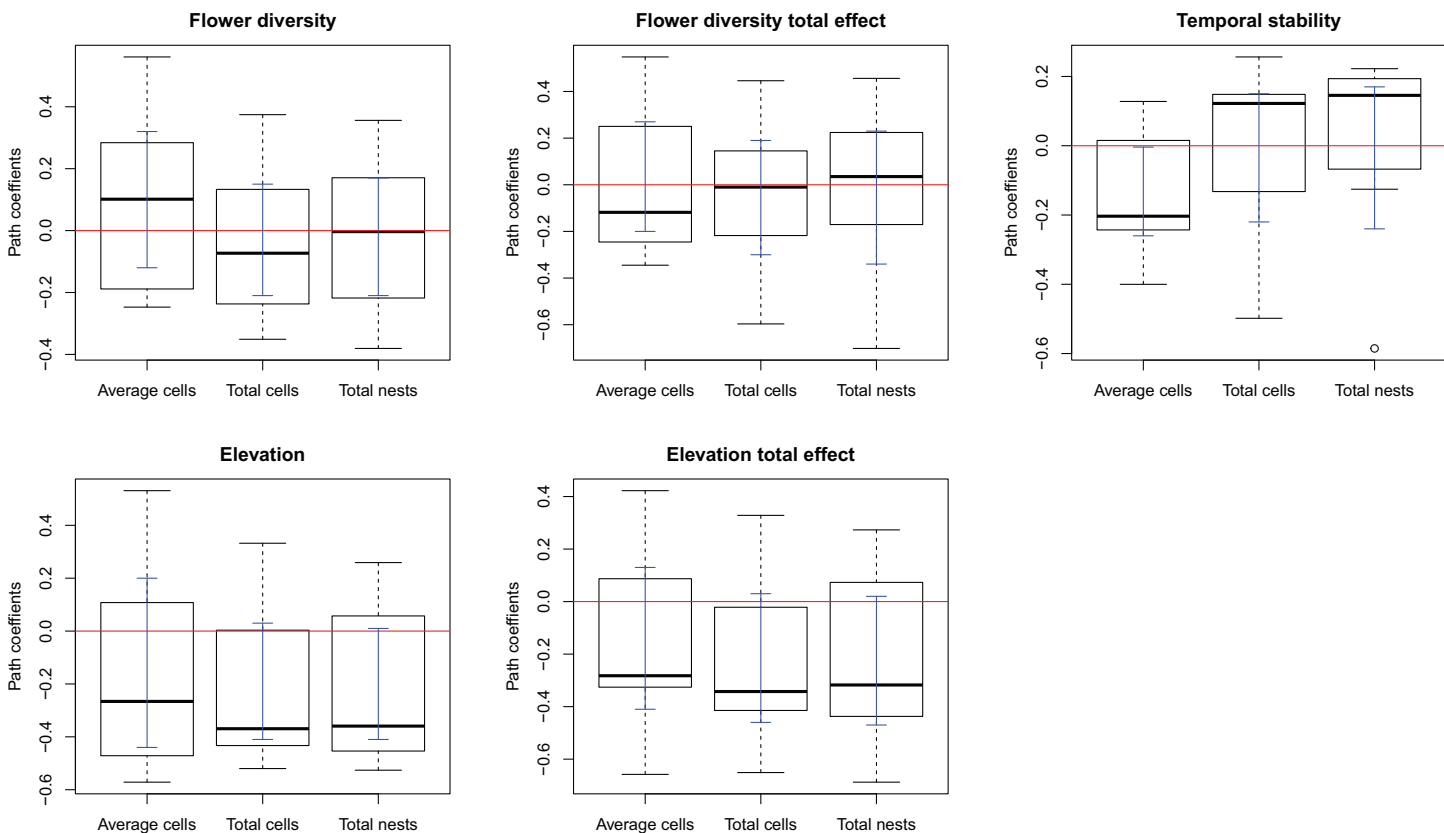


Figure 2 Box-plot summarizing the path coefficients of Model 2 (see Fig. 1) for the seven bee species studied here. In each box plot, the middle line indicates median, box limits are the first and third quartiles, whiskers indicate most extreme points ≤ 1.5 times the interquartile range, and circles indicate outliers of the seven path coefficients of the corresponding effect. 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) on three bee reproductive variables: “Average cells,” the average number of brood cells per nest per site; “Total cells,” the total number of brood cells per site; and “Total nests,” the total number of nests per site. The ordinates represent the path coefficients; the abscissa represent the effect of the above ecological variables on bee reproductive variables. Blue error bars are the ninety-five percent confidence limits of path coefficients obtained from bootstrap sampling of the distribution of path coefficients.

Table 3 Correlation coefficients between effect of flower diversity on pollinator reproduction and bee generalization.

Generalization index	Reproductive variable	Correlation coefficient (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

DISCUSSION

Contrary to our expectations, we found no effects of flower diversity and flower abundance on bee reproduction, either at the community or at the species level. Thus, flower diversity did not matter for the reproduction of the solitary bees studied here.

Considering the ecosystem functioning context where relationships are commonly saturating (*Cardinale et al., 2012*), there is a possibility that we have sampled plant diversities corresponding only to the saturating part of the diversity-productivity curve. In addition, this result could stem from the context dependence of the diversity-stability relationship (*Griffin et al., 2010*), given that elevation had a positive effect on flower diversity (*Dorado & Vázquez, 2014*) but a negative effect on bee reproduction (*Table 2*). This trend in the effect of elevation on bee reproduction was observed despite the narrow elevation range encompassed by our sites (1,100–1,500 m), which suggests that the environmental conditions of the study sites could have influenced the relationship between floral diversity and bee reproduction.

An explanation of the negative effect of temporal stability on brood cell production concerns a compensatory behavior of females to avoid parasitism. In sites with high temporal stability in flower production, females might lay fewer eggs per nest while building more nests, so as to maximize larval survival per site. This reasoning makes two implicit assumptions. First, that the bee species are parasitized, which we indeed observed for many of the bee species studied here. Second, that nesting sites are not limited for the population. In fact, the trap nest sampling with replacement highly increased the nest availability in our study sites. If this mechanism were responsible for the observed negative effect of temporal stability in flower production on the average number of brood cells per nest, we would expect the number of cells per site to be either unrelated to temporal stability or to be higher in the more temporally stable sites, and the number of nests to be higher in the more temporally stable sites, as females would be laying eggs at their maximum capacity but distributing them in more nests. Matching these expectations, the total number of brood cells per site was unrelated to temporal stability (*Fig. 2*, flower stability), while the number of nests per site tends to increase with temporal stability for most species, although the effect was statistically non-significant.

An alternative explanation of the negative effect of temporal stability on brood cell production per nest could be that elevation might be weakening the effects of other variables on pollinator reproduction. This is particularly likely considering the positive direct effect of elevation on flower diversity, the positive indirect effect of elevation on stability, and the negative effect of elevation on bee reproduction (*Table 2* and *Fig. 2*); these effects could be neutralizing the effect of the flower diversity and temporal stability in flower production on bee reproduction. The upper sites are located at the mouth of ravines, which are probably wetter and cooler than the lower sites, located in open land. Thus, changes in humidity and temperature associated to elevation could be influencing bee reproduction more strongly than the other ecological factors studied here.

We found no support for the idea that generalist bees are more favored in their reproduction by flower diversity than specialized ones, despite bee species included in this study having contrasting degrees of feeding specialization. Again, we think the negative effect of elevation on bee reproduction can be responsible for this unexpected result. It seems reasonable to think that species will respond idiosyncratically to flower

diversity and stability when there is context dependency, given our finding of no general effects of flower diversity on bee reproduction.

Although there is a consensus that diversity promotes ecosystem-level productivity (*Cardinale et al., 2012*), we failed to find this relationship at the community and population levels in our study. However, 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. These studies are becoming priority, as wild bees are known to enhance fruit production in crops, beyond the pollination service provided by honeybees (*Garibaldi et al., 2013*). 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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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Jimena Dorado conceived and designed the study, conducted fieldwork, analyzed the data, and wrote the paper, prepared figures and/or tables.
- Diego P. Vázquez conducted fieldwork, and reviewed drafts of the paper, supervised the work for this article in his capacity as Ph.D. advisor.

Field Study Permissions

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

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Data Deposition

The following information was supplied regarding data availability:

The raw data was supplied as [Supplemental Dataset Files](#).

Supplemental Information

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