

The diversity–stability relationship in floral production

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The diversity–stability hypothesis posits that species diversity confers redundancy in function, so that richer communities show higher temporal stability in ecosystem processes than poorer communities. The diversity–stability relationship has not been studied in terms of flower production before. A diverse flower community may stabilize the availability of floral resources along the floral season. Considering this type of stability is important because it could promote the stability and persistence of the pollination service. We evaluated 1) the diversity–stability relationship in floral production along a flowering season; 2) the effect of additional factors that could blur the diversity–stability relationship, such as flower abundance, elevation, and the time elapsed since the last fire, a common human disturbance in the study area; and 3) whether the most important plants for pollinators in terms of interspecific interactions contribute differentially to temporal stability. The most diverse communities were more stable in floral resource production along the flowering season. Stability of flower production was also influenced by a positive indirect effect of elevation. The plants that contributed the most to temporal stability were the most abundant and densely connected species, those at the core of the plant–pollinator network. Our study shows that species richness enhances the availability of floral resources for pollinators, providing a strong support for the diversity–stability hypothesis.

A central issue in the study of biodiversity is its role in stabilizing ecosystems and the services they provide. Species diversity confers redundancy in function, so that ecological processes are more stable in more diverse communities (MacArthur 1955, Elton 1958). The study of the relationship between diversity and stability has a long history, and although the effect of species diversity on the stability of ecosystem properties has been controversial (Hooper et al. 2005), there is an emerging consensus that the effect is positive (Cardinale et al. 2012, Naeem et al. 2012). Stability has multiple definitions, which result in multiple diversity–stability relationships (Ives and Carpenter 2007). We will focus on temporal stability, which describes the variability along a period of time of a community-level property such as biomass or production. It is usually measured as the reciprocal of the coefficient of variation of the community property of interest, thus representing a standardized measure of stability that accounts for the tendency of variability to increase with the mean (Tilman 1999, Lehman and Tilman 2000, Tilman et al. 2006). The diversity–stability relationship has been well studied in plant communities for biomass production (Caldeira et al. 2005, Tilman et al. 2006, Isbell et al. 2009, Hector et al. 2010), but not for flower production.

Considering stability in flower production is relevant because it could be important for pollinator populations and the ecosystem service they provide. Pollination constitutes a

key ecosystem service that promotes and maintains biodiversity and crop production (Klein et al. 2007, Garibaldi et al. 2011a). Even if floral resources were abundant in the community, they might be insufficient to support pollinator populations if they were temporally unstable (Westphal 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 et al. 2009). Temporal stability of floral resources should be higher in diverse plant communities, as they are likely to occupy the flowering phenological space more broadly, stabilizing floral availability throughout the flowering season, as occurs for plant biomass. For example, diverse assemblages of *Clarkia* spp. (Onagraceae) provide more floral resources along the flowering season than poorer assemblages, resulting in a higher number of pollinators per plant (Moeller 2004).

Plant species will likely differ in their contribution to the temporal stability of flower production. A relevant question is thus whether a plant's contribution to stability relates to its importance for pollinators. Such importance can be measured using a network approach (Memmott 1999, Bascompte and Jordano 2007), which allows identification of the most densely connected species (the network “core”; Bascompte et al. 2003). Plants in the network core are important for many visitor species, as they are the most generalized, abundant and temporally stable species in the network (Bascompte and Jordano 2007). Thus, plant species in

the network core are likely to contribute the most to stability of flower production.

When studying the diversity–stability relationship, it is important to go beyond a correlative approach, so as to understand the underlying mechanisms that drive the relationship. An important factor that could influence the diversity–stability relationship in flower production is total flower abundance in the community. Flower abundance and flower richness could be positively related, as suggested by Tilman (1999) for total biomass in plant communities. If flower abundance were highly correlated with flower richness and stability of floral resources, there could be a spurious positive correlation between flower richness and stability even if they were not causally related. In addition, the functional form and the strength of this relationship may depend on local environmental conditions (Ives and Carpenter 2007, Griffin et al. 2010). Thus, when evaluating the diversity–stability relationship it would be important to consider the local environmental factors such as elevation or disturbance history, which are known to influence species diversity (Potts et al. 2003a, Grytnes and McCain 2007).

Here we evaluate two questions concerning the diversity–stability relationship in floral production. First, we ask whether there is a positive diversity–stability relationship in floral production along a flowering season. As the diversity–stability relationship is studied in a natural diversity gradient of a desert ecosystem in Argentina, we include in the analysis other attributes of the study sites that may influence stability besides diversity, namely flower abundance, elevation and the time elapsed since the last fire. Our second question is whether plants in the network core are key drivers of the temporal stability in flower production. If so, we expect that the simulated removal of plants will lead to a greater decrease in stability of flower production according to their distance to the network core. As plants in the network core tend to be the most abundant, we also expect that species' contribution to stability is positively related to their abundance.

Methods

Study area and field methods

This study was carried out in the Monte desert in Villavicencio Natural Reserve, located ca. 40 km north of Mendoza city, Argentina, during the 2008 flowering season (15 October – 8 December 2008). This study was part of a broader research program aimed at addressing multiple related questions about the structure and functioning of plant–pollinator interactions (Dorado et al. 2011, Chacoff et al. 2012, Vázquez et al. 2012). We selected fourteen 100 × 200 m rectangular study sites, located between 1100 and 1500 m a.s.l. (Supplementary material Appendix 1 Table A1). These sites lie at the ecotone between the Monte desert and the Prepuna biomes (Ambrosetti et al. 1986). This 2 m tall shrubland is dominated mainly by *Larrea divaricata* (Zygophyllaceae), *Zuccagnia punctata* (Fabaceae), *Prosopis flexuosa* (Fabaceae), *Condalia microphylla* (Rhamnaceae), *Acantholippia seriphoides* (Verbenaceae) and *Opuntia sulphurea* (Cactaceae). Flower abundance, composition and

diversity differed markedly among sites. Fire is the most common human disturbance in the area (E. L. Stevani pers. comm.), and the time elapsed since the last fire varied substantially among our study sites (Supplementary material Appendix 1 Table A1).

In each site, we estimated floral resource availability using two measures: flower density and overall pollen availability (i.e. flower density × number of pollen grains per flower). Density of flowers is arguably an appropriate measure of pollinator resource abundance, because pollinators focus on flowers as resource units for both pollen and nectar. However, as flowers of different species vary substantially in their pollen content, we used overall pollen availability as an alternative measure of floral resource availability. We also attempted to obtain nectar from flowers, so as to estimate overall nectar availability, which is also an important component of floral resources; however, we were unable to extract nectar from flowers of most plant species, as flowers in this system usually have very small standing volumes of nectar. We included in the study all flowering plant species except grasses, which are known not to be animal pollinated.

Flower density was measured weekly (a reasonable frequency, given that flowers in our system do not last more than a week) at four 8 × 20 m plots and two 2 × 50 m transects per site as described in Supplementary material Appendix 1 Fig. A1. For plant species for which individuals could be distinguished (shrubs and some herbs), we counted the number of all flowering individuals of each species and the number of flowers (or inflorescences, in the case of the Asteraceae) for the first ten individuals encountered in each plot or transect, and then multiplied the average number of flowers or inflorescences per individual by the total number of individuals in each plot. For plant species for which it was not possible to identify individuals (some herbaceous species), all flowers in a plot or transect were counted.

Pollen grains per flower or inflorescence were estimated in two different flowering seasons (2006 and 2008). We collected 30 fresh flowers from several individuals. Fresh flowers were stored in 70% ethanol. Once in the laboratory, vials containing flowers were vigorously shaken to suspend pollen and remove the flower, and then centrifuged at 2000 rpm during 5 min to precipitate pollen. The pellet was suspended in 50 µl, or in 1 ml when the flower or inflorescences had large pollen quantities. Two samples of this suspension per flower were observed in a Neubauer chamber to estimate pollen content per flower. In spite of substantial sampling effort, we detected pollen grains in only 57 of 113 species. For seven of the remaining species, we could not detect pollen in the flowers collected; the remaining 49 species were extremely rare, which precluded flower collection for pollen quantification. Thus, for our analyses we assumed that flowers of these extremely rare species had half of the smallest pollen quantity detected for other species. The results were unaffected by the inclusion of these species (Supplementary material Appendix 1 Table A2, Fig. A2).

Statistical analyses

Diversity–stability relationship in floral production

To evaluate the hypothesis that floral diversity stabilizes floral production along a flowering season, we calculated

Spearman's rank correlation coefficient between flower/pollen richness and temporal stability in flower/pollen abundance respectively; a positive correlation would support the hypothesis. Flower/pollen richness was used as a measure of flower/pollen diversity. Flower/pollen richness per site ($n = 14$) was estimated from species abundance data in the study plots using rarefaction (Gotelli and Colwell 2001) to remove the confounding effect of flower/pollen abundance (measured as total number of flowers/pollen grains per site). Stability was defined as the inverse of the coefficient of variation (CV) of weekly flower/pollen abundance per site, calculated as mean weekly flower/pollen abundance per site divided by the standard deviation of that mean (stability = $1/CV = \mu/\sigma$; Tilman 1999, Lehman and Tilman 2000, Tilman et al. 2006).

To assess the influence of other ecological factors on the diversity–stability relationship, we used structural equation models (hereafter SEM). We built a general initial model to explore the effects of flower/pollen abundance, time elapsed since the last fire and elevation on flower richness and temporal stability in flower production, and then generated more parsimonious nested models by removing variables with non-significant effects or small, non-significant path coefficients (see models in Fig. 1; see also Maestre et al. 2010). As the number of replicate plots in this study was too small to evaluate alternative SEM models using conventional SEM methods (Grace 2006), we selected the best fitting model based on Akaike's information

criterion (AIC) calculated with a d-separation test (Shipley 2000, 2013), a method robust to small sample sizes. The d-separation test considers a basis set, i.e. the k pairs of variables that are not directly connected with an arrow in the causal model (Supplementary material Appendix 1 Table A3). For each pair of variables i in the basis set, it is possible to calculate their probability of independence, p_i , with an appropriate test. We used here the p -value associated to Spearman's rank correlation-test as an estimate of p_i . With this information, we can then calculate the maximum likelihood estimate for each model, based on Fisher's C statistic,

$$C = -2 \sum_{i=1}^k (\ln p_i) \quad (\text{Shipley 2000, 2013}).$$

Using the C value associated to each causal model, we calculated the corrected Akaike's information criterion as $AIC_c = C + 2K [n/(n - K - 1)]$, where K is the total number of free parameters in the model and n is the sample size. The best fitting model was that with the lowest value of AIC_c . To discriminate among competing models we used the AIC_c difference, ΔAIC_c , calculated as the difference between a given model and the best-fitting model. Models whose ΔAIC_c values are less than 3 are generally considered to have substantial support, models whose ΔAIC_c are between 3 and 7 are considered to have considerably less support, and models whose ΔAIC_c are greater than 10 have essentially no support relative to the best model of the set (Richards 2005, Burnham and Anderson 2010).

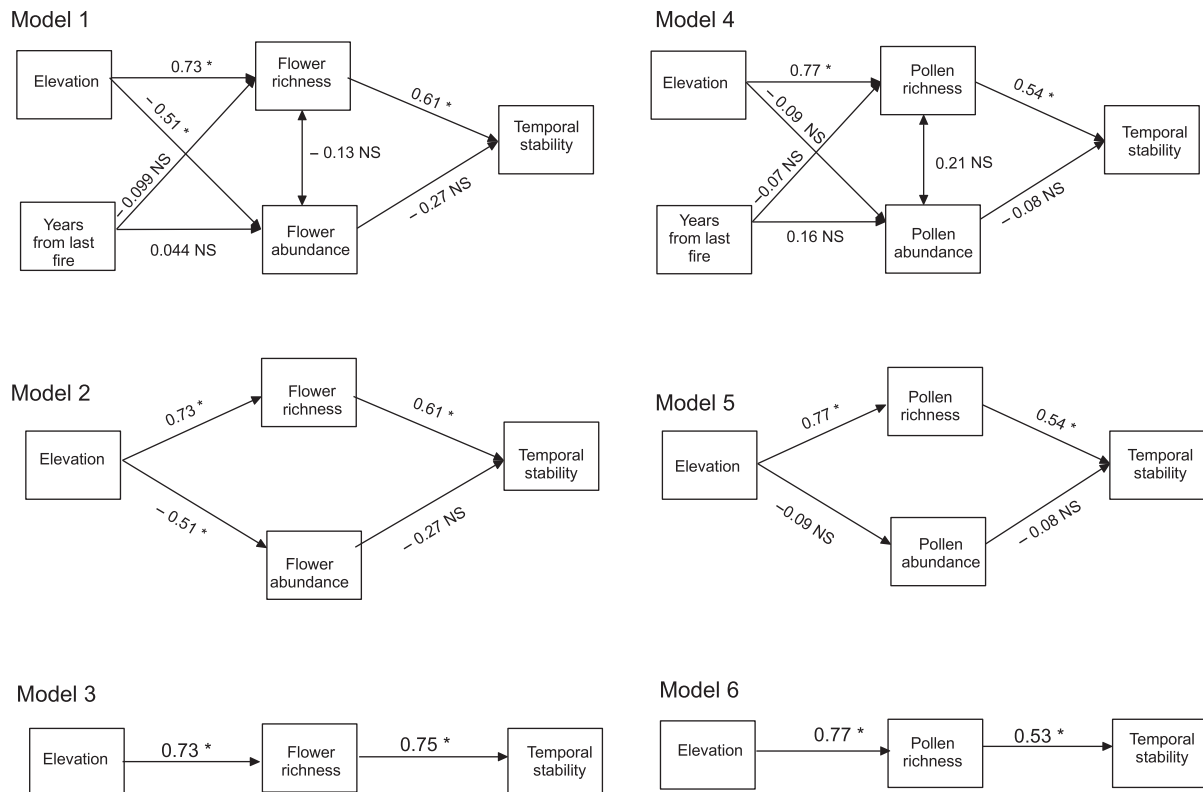


Figure 1. Models evaluating the effect of ecological factors on the diversity–stability relationship for flower production in the natural diversity gradient of the 14 study sites. We generated nested models by removing variables with non-significant effects or small path coefficients that were non-significant. Model 3 and 6 were selected (Table 1). Numbers above the arrows are the path coefficients; asterisks indicate statistical significance at the $\alpha = 0.05$ level.

Species' individual contribution to stability in floral production

We evaluated if the plants belonging to the network core contribute significantly more to temporal stability in flower production of the community. To this end, we considered plant species' rank order in the nested interaction matrix as a measure of their membership to the network core, which represents the most densely connected group of species (species at the network core have the lowest rank orders). Data for this analysis came from a previous study describing the plant–pollinator network in three of our study sites (Chacoff et al. 2012). We then calculated Spearman's rank correlation between each species' rank order and temporal stability re-calculated without the corresponding plant species, pooling the data for the three sites for which we had information on the interaction network. Thus, if stability and rank order were positively correlated we would accept that the core plants are contributing more than the rest. The above analysis was repeated using species abundance ranks instead of the rank order in the interaction matrix (with the lowest rank corresponding to the most abundant species); we expected a positive correlation between rank abundance and contribution to stability.

All analyses were done using R statistical software (<www.r-project.org>; R ver. 3.0.2). Rarefaction was performed using the rarefy function of the vegan package (Oksanen et al. 2013). Structural equation modeling was performed using the sem function of the sem package to obtain the path coefficients (Fox et al. 2013).

Results

Flowering plant assemblage in the study sites

The plant species with the highest flower abundance in our study area were *Zuccagnia punctata*, *Condalia microphylla*, *Junellia aspera*, *Larrea divaricata*, *Thymophylla pentachaeta*, *Acantholippia seriphioides* and *Schinus fasciculata*. Rarefied flowering species richness per site was 24.92 ± 7.60 (mean \pm SD) using flower abundance to estimate resource availability, and 32.78 ± 9.33 using pollen abundance. Unrarified flower abundance was $95.10 \times 10^3 \pm 47.47 \times 10^3$ flowers, and pollen abundance was $11.38 \times 10^{10} \pm 10.47 \times 10^{10}$ pollen grains per site. The most connected plants in the plant–pollinator network were *Prosopis flexuosa*, *Condalia microphylla*, *Larrea divaricata*, *L. nitida*, *Zuccagnia punctata*, *Aloysia gratissima* (see Fig. 1, and Table S1, S2 in Chacoff et al. 2012).

Diversity–stability relationship in floral production

Flower richness and stability of flower production were positively correlated ($r = 0.72$, $p = 0.0035$, $n = 14$; Fig. 2a). Pollen richness and stability of pollen production were also positively correlated, although the correlation was weaker than for flower richness ($r = 0.54$, $p = 0.0471$, $n = 14$; Fig. 2b). Thus, flower and pollen abundance along a floral season were more stable in diverse communities.

The purported causal relationship between flower richness and temporal stability was further evaluated by the

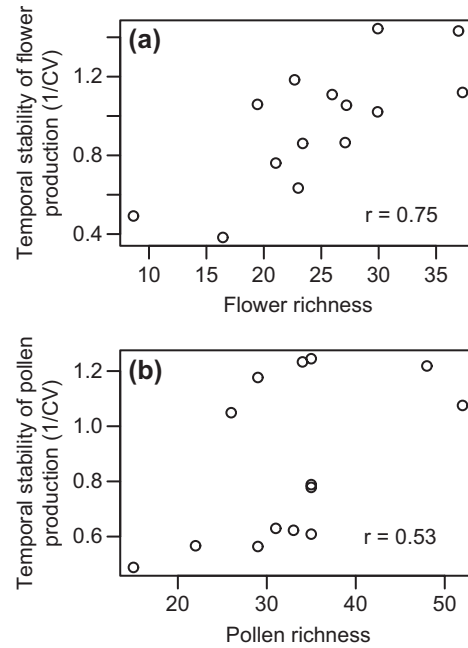


Figure 2. Relationship between (a) flower richness and stability of flower production along a floral season, and (b) pollen richness and stability of pollen production along a floral season. Temporal stability was estimated as the inverse of the coefficient of variation of mean weekly flower abundance (1/CV).

analysis of structural equation models (Fig. 1). The best-fitting model according to ΔAIC_c fit the data well when flowers were used to the floral resource abundance, but not when pollen was used instead (Fig. 1, model 3 and 6; Table 1). Both models included a positive direct effect of flower or pollen richness and a positive indirect effect of elevation on temporal stability of flower or pollen production, respectively (Fig. 1, model 3 and 6; Table 1). Thus, even though the model for pollen provided a poor overall fit to the data, suggesting that the overall causal structure assumed by the model is incorrect, the model still provides positive evidence for the diversity–stability hypothesis.

Species' individual contribution to stability in floral production

The contribution of different plant species to temporal stability in flower and pollen production increased with

Table 1. Statistical parameters to evaluate the models from Fig. 1.

Model	C	DF	p	K	AIC _c	ΔAIC_c
1	5.79505	6	0.45	11	159.7951	137.7051
2	8.44116	4	0.92	8	53.2411	31.1511
3	4.58999	2	0.90	5	22.0899	0.0000
4	13.27830	6	0.04	11	167.2783	138.7988
5	12.77265	4	0.01	8	57.57265	29.0931
6	10.97953	2	0.004	5	28.47953	0.0000

Notes: C is the Fisher's C statistic used for the d-sep test, DF are the corresponding model degrees of freedom, p is the null probability, K is the number of parameters needed to fit the model, AIC_c is Akaike's information criterion, and ΔAIC_c is each model's difference in AIC_c relative to model 3 and 6 respectively.

increasing rank order according to core position (Spearman's $r = 0.39$, $n = 49$, $p = 0.0050$ for flowers; Spearman's $r = 0.38$, $n = 49$, $p = 0.0068$ for pollen; Fig. 3a, c). The correlation was even stronger when plant rank abundance was considered instead of distance to the core (Spearman's $r = 0.41$, $n = 44$, $p = 0.0043$ for flowers; Spearman's $r = 0.71$, $n = 44$, $p < 0.0001$ for pollen; Fig. 3b, d). It is noteworthy that species' contribution to stability saturates rapidly with decreasing rank order according to both core position and abundance. It is only abundant species in the network core that contribute to stability (Fig. 3a, c); the contribution of other species appears to be nil. Notice that for pollen analysis there is one abundant species (*Larrea divaricata*) that when removed produces a high increase in temporal stability (instead of the substantial decrease observed for all other abundant species in the network core). This species had an extremely high abundance of pollen in our study sites, as it produced large quantities of pollen per flower and flowered profusely, with a peak in the middle of the flowering season. The disproportionately large amount of pollen produced by this species during three weeks in the season had thus the paradoxical effect of causing a destabilizing effect in the community, as its presence greatly increases variability. Thus, removal of *L. divaricata* greatly increases stability (Supplementary material Appendix 1 Fig. A3).

Discussion

We found that the most diverse flower communities were the most stable in terms of flower and pollen production along

the flowering season, which supports the diversity–stability hypothesis for floral production in a natural diversity gradient. Our results broaden the generality of the diversity–stability hypothesis by focusing on a previously unstudied aspect of ecosystem functioning, flower production (cf. Cardinale et al. 2012). We also found that it is abundant plants in the network core those that usually contribute the most to stability (with the exception of the disproportionately abundant pollen production of *Larrea divaricata*; Supplementary material Appendix 1 Fig. A3).

In agreement with previous predictions (Ives and Carpenter 2007, Griffin et al. 2010), our study also shows that the diversity–stability relationship can be context dependent in natural diversity gradients, as stability of floral resources was indirectly determined by elevation, in spite of the relatively narrow elevational range encompassed by our study (ca 1050–1500 m a.s.l.). The positive effect of elevation on flower richness observed in our study agrees with previous studies of elevational gradients in species richness, which indicate that species richness does not necessarily decrease monotonically with increasing elevation (Rahbek 1995). In our study, the positive relationship between richness and elevation is probably explained by the fact that our study area lies at an ecotone zone, ranging from Monte desert at lower elevations to the ecotone between the Monte and high–Andean vegetation at higher elevations.

In natural ecosystems, richness is often so correlated with abundance that disentangling these factors is not possible. This is probably the reason why the field is currently dominated by small-scale experiments where abundance can be held constant and richness is allowed to vary.

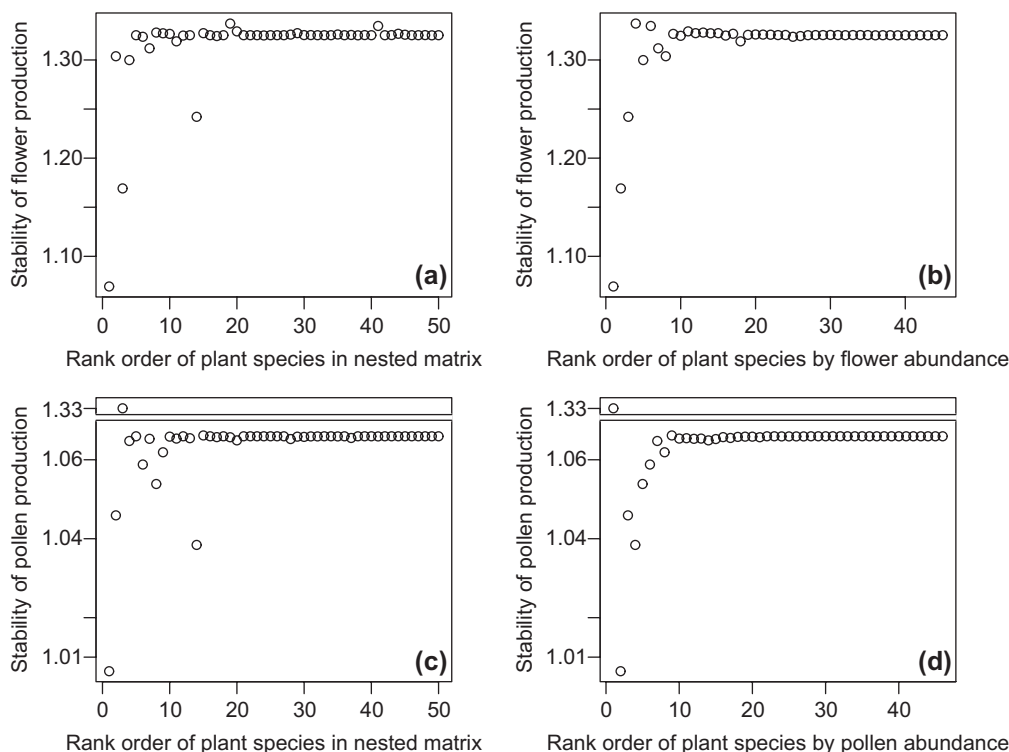


Figure 3. Plant species contribution to temporal stability in flower production. The abscissas represent (a and c) the rank order of plant species according to their membership to the network core (see Methods), and (b and d) the rank order of plant species according to their flower/pollen abundance. The ordinates represent temporal stability without the corresponding plant species. *Larrea divaricata* is represented by the third point from left to right in panel (a), the second in panel (b), the third in panel (c), and the first in panel (d).

The SEM approach used here represents a valuable tool to deal with this problem in natural ecosystems, thus allowing an evaluation of the diversity–stability hypothesis at broader spatial scales, arguably more relevant for ecological processes involving mobile organisms, such as pollination. Even though the selected SEM for pollen did not fit the data well, the diversity–stability relationship in this model was significantly positive, as also observed for the best-fitting SEM model for flowers, which had a good fit to the data (Fig. 1). Taken together, these results provide support for the diversity–stability relationship in flower production. Furthermore, our structural equation model indicated no significant relationship between flower richness and flower abundance, which suggests that the effect of flower richness on stability is not spurious. These results underscore the importance of considering other factors besides diversity when studying the diversity–stability relationship in natural diversity gradients, as suggested by Griffin et al. (2010).

An important limitation of our study is that we have used an incomplete quantification of pollinator rewards, as we have not quantified nectar availability in our study system. Unfortunately, quantifying nectar availability in our study system was not feasible, as flowers usually have extremely low nectar standing volumes (Vazquez et al. 2009). It would be interesting to include nectar quantification in future studies of the diversity–stability in floral resource production, especially in other systems where measuring nectar availability is more feasible.

When studying the diversity–stability relationship, it is important to identify the functional traits of species that contribute to stability (Díaz et al. 2007, Hooper et al. 2005). In this study, we found that abundant and highly connected members of the network core drive the stability on floral and pollen production in our study system. Yet, some highly connected species did not contribute substantially to stability (Fig. 3a, c), and flower and pollen abundance alone appear to be the best predictors of temporal stability of flower resources (Fig. 3b, d). We also had the paradoxical result that a species that produced a disproportionately high amount of resource compared to overall community production (*L. divaricata*), contributed negatively to temporal stability. The latter result was observed when using pollen to estimate floral resource abundance; however, this destabilizing effect of *L. divaricata* was not observed when using flowers to estimate resource abundance, as flower abundance of this species was comparable to that of other species in the community (*Larrea divaricata* is the second most abundant species in terms of flower abundance; Fig. 3b).

Studies of the diversity–stability relationship are important not only to understand the functioning of ecosystems but because of the services they provide to human society. Several studies have shown that distance to natural and semi-natural areas affects pollination services negatively (Garibaldi et al. 2011b). For example, Kremen et al. (2002, 2004) found that crop pollination services provided by native bee communities strongly depend on the proportion of natural habitats surrounding agricultural fields. A recent world-wide study including many crop species

concluded that wild bees have a significant, positive effect on crop production (Garibaldi et al. 2013). Thus, assuming that natural areas are particularly diverse, and that plant diversity can enhance pollinator diversity, we can infer that plant diversity will favor pollination service. Our study suggests that temporal stability in flower production enhanced by plant diversity could be a mechanism responsible for driving the positive relationship between plant and pollinator diversity and crop production.

We have considered the temporal stability of flower production in one flowering season, which is arguably limited. In the future, it will be interesting to study the inter-annual variation of the diversity–stability relationship for flower production, to evaluate whether long term variations in plant diversity translate into variations in stability of flower production. The latter is particularly important to assess the importance of preserving biodiversity to sustain plant–pollinator interactions and the ecosystem services they provide, especially considering that climatic variability is expected to increase in the future (Meehl et al. 2007). Furthermore, these results parallel those of previous studies showing that plant and pollinator diversity are positively related (Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003b, Fründ et al. 2010), and that high pollinator diversity confers high temporal stability in pollinator visits to flowers (Ebeling et al. 2008, Garibaldi et al. 2011b), enhancing pollination services (Kremen et al. 2002.). Taken together, this evidence indicates that species richness enhances the functioning of plant–pollinator interactions, providing strong support for the diversity–stability hypothesis in plant–pollinator systems.

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Supplementary material (available online as Appendix oik-00983 at <www.oikosjournal.org/readers/appendix>). Appendix 1.