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Patterns of among- and within-species variation in heterospecific pollen receipt: the importance of ecological generalization[1]

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- *Premise of the study:* Co-flowering plants are at risk of receiving pollen from heterospecifics as well as conspecifics, yet evidence shows wide variation in the degree that this occurs. Evaluation of patterns and correlates of among- and within-species variation in heterospecific pollen (HP) receipt is key to understanding its importance for floral evolution and species coexistence; however, the rarity of deeply-sampled multispecies comparisons has precluded such an evaluation.

- *Methods:* We evaluated patterns of among- and within-species variation in HP load size and diversity in 19 species across three distinct plant communities. We assessed the importance of phenotypic specialization (floral phenotype), ecological specialization (contemporary visitor assemblage) and conspecific flower density as determinants of among-species variation. We present hypotheses for different accrual patterns of HP within species based on the evenness and quality of floral visitors, and evaluated these by characterizing the relationship between conspecific pollen (CP) and HP receipt.

- *Key results:* We found that within-species variation in HP receipt was greater than among-species and among-communities variation. Among species, ecological generalization emerged as the strongest driver of variation in HP receipt irrespective of phenotypic specialization. Within-species variation in HP load size and diversity was predicted most often from two CP-HP relationships (linear or exponentially decreasing) suggesting that two distinct types of plant-pollinator interactions prevail.

- *Conclusions:* Our results give important insights into the potential drivers of among- and within-species variation in HP receipt. They also highlight the value of explorations of

patterns at the intraspecific level which can ultimately shed light on plant-pollinator-mediated selection in diverse communities.

Keywords: co-flowering community, diversity, ecological generalization, floral specialization, heterospecific pollen, floral visitor assemblage, pollinator sharing

The movement of pollinators between plants in multi-species plant communities can result in the transfer of pollen from heterospecifics as well as conspecifics (e.g., Feinsinger et al., 1986; Montgomery and Rathcke, 2012; Fang and Huang, 2013). However, the likelihood of heterospecific pollen (hereafter, HP) receipt varies widely among species. For instance, a review of published studies (Ashman and Arceo-Gómez, 2013) revealed variation among species in both the percentage of flowers that received any HP (2-100%), as well as in the average intensity of HP receipt (% HP in total stigmatic pollen load: 0.1% to 80%). Furthermore, Fang and Huang (2013) uncovered variation among species within a single community not only in HP load size but also in the number and identity of HP donors. Some species received large multispecies loads while others received small monospecific loads of HP (Fang and Huang, 2013). Variation in HP receipt among individuals within a single species can also be extensive (e.g., 1-95% of total load in *Mimulus guttatus*; Arceo-Gómez and Ashman, unpublished data), but variation at this level has received much less attention. In fact, a systematic comparison of all aspects of HP receipt (e.g., mean and variance of HP load size and diversity) among and within species has not been attempted in any community. Characterization of the pattern of variation at inter- and intra-specific levels as well as identifying the factors that contribute to variation at both levels are crucial for gaining a complete understanding of the role of HP transfer in floral evolution and species coexistence in diverse plant communities.

Phenotypic specialization is thought to reflect past selection to maximize conspecific pollen (hereafter, CP) receipt and export while minimizing HP transfer (Rathcke, 1983; Waser, 1983; Armbruster, 1995; Waser et al., 1996; Muchhala and Potts, 2007; Pauw, 2013). Flower shape (e.g., symmetry), in particular, can restrict visitors by body size, tongue length and/or learning capabilities leading to predictions of lower HP receipt by zygomorphic flowers than

actinomorphic ones (Faegri and van der Pijl, 1979; Feinsinger et al., 1986; Waser, 1986; McLernon et al., 1996). Irrespective of floral symmetry, however, species with large flowers, long life times and/or large exerted stigmas are accessible to a wide array of pollinators (see below) and thus are expected to receive large and possibly diverse loads of HP (Montgomery and Rathcke, 2012; Ashman and Arceo-Gómez, 2013; Fang and Huang, 2013; Huang and Shi, 2013). In addition, species with such floral features (i.e., actinomorphic and large, long-lived flowers) would be predicted to also exhibit less variation among plants, as every flower would receive at least some HP over their life time. In contrast, species with more restrictive floral phenotypes and small, short-lived flowers are expected to receive, on average, smaller and less diverse HP loads, but may have higher variance among conspecifics as HP delivery is predicted to be more stochastic. These predictions for HP load size among species have been partially borne out (McLernon et al., 1996; Eaton et al., 2012; Montgomery and Rathcke, 2012; Fang and Huang, 2013; Huang and Shi, 2013), but those for variance among and within species have yet to be explored.

Separate from the evolutionary state of specialization reflected in floral phenotype addressed above, the ecological state of specialization, that is, the contemporary community of floral visitors (*sensu* Feinsinger et al., 1986; Waser et al., 1996; Fenster et al., 2004) is expected to be an important determinant of the among-species variation in amount and diversity of HP deposited on stigmas. From this perspective, a plant species can range from being highly specialized, i.e., visited by only a single taxon (Pellmyr et al., 1996; Flemming and Holland, 1998; Weiblen, 2004) to widely generalized, for example, be visited by up to 70 different taxa (Waser et al., 1996; Olesen and Jordano, 2002; Vazquez and Aizen, 2003; Alarcón et al., 2008; Bosch et al., 2009). As a consequence, plant species that host a wider array of visitors (that may

104 also visit other plant species) are predicted to receive larger, more diverse loads of HP with little
105 variance among flowers than species with less diverse pollinator assemblages, all else being
106 equal (e.g., pollen placement). This relationship between HP receipt and pollinator diversity has
107 been explored indirectly via the presumed association between ecological specialization and
108 phenotypic specialization (e.g., generalized pollination-actinomorphic flowers vs. specialized
109 pollination-zygomorphic flowers; McLernon et al., 1996). A direct test of the effect of ecological
110 specialization on HP receipt, however, requires measures of the contemporary community of
111 floral visitors. Simultaneous tests of floral morphology and the degree of ecological
112 specialization are needed to evaluate their relative importance in determining patterns of HP
113 receipt across species (see Fang and Huang, 2013). Furthermore, for species visited by generalist
114 pollinators, the floral neighborhood can also be important in influencing patterns of HP receipt
115 (Rathcke, 1983; Feinsinger et al., 1986). For instance, the local abundance of conspecifics
116 relative to heterospecifics may affect HP receipt, as rare species are expected to receive more
117 (and more diverse) HP than common species (Rathcke, 1983; Vamosi et al., 2006; Alonso et al.,
118 2010). To date, only a small handful of comparative studies have addressed these factors (see
119 McLernon et al., 1996; Fang and Huang, 2013) and as of yet no study has incorporated all three.

120 Additional insight into the dynamics of HP transfer in natural communities can be gained
121 from more detailed analysis of intraspecific variation. For instance, the evenness of pollinator
122 quality within the assemblage could affect the pattern and variance in HP receipt among
123 conspecific individuals. Specifically, because flower-visiting taxa (or functional groups) have
124 differences in body size, flight distances and floral constancy they can vary in the size and purity
125 (i.e., CP vs. HP) of the pollen load they deposit (‘pollination quality’; Herrera, 1987). For
126 instance, Hymenoptera deposited more CP than Lepidoptera and Diptera in Mediterranean

Lavandula latifolia (Herrera, 1987) and bats deposited larger amounts of HP relative to hummingbirds and hawkmoths in tropical *Aphelandra acanthus* (Muchhala et al., 2009). Thus, low quality floral visitors are those that deposit little CP but large amounts of HP, whereas high quality visitors deposit a lot of CP but little or no HP (Herrera, 1987). As a result, within an assemblage, the evenness of flower-visiting taxa (or functional groups) that differ in their quality may be an important determinant of the distribution of HP among flowers. This hypothesis can be assessed for a single plant species by estimating the pollination quality of each visiting group within its assemblage (e.g., Herrera, 1987; Muchhala et al., 2009), but such an approach is prohibitive for comparing among multiple plant species. Here we propose that the pattern of CP and HP receipt among plants within a species will reflect the joint effect of quality and evenness of their floral visitor assemblage and that these CP-HP relationships can be readily compared among species.

Specifically, we envision three ways HP receipt could covary with CP receipt in flowers within a species. In the first, HP receipt increases monotonically as CP increases (type 1 in Fig. 1). This relationship would occur when both CP and HP grains are deposited with each pollinator visit, as expected when an evenly diverse assemblage of pollinators of similar quality visit flowers. Little variation in HP load size is expected among flowers and HP loads should be diverse because the diverse visitors are also visiting many other plant species (i.e., generalists; Neiland and Wilcock, 1999). The second possibility is that the delivery of HP is independent of delivery of CP, leading to no relationship between CP and HP receipt across conspecifics (type 2 in Fig. 1). This pattern could occur when a species is visited by only one or very few high quality pollinators that deliver almost pure CP loads (e.g., specialists) and thus HP receipt occurs only as a result of pollinator ‘mistakes’ (e.g., Wang et al., 2013) which lead to unpredictable patterns of

HP deposition. A third alternative is that HP receipt decreases or increases exponentially as CP receipt increases (type 3A and 3B in Fig. 1). These patterns are expected to occur when a species is visited by a highly uneven pollinator assemblage that is composed of one or few frequent, high-quality pollinators and also several less frequent, low-quality pollinators (e.g., Gómez et al., 2010). We note that these predictions rest on the assumption that high quality pollinators also tend to visit flowers more frequently than low quality ones-- a pattern often observed in natural communities (e.g., Motten et al., 1981; Herrera 1987; Sahli and Conner 2006; Gómez 2000; Gómez et al., 2007; Gómez et al., 2010). Thus in species with exponential patterns of CP-HP, receipt HP would be deposited mostly during visits by low-quality pollinators that are less frequent and exhibit low constancy. As a result the HP load varies with CP (either positively or negatively) depending on the CP load size deposited by the more frequent high-quality pollinators in the assemblage. For instance, if high-quality pollinators deliver large and pure CP loads whereas HP is delivered along with few CP grains by low-quality pollinators then HP would decrease exponentially as CP receipt increases (type 3A in Fig. 1). Alternatively, if numerous high-quality pollinators deliver small but pure CP loads and infrequent low-quality pollinators deliver large, mixed pollen loads then HP will increase exponentially with CP (type 3B in Fig. 1). Due to the unevenness of pollinator quality in the assemblage, HP loads will be unequally distributed across flowers, i.e., HP will be aggregated in only a few flowers, and there will be high within-species variance in HP load size. Moreover, the diversity of HP loads is predicted to be lower than that of species with a linear CP-HP relationship (type 1) because it reflects infrequent and random visitation events, rather than regular, consistent co-transport. These predictions can be tested by fitting curves to natural variation in CP and HP in flowers within species and comparing the evenness of pollinator assemblages and diversity of HP between groups defined by HP-CP relationships.

Accordingly, the aim of this study is to evaluate patterns of among- and within-species variation in HP receipt (load size and diversity) and identify potential drivers of such variation. First, we assess the relative importance of phenotypic and ecological (i.e., contemporary floral visitor assemblage) specialization, as well as conspecific flower density as determinants of among-species differences in mean and variance of HP load size and diversity received by flowers. Second, we evaluate patterns of within-species variation by characterizing CP-HP relationships (Fig. 1) and the diversity in the HP load and determine whether differences among species are related to the evenness of their floral visitor assemblage. We conduct these analyses with 19 plant species from three geographically distinct co-flowering communities and thereby assess the generality of these patterns across a wide range of ecological contexts.

MATERIALS AND METHODS

Study systems- Heterospecific pollen receipt was studied in 19 species sampled across three geographically and ecologically distinct coflowering plant communities: serpentine seeps of California, USA (SS), dolomite outcrops in Andalusia, Spain (DO) and dry scrublands in Yucatan, Mexico (DS) (Table 1). While each community has a unique evolutionary history, all three are seasonal flowering, species-rich communities dominated by small woody or herbaceous perennials and annuals (Estrada-Loera, 1991; Médail and Quezel, 1997, 1999; Safford et al., 2005; Freestone and Inouye, 2006; Alonso et al., 2013) that support many functional groups of insect flower visitors (e.g., Herrera et al., 2006; Campos-Navarrete et al., 2013; Koski et al., 2015). Thus, these communities reflect ecologically and evolutionarily independent replicates of similarly diverse plant-pollinator communities (Table 1).

Within each community four to nine insect-pollinated plant species with overlapping flowering times were selected (Table 1). Plant species represented nine families and varied in flower color, size, longevity, mating system and type of rewards (Table 2, Appendix 1, Alonso et al., 2013). Both, zygomorphic and actinomorphic species were included from each community and were similarly represented in the data set (10 vs. 9; Appendix 1).

Data collection-

Pollen receipt– Within each community an average of 135 wilted flowers (range: 52-222) was collected from each species along 3-5 transects at bi-weekly intervals during peak flowering (Table 2). This sampling scheme allowed us to capture both temporal and spatial variation in pollen receipt for each species. Across the 19 species, styles from a total of 2,566 flowers were collected and stored in 70 % ethanol until they were stained with decolorized aniline blue and prepared for scoring. Conspecific pollen and HP on stigmas were visualized with the aid of fluorescence microscopy (Kearns and Inouye, 1993). Both CP and HP were counted and summed across all styles within a flower when more than one style was present. A pollen library was constructed for each community to aid in the identification of pollen to species when possible or to morphotype when not. Heterospecific pollen was classified based on morphology (size, shape and exine ornamentation). For analysis HP was pooled into16 to 32 morphotype categories per community (Table 1). Each morphotype consisted of 1-6 possible species known to co-flower (Koski et al., 2015; Alonso, Ashman and Parra-Tabla unpublished data). The mean and coefficient of variation [CV] in HP load size (number of HP grains per flower) and diversity (number of HP morphotypes per flower) were calculated for each species (Appendix 1).

Floral visitors– The contemporary assemblage of floral visitors was characterized for each species by conducting 3-5 min observations of flowers within fixed plots scaled appropriately for each community (119 $2m^2$ plots in SS, 112 $4m^2$ plots in DO, and 60 $4m^2$ plots in DS). Pollinator censuses were conducted during the period of highest pollinator activity (i.e., between 8:00 and 16:00h) twice per plot per week for the duration of the flowering season. A total of 252.5, 32.5 and 183.7 hrs of observation was conducted at SS, DO and DS respectively. During each census the number of open flowers and the number and identity of floral visitors on a given species was recorded. Only species that received at least 25 visits were analyzed (N = 15 species; Appendix 1).

Floral visitors are often categorized into functional groups based on their morphology (e.g., body size), energetic requirements and flight ability, which can determine their foraging and flower-handling behavior, the range of flowers they can visit, as well as their conspecific pollen transfer abilities and thus the type of selection they generate (Fenster et al., 2004; Moretti et al., 2009). In this sense, insects within a pollinator functional group are also expected to be equivalent in their contribution to HP transfer to a given plant species. Members of a functional group are thus more similar to each other in their quality as pollinators than to members of other groups (Zamora, 2000; Fenster et al., 2004; Greenleaf et al., 2007; Geslin et al., 2013; Rosas-Guerrero et al., 2014; Koski et al., 2015) and the presence/absence of a particular group can have important effects on plant fitness (Gómez et al., 2010; Albrecht et al., 2012; Fründ et al., 2013). Thus, in this study, floral visitor diversity was calculated based on 11 behaviorally and functionally defined groups based on their body size, energetic requirements and foraging/feeding behavior (Appendix 2). These functional groups were present across all three communities and included: large solitary bees, small solitary bees, large social bees, beetles, bee

flies, large syrphid flies, small syrphid flies, other flies, butterflies, walking insects (e.g., ants) and wasps (Appendix 2). Simpson's reciprocal diversity index (1/D) and evenness were calculated for each study species using data on number of visits by these functional groups. Simpson's reciprocal index (1/*D*) was chosen because it is an abundance weighted diversity estimate ($1/D = 1/\Sigma[n / N]^2$ where n = total number of organisms in a particular functional group, and N = total number of organisms in all functional groups) that is very robust even with small sample sizes and thus is a reliable measure of diversity (Magurran, 2004). Rarefaction analyses demonstrated that our sampling effort was sufficient to adequately characterize the diversity of pollinator functional groups visiting plant species as we were able to capture between 80-98% of all possible plant-pollinator interactions (Koski et al., 2015; Alonso et al., unpubl. data). Functional group diversity was not correlated with the total number of visits observed for a given species ($r = 0.09$, $P = 0.7$).

Simpson's evenness was calculated by dividing Simpson's reciprocal index by the total number of pollinator functional groups in the sample (Magurran, 2004). Thus, evenness varies from 0 (completely uneven) to 1 (complete evenness).

Conspecific density– Conspecific flower density for each focal plant species was determined from the records of the number of open flowers per plot during each floral visitor census. To produce a single value per species of local conspecific density (flowers/m^2) flower densities were averaged across the season for every plot where that species flowered. This estimate of local conspecific flower density is correlated with its global floral abundance in the community ($r = 0.99$; $P = 0.001$, $N = 19$).

Flower traits– Flower biomass was used as a proxy of flower size. For each species, we collected a minimum of 15 flowers and these were dried in bulk at 60°C for 24 h and then weighed to the nearest 0.0001 g on an AE200 Mettler analytical balance (Mettler-Toledo, Columbus, Ohio, USA). Total dry weight was then divided by the total number of flowers to estimate average flower biomass for each species. Flower longevity was estimated by recording the number of days a flower remained open (from anthesis to senescence) on a minimum of five individuals (excluded from pollinators) per species during peak flowering in each community. The average flower size and longevity for each species was used in analyses. Floral shape was scored as zygomorphic (bilateral symmetry) or actinomorphic (radial symmetry).

Data Analyses-

Sources of variation in HP receipt- To evaluate the pattern of variation in size (number of HP grains) and diversity (number of HP types) of the HP load per flower, we conducted nested mixed effects ANOVAs (proc mixed; SAS 2010). To account for the potential influence of shared evolutionary history on species patterns of HP receipt, family and species (nested within family) were treated as random effects, while community was treated as a fixed effect. We then used this same model to partition the total variance in HP load size and diversity among families, species, communities and individuals within species (residual variation; proc varcomp, method = MIVQUE0; SAS 2010). Load size and diversity of HP types were (square root + 0.5) transformed in order to meet assumptions of normality of residuals.

Among-species variation in HP receipt- Means and CV of HP load size and diversity were calculated for each species and used in among-species regressions to determine the relative importance of ecological specialization (contemporary floral visitor diversity), conspecific

283 flower density and phenotypic specialization (flower size, longevity and symmetry) in explaining
284 interspecific variation in HP receipt. Given the minor, but significant, effect of community on
285 HP load size and diversity (see results), the effect of community was removed using a single
286 effect linear model (proc glm; SAS 2010) and using the residuals in subsequent regression
287 analyses across all species regardless of their community (e.g., Jakob et al., 1996; Essenberg,
288 2013). There was no effect of community on any of the independent variables studied (all $P >$
289 0.3) so raw data were used in the regression analyses. Standardized regression coefficients were
290 calculated for each variable (each observation minus the mean and divided by the variance) to
291 facilitate comparisons among independent variables. To test for an effect of continuous variation
292 in phenotypic specialization (flower size and longevity), ecological specialization and
293 conspecific flower density, multiple regressions were conducted. To test for an effect of
294 categorical variation in phenotypic specialization (flower symmetry: actinomorphic vs.
295 zygomorphic) and its potential interaction with floral visitor diversity and conspecific density an
296 ANCOVA was run (proc glm; SAS 2010). When interactions between flower symmetry and
297 visitor diversity or conspecific density were non-significant ($P > 0.5$) they were removed from
298 the models. Heterospecific pollen load size, diversity of HP types (square root + 0.5) and
299 conspecific flower density (log10) were transformed to improve the distribution of residuals.
300 Insect visitation and flower size data were not available for four and one species respectively,
301 (Appendix 1), so the final data set for the analysis of species-specific traits on HP receipt
302 included a total of 14 species.

303 *Within-species variation in HP receipt*- To characterize within-species relationships between HP
304 and CP receipt (Fig. 1), linear and non-linear regressions between the amount of CP and HP
305 received per flower were performed separately for each species. First we tested for the

significance of both linear (proc reg; SAS 2010) and non-linear relationships between CP and HP receipt. The non-linearity of the relationship was tested with the inclusion of a non-parametric component (spline) using a generalized additive model with a cubic spline and a Poisson error distribution (proc gam; SAS 2010). If only a significant linear relationship was found then the species was classified as type 1. If both (linear and non-linear) were found to be non-significant then the species was categorized as type 2 (amount of HP received independent of the amount of CP). Only when the non-linear relationship was found significant was an exponential model ($HP=a*(\exp[b_1*CP])$) then fit to the data (proc nlin; SAS 2010). Species with a significant negative *b* have an exponentially decreasing CP-HP relationship (type 3A), while those with positive *b* have an exponentially increasing CP-HP relationship (type 3B). If both linear and non-linear relationships were found to be significant, then we assessed the fit of the models by comparing adjusted R^2s and the model with the best fit was selected (larger R^2 values). Pseudo R^2 for non-linear models was estimated as 1- (Error sum of squares/Total sum of squares [corrected]) (Introduction to SAS. UCLA: Statistical Consulting Group [online]. Website http://www.ats.ucla.edu/stat/sas/notes2 [accessed 29 May 2015]). Finally, we performed linear models to evaluate whether species with different patterns of CP-HP receipt (linear vs. nonlinear: type 1 vs. 3A and 3B; see results) also differed significantly in evenness of flower visiting fauna, CV of HP load size or total HP diversity received. These models were based upon the residuals from a one-way ANOVA where community was the predictor of each response variable.

RESULTS

Sources of variation in HP receipt- We found extensive variation among species in mean HP load size (mean ± SE: 24.7 ± 11.4; range: 0.04-191.5 pollen grains) and diversity (1.3 ± 0.25;

0.03-3.8 morphotypes) per flower as well as in their respective CVs (302.6 ± 30.5; 102.9-612.1 and 140.6 ± 27.1; 42.1-547.6 for HP load size and diversity respectively; Fig 2; Appendix 1).

Variation among individuals within a species (residual variation) accounted for the highest proportion of the total variation in HP load size and diversity (46 and 50% respectively). Nevertheless, the contribution of species-level variation to total variation for both response variables was also substantial (28 and 10% respectively). Variation among communities explained 23 and 7%, and plant family explained 3 and 33% of the total variation in HP load size and diversity, respectively.

In the global analysis, the average HP load size and diversity received per flower was significantly different among species ($Z = 1.86$, $P < 0.03$ and $Z = 2.18$, $P < 0.01$, respectively). Heterospecific pollen load size and diversity also varied significantly among communities ($F_{2, 2547} = 5.77$, $P = 0.003$ and $F_{2, 2547} = 4.28$, $P = 0.01$, respectively) while family had no effect in either response variable (both $Z < 1.4$, $P > 0.05$).

Among-species variation in HP receipt- There was wide variation in floral visitor diversity (2.02 ± 0.25; 1.05-4.09), conspecific flower density (19.7 ± 1.25; 0.6–217.2 flowers/m^2), flower longevity (3.8 ± 0.79; 0.5-12 days) and flower biomass (0.008 ± 0.001; 0.0006-0.29g) among species providing ample discriminatory ability in regressions even with a small number of species (Appendix 1).

Among species, mean HP load size increased significantly with increasing floral visitor diversity and flower biomass (Table 3A). Floral visitor diversity was the only significant factor affecting HP load diversity and this was a positive effect (Table 3B). Conspecific flower density and flower longevity did not significantly affect either aspect of HP receipt (Table 3A, B).

Although there was substantial variation among species in the CV of HP load size and diversity (see above), none of the factors we measured significantly explained this variation (Table 3C, D).

When flower symmetry was included in a separate model to account for categorical variation in floral phenotype (see data analysis above) the results did not change. That is, the strong effect of floral visitor diversity and the non-significant effect of conspecific density, ($F_{1, 9}$= 14.5, P = 0.004; $F_{1, 11}$ = 0.4, P > 0.5 respectively) and diversity ($F_{1, 9}$= 9.96, P = 0.01; $F_{1, 9}$ = 0.8, P > 0.4) on HP load size remained. There were no significant interactions of flower symmetry with either continuous variable ($F_{1, 9}$ = 0.04-1.3; all P > 0.3). And even though average HP load size and diversity were slightly elevated in actinomorphic flowers compared to zygomorphic ones, these were not statistically significant differences (HP load size: 27.2 ± 18.3 vs. 22.1 ± 14.2 grains; $F_{1, 11}$ = 0.18, P > 0.6; HP diversity: 1.6 ± 0.3 vs. 0.9 ± 0.3; $F_{1, 11}$= 1.5, P = 0.24).

Within-species variation in HP receipt- Of the 19 species evaluated seven exhibited significant linear relationships between the amount of CP and HP received (type 1 in Fig. 1; Fig. 3A for an example), eight showed an exponentially decreasing relationship (type 3A in Fig. 1; Fig. 3C) and three showed an exponentially increasing relationship (type 3B in Fig. 1; Fig. 3D; Table 2). Only in one species did HP vary independently of CP (type 2 in Fig. 1; Fig. 3B; Table 2). Furthermore, differences in CP-HP patterns (linear type 1 vs. exponential type 3A and 3B) reflected differences in HP load size and diversity and pollinator evenness in the predicted directions, although none of these relationships were statistically significant (HP diversity: 1.8 ± 0.3 vs. 0.9 ± 0.3; $F_{1, 16}$ = 3.21, P = 0.09; CV in HP load size: 291 ± 36 vs. 270 ± 42; $F_{1, 16}$ = 0.11,

372 $P > 0.7$; pollinator evenness: 0.44 ± 0.08 vs. 0.34 ± 0.06; $F_{1, 16} = 1.16$, $P > 0.4$). There was also
373 no association between flower symmetry and CP-HP relationship type ($\chi 2_{16} = 0.01$, $P > 0.9$).

374 DISCUSSION

375 Wide variation in mean HP load size and diversity in naturally pollinated flowers was
376 revealed in this detailed comparison of 19 species across three plant communities. Diversity of
377 the contemporary flower-visiting community emerged as a strong and consistent driver of
378 variation in HP receipt among species, more so than evolutionary degree of specialization, as
379 represented by floral phenotype (symmetry, biomass and longevity). Furthermore, within-species
380 variation in HP load size and diversity could be associated with patterns of CP receipt and two
381 dominant CP-HP relationships emerged (linear or exponentially decreasing) indicating the
382 potential for promising explorations of mechanisms at this level in the future. We discuss these
383 results and their broader ecological implications in detail below.

384 ***Among-species variation in HP receipt-*** Plant species identity accounted for more variation in
385 HP load size than family membership suggesting that the processes that influence variation in HP
386 load size are likely independent of common evolutionary history. However, this was not the case
387 for HP load diversity where among-family variation was more important. This latter result is
388 consistent with studies that have shown, across many plant-pollinator communities, that
389 pollinator guilds tend to visit closely related plant species (e.g., Vamosi et al. 2014) and thus
390 species within the same plant family are likely to receive similar diversity of HP grains.
391 Furthermore, HP receipt varied across communities but variation among them explained less
392 than variation among species and individuals in both HP load size and diversity, suggesting that
393 underlying processes that influence HP receipt may operate across a wide range of ecological

394 and evolutionary contexts. Interestingly, each community had both species with high mean HP
395 receipt and species with very low HP receipt (Fig. 2). For example, in the serpentine seeps
396 *Delphinium uliginosum* and *Triteleia peduncularis* received hundreds of HP grains—ten times
397 the HP per flower received by *Zigadenus venenosus*, and in the dolomite outcrops *Silene*
398 *lasiostyla* received twenty times that of *Thymus orospedanus* or *Sideritis incana* (Fig. 2;
399 Appendix 1). Similar dramatic differences have been observed between species within alpine
400 (Fang and Huang, 2013), prairie (Montgomery and Rathcke, 2012), and old field communities
401 (McLernon et al., 1996) suggesting that avoidance of HP may not be the only evolutionary stable
402 strategy for co-existence. That is, there may be two evolutionary strategies: selection for
403 avoidance of HP on one hand and selection for tolerance of the effects of HP receipt on the other
404 that could contribute to species coexistence (Ashman and Arceo-Gómez, 2013). Studies that link
405 natural patterns of HP receipt to their causes (see below) as well as fitness costs are needed to
406 test these ideas (Ashman and Arceo-Gómez, 2013).

407 There was also substantial among-species variation in the diversity of HP loads.
408 However, given our use of morphotypes (which each could represent 1-6 species) these data
409 most likely represent underestimates of the diversity of interactions. In fact, when species have
410 been identified up to 15 species of HP can occur on one flower (Bartomeus et al., 2008; Fang and
411 Huang, 2013). Such extensive HP transfer indicates that pollinator sharing is leading to
412 multispecies interactions on the style for most plants in the community, the consequences of
413 which can be greater than just the sum of individual species' effects (Arceo-Gómez and Ashman,
414 2011). What is clear, however, is that this variation in load size and diversity provides a window
415 into understanding the ecological drivers of HP receipt, as well as can help pinpoint where
416 opportunities for natural selection to avoid or tolerate HP receipt lie (see below).

After accounting for community differences, HP load size and diversity reflected species-specific floral visitor diversity, more than other measures of ecological context (conspecific density) or phenotypic specialization (floral symmetry, longevity and biomass). The only other study of HP patterns that directly characterized contemporary floral visitor assemblages also found that more generalized plants tended to receive larger and more diverse loads of HP than specialized ones (Fang and Huang, 2013). Moreover, in our study the increase in HP load size and diversity with increasing floral visitor diversity occurred irrespective of flower symmetry, a finding that supports the notion that phenotypic specialization may not always reflect ecological specialization (Ollerton, 1996). Such a disconnect may also explain patterns of HP receipt contrary to the presumed level of specialization based on symmetry, i.e., higher HP receipt in zygomorphic than actinomorphic flowers found in other studies (McLernon et al., 1996).

Floral traits that defined specialization or restrictiveness, while being quite varied in our data set (Appendix 1), were not strong determinants of variation in any aspect of HP receipt. Only flower biomass affected HP load size among-species, with species with heavier (larger) flowers receiving larger and more divers HP loads than lighter (smaller) ones. Because we accounted for visitor diversity, the effect of flower biomass is not through differences in generalization level but rather may be mediated through enhanced visitation rates (e.g., Galen and Newport, 1987; Conner and Rush, 1996) or larger/more exposed stigmas (Montgomery and Rathcke, 2012; Fang and Huang, 2013). Interestingly, flower symmetry only had a minor effect on mean HP load size, and HP receipt appeared to scale similarly with floral visitor diversity in both actinomorphic and zygomorphic flowers. Furthermore, we did not find any evidence to support the prediction that sparse (rare) species are more likely to receive HP than abundant ones (Rathcke, 1983; McLernon et al., 1996), contrasting with the results of Jakobsson et al. (2009).

Despite the observation of a wide range in CVs of HP load size and diversity across species (Appendix 1), none of the predictors we tested could account for this variation (Table 3). The strongest non-significant indicator of this variation was flower longevity, possibly reflecting increased visitation rate per flower, and/or increased likelihood of stochastic visitation events by inconstant visitors. But more study is needed to pinpoint the sources of variation in this important aspect of HP receipt.

Within-species variation in HP receipt- Within species, HP load size and diversity varied 6-10 fold in magnitude (Appendix 1) and variance at this level was greater than the combined contributions of family and species identity (> 46% of the total). Our exploration of within-species variation in HP load size could be predicted from two dominant CP-HP relationships (type 1 vs. 3A in Fig. 1; Table 2) and suggests that two distinct types of plant-pollinator interactions prevail. We found approximately half of the species studied showed significant linear increases in HP with CP (and also tended to have higher diversity of HP types) while most of the remaining species showed exponentially decreasing relationships (and fewer HP types). And while the difference in pollinator evenness between these two groups was in the predicted direction (greater for species with type 1), it was not significant. Nevertheless, the evaluation of CP-HP relationships among flowers provides insight into the genesis of variation in HP receipt that cannot be discerned from means or variances alone and our comparative data provide first insight into the possible factors responsible for within-species variation in HP receipt. For instance, the fact that evenness alone did not capture the within-species variance in pollen transfer dynamics may suggest that variation in pollinator quality is more important than variation in abundance in influencing deposition dynamics, or that variation not captured by our floral visitor functional groups is important. Pollinator quality, in particular, is likely a complex

463 trait that results from not only inconstancy but also pollinator grooming (Thomson, 1986;
464 Holmquist et al., 2012), pollen carryover (Thomson and Plowright 1980) and pollen loss during
465 transport (Wilcock and Neiland, 2002), and thus, it may be difficult to capture with only
466 information on the visitor functional groups defined herein.

467 Nevertheless, more species–level studies are needed to tease apart the contribution of
468 pollinator evenness from pollinator quality as well as to take into account fine-scale
469 neighborhood variation in flower diversity and abundance. Such work would provide insight into
470 the potential for ongoing evolution of either avoidance (e.g., pollen placement [Armbruster et al.,
471 1994], site of stigma contact [Armbruster et al., 2014], stigma size [Montgomery and Rathcke,
472 2012]) or tolerance strategies (e.g., stigma secretions [Ashman and Arceo-Gómez, 2013]) in
473 contemporary communities. While it is a daunting task to perform these studies across many
474 species within communities, such studies are needed to understand how traits evolve in multi-
475 species contexts.

476 ***Conclusions***- This study illustrates how widespread the phenomenon of HP receipt is both
477 within and across diverse plant communities. In doing so it highlights ecological generalization
478 as an important determinant of interspecific variation in both the size and diversity of HP load.
479 Indicating that contemporary changes in pollinating fauna (loss of species, shifts in flowering
480 time) will likely translate into changes in the plant-plant interactions on the style (e.g., Brosi and
481 Briggs 2013) We further confirm that HP and CP receipt are not independent of each other at
482 intraspecific level for some species and propose that the shape of such relationship reflects past
483 evolution and may provide substrate for future evolution to shape avoidance of HP transfer.

484

485 LITERATURE CITED

486 ALARCÓN, R., N. M. WASER, AND J. OLLERTON. Year-to-year variation in the topology of a
487 plant–pollinator interaction network. *Oikos* 117: 1796–1807.

488 ALBRECHT, M., B. SCHMID, Y. HAUTIER, AND C. B. MÜLLER. 2012. Diverse pollinator
489 communities enhance plant reproductive success. *Proceedings of the Royal Society B*
490 279:4845-4852.

491 ALONSO, C., J. C. VAMOSI, T. M. KNIGHT, J. A. STEETS, AND T-L. ASHMAN. 2010. Is reproduction
492 of endemic plant species particularly pollen limited in biodiversity hotspots? *Oikos* 119:
493 1192–1200.

494 ALONSO, C., C. M. HERRERA, AND T-L. ASHMAN. 2012. A piece of the puzzle: a method for
495 comparing pollination quality and quantity across multiple species and reproductive events.
496 *New Phytologist* 193: 532–542.

497 ALONSO, C., C. M. NAVARRO-FERNÁNDEZ, G. ARCEO-GÓMEZ, G. A. MEINDL, V. PARRA-TABLA,
498 AND T-L. ASHMAN. 2013. Among-species differences in pollen quality and quantity
499 limitation: implications for endemics in biodiverse hotspots. *Annals of Botany*112: 1462-
500 1469.

501 ARCEO-GÓMEZ, G., AND T-L. ASHMAN. 2011. Heterospecific pollen deposition: does diversity
502 alter the consequences? *New Phytologist* 192: 738–746.

503 ARMBRUSTER, W. S. 1995. The origins and detection of plant community structure: reproductive
504 versus vegetative processes. *Folia Geobotanica* 30: 483–497.

505 ARMBRUSTER, W. S., M. E. EDWARDS, AND E. M. DEBEVEC. 1994. Floral character displacement
506 generates assemblage structure of western Australian triggerplants (*Stylidium*). *Ecology* 75:
507 315-329.

508 ARMBRUSTER, W. S., T. F. HANSEN, C. PELABON, R. PEREZ-BARRALES, AND J. MAAD. 2009. The
509 adaptive accuracy of flowers: measurement and microevolutionary patterns. *Annals of*
510 *Botany* 103: 1529–1545.

511 ARMBRUSTER, W. S., X-Q. SHI, AND S-Q. HUANG. 2014. Do specialized flowers promote
512 reproductive isolation? Realized pollination accuracy of three sympatric *Pedicularis*
513 species. *Annals of Botany* 113: 331-340.

514 ASHMAN, T-L., AND G. ARCEO-GÓMEZ. 2013. Toward a predictive understanding of the fitness
515 costs of heterospecific pollen receipt and its importance in co-flowering communities.
516 *American Journal of Botany* 100: 1061–1070.

517 BARTOMEUS, I., J.BOSCH, AND M. VILA. 2008. High invasive pollen transfer, yet low deposition
518 on native stigmas in a *Carpobrotus*-invaded community. *Annals of Botany* 102: 417–424.

519 BOSCH, J., A. M. M. GONZALEZ, A. RODRIGO AND D. NAVARRO. 2009. Plant–pollinator networks:
520 adding the pollinator's perspective. *Ecology Letters* 12: 409–419.

521 BROSI, B. J., AND H. M. BRIGGS. 2013. Single pollinator species losses reduce floral fidelity and
522 plant reproductive function. *Proceedings of the National Academy of Sciences* 110: 13044-
523 13048.

524 CAMPOS-NAVARRETE, M. J., V. PARRA-TABLA, J. RAMOS-ZAPATA, C. DÍAZ-CASTELAZO, AND E.
525 REYES-NOVELO. 2013. Structure of plant–Hymenoptera networks in two coastal shrub sites
526 in Mexico. *Arthropod-Plant Interactions* 7: 607-617.

527 CONNER, J. K., AND S. RUSH. 1996. Effects of flower size and number on pollinator visitation to
528 wild radish, *Raphanus raphanistrum*. *Oecologia* 105: 509–516.

529 DORMANN, C. F. 2011. How to be a specialist? Quantifying specialisation in pollination
530 networks. *Network Biology* 1: 1-20.

531 EATON, D. A. R., C. B. FENSTER, J. HEREFORD, S-Q. HUANG, AND R. H. REE. 2012. Floral
532 diversity and community structure in *Pedicularis* (Orobanchaceae). *Ecology* 93: S182–
533 S194.

534 ESSENBERG, C. J. 2013. Explaining the effects of floral density on flower visitor species
535 composition. *The American Naturalist* 181: 344–356.

536 ESTRADA-LOERA, E. 1991. Phytogeographic relationships of the Yucatan Peninsula. *Journal of*
537 *Biogeography* 18: 687–697.

538 FAEGRI, K., AND L. VAN DER PIJL. 1979. The principles of pollination ecology. Pergamon Press,
539 Oxford, UK.

540 FANG, Q., AND S-Q. HUANG. 2013. A directed network analysis of heterospecific pollen transfer
541 in a biodiverse community. *Ecology* 94: 1176–1185.

542 FEINSINGER, P., K. G. MURRAY, S. KINSMAN, AND W. H. BUSBY. 1986. Floral neighborhood and
543 pollination success in four hummingbird-pollinated cloud forest plant species. *Ecology* 67:
544 449–464.

545 FENSTER, C. B., W. S. ARMBRUSTER, P. WILSON, M. R. DUDASH, AND J. D. THOMSON. 2004.
546 Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution and*
547 *Systematics* 35: 375–403.

548 FLEMING, T. H., AND J. N. HOLLAND. 1998. The evolution of obligate pollination mutualisms:
549 senita cactus and senita moth. *Oecologia* 114: 368–375.

550 FREESTONE, A. L., AND B. D. INOUYE. 2006. Dispersal limitation and environmental
551 heterogeneity shape scale-dependant diversity patterns in plant communities. *Ecology* 87:
552 2425–2432.

553 FRÜND, J., C. F. DORMANN, A. HOLZSCHUH, AND T. TSCHARNTKE. 2013. Bee diversity effects on
554 pollination depend on functional complementary and niche shifts. *Ecology* 94:2042-2054.

555 GALEN, C., AND M. E. A. NEWPORT. 1987. Bumble bee behavior and selection on flower size in
556 the sky pilot, *Polemonium viscosum*. *Oecologia* 74: 20–23.

557 GESLIN, B., B. GAUZENS, E. THEBAULT, AND I. DAJOZ. 2013. Plant pollinator networks along a
558 gradient of urbanization. *PLoS ONE* 8: e63421.

559 GÓMEZ, J. M. 2000. Effectiveness of ants as pollinators of *Lobularia maritima*: effects of main
560 sequential fitness components of the host plant. *Oecologia* 122: 90.97.

561 GÓMEZ, J. M., M. ABDELAZIZ, J. LORITE, A. J. MUÑOZ-PAJARES, AND F. PERFECTTI. 2010. Changes in
562 pollinator fauna cause spatial variation in pollen limitation. *Journal of Ecology* 98: 1243–
563 1252.

564 GÓMEZ, J. M., J. BOSCH, F. PERFFECTI, J. FERNANDEZ, AND M. ABDELAZIZ. Pollinator diversity
565 affects plant reproduction and recruitment: the tradeoffs of generalization. *Oecologia* 157:
566 597-605.

567 GREENLEAF, S. S., N. M. WILLIAMS, R. WINFREE, AND C. KREMEN. 2007. Bee foraging ranges
568 and their relationship to body size. *Oecologia* 153: 589–596.

569 HERRERA, C. M. 1987. Components of pollinator "quality": comparative analysis of a diverse
570 insect assemblage. *Oikos* 50: 79–90.

571 HERRERA C. M., M. C. CASTELLANOS, M. MEDRANO. 2006. Geographical context of floral
572 evolution: towards an improved research programme in floral diversification. In: Harder L.
573 D., and S. C. H. Barrett (eds.) Ecology and Evolution of Flowers. pp. 278–294. Oxford
574 University Press, Oxford.

575 HOLMQUIST, K. G., R. J. MITHCELL, AND J. D. KARRON. 2012. Influence of pollinator grooming
576 on pollen-mediated gene dispersal in *Mimulusringens* (Phrymaceae). *Plant Species Biology*
577 27: 77–85.

578 HUANG, S-Q., AND X-Q. Shi. 2013. Floral isolation in *Pedicularis*: how do congeners with shared
579 pollinators minimize reproductive interference? *New Phytologist* 199: 858–865.

580 JAKOB, E. M., S. D. MARSHALL, AND G. W. UETZ et al. 1996. Estimating fitness: a comparison of
581 body condition indices. *Oikos* 77: 61–67.

582 JAKOBSSON, A., A. LAZARO, Ø. TOTLAND. 2009. Relationships between the floral neighborhood
583 and individual pollen limitation in two self-incompatible herbs. *Oecologia* 160: 707–719.

584 KEARNS, C. A., AND D. W. INOUYE. 1993. Techniques for pollination biologists. - University
585 Press of Colorado, USA.

586 KOSKI, M H., G. A. MEINDL, G. ARCEO-GOMEZ, M. WOLOWSKI, K. A. LECROY, AND T-L.
587 ASHMAN. 2015. Plant-flower visitor networks in a serpentine metacommunity: assessing
588 traits associated with keystone plant species. *Arthropod-Plant Interactions* 9: 9-21.

589 MAGURRAN, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Malden, USA.

590 MCLERNON, S. M., S. D. MURPHY, AND L. W. AARSSEN. 1996. Heterospecific pollen transfer
591 between sympatric species in a midsuccessional old-field community. *American Journal of*
592 *Botany* 83: 1168–1174.

593 MEDAIL, F., AND P. QUEZEL. 1997. Hot-spots analysis for conservation of plant biodiversity in
594 the Mediterranean Basin. *Annals of the Missouri Botanical Garden* 84: 112–127.

595 MÉDAIL, F., AND P. QUÉZEL. 1999. Biodiversity hotspots in the Mediterranean Basin: setting
596 global conservation priorities. *Conservation Biology* 13: 1510–1513.

597 MONTGOMERY, B. R., AND B. J. RATHCKE. 2012. Effects of floral restrictiveness and stigma size
598 on heterospecific pollen receipt in a prairie community. *Oecologia* 168: 449–458.

599 MORALES, C. L., AND A. TRAVESET. 2008. Interspecific pollen transfer: magnitude, prevalence
600 and consequences for plant fitness. *Critical Reviews of Plant Science* 27: 221–238.

601 MORETTI, M., F. DE BELLO, S. P. M. ROBERTS, AND S. G. POTTS. 2009. Taxonomical vs.
602 functional responses of bee communities to fire in two contrasting climatic regions. *Journal*
603 *of Animal Ecology* 78: 98-108.

MOTTEN, A. F., D. R. CAMPBELL, D. E. ALEXANDER, AND H. L. MILLER. 1981. Pollination effectiveness of specialist and generalists visitors to a North Carolina population of *Claytonia virginica*. *Ecology* 62: 1278-1287.

MUCHHALA, N., AND M. D. POTTS. 2007. Character displacement among bat-pollinated flowers of the genus *Burmeistera*: analysis of mechanism, process and pattern. *Proceedings of the Royal Society B* 274: 2731–2737.

MUCHHALA, N., A. CAIZA, J. C. VIZUETE, AND J. D. THOMSON. 2009. A generalized pollination system in the tropics: bats, birds and *Aphelandra acanthus*. *Annals of Botany* 103: 1481–1487.

NEILAND, M. R. M., AND C. C. WILCOCK. 1999. The presence of heterospecific pollen on stigmas of nectariferous and nectarless orchids and its consequences for their reproductive success. *Protoplasma* 208: 65–75.

OLESEN, J. M., AND P. JORDANO. 2002. Geographic patterns in plant-pollinator mutualistic networks. *Ecology* 83: 2416–2424.

OLLERTON, J. 1996. Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant–pollinator systems. *Journal of Ecology* 84: 767–769.

PAUW, A. 2013. Can pollination niches facilitate plant coexistence? *Trends in Ecology and Evolution* 28: 30–37.

PELLMYR, O., J. N. THOMPSON, J. M. BROWN, AND R. G. HARRISON. 1996. Evolution of pollination and mutualism in the yucca moth lineage. *The American Naturalist* 148: 827–847.

RATHCKE, B. 1983. Competition and facilitation among plants for pollination. In: Real, L. (ed.), Pollination biology. Pp. 305-329. Academic Press, New York, USA.

ROSAS-GUERRERO, V., R. AGUILAR, S. MARTEN-RODRIGUEZ, L. ASHWORTH, M. LOPEZARAIZA-MIKEL, J. M. BASTIDA, AND M. QUESADA. 2014. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? *Ecology Letters* 17: 388-400.

SAFFORD, H. D., J. H. VIERS, AND S. P. HARRISON. 2005. Serpentine endemism in the California flora: a database of serpentine affinity. *Madroño* 52: 222–257.

SAHLI, H. F., J. K. CONNER. 2006. Characterizing ecological generalization in plant-pollination systems. *Oecologia* 148: 365-372.

SAS INSTITUTE. 2010. SAS/IML software. Version 9.2.SAS Institute, Cary, North Carolina, USA.

THOMSON, J. D. 1986. Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. *Journal of Ecology* 74: 329–341.

THOMSON, J. D., AND R. C. PLOWRIGHT. 1980. Pollen carryover, nectar rewards, and pollinator behavior with special reference to *Diervillalonicera*. *Oecologia* 46: 68–74.

THOMSON, J. D., B. J. ANDREWS, AND R. C. PLOWRIGHT. 1982. The Effect of foreign pollen on ovule development in *Diervilla lonicera* (Caprifoliaceae). *New Phytologist* 90: 777–783.

VAMOSI, J. C., C. M. MORAY, N. K. GARCHA, S. A. CHAMBERLAIN AND A. Ø. MOOERS. 2014. Pollinators visit related plant species across 29 plant-pollinator networks. *Ecology and Evolution* 4: 2303-2315.

645 VAMOSI, J. C., T. M. KNIGHT, J. A. STEETS, S. J. MAZER, M. BURD AND T-L. ASHMAN. 2006.
646 Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of*
647 *Science* 103: 956–961.

648 VÁZQUEZ, D. P. AND M. A. AIZEN. 2003. Null model analyses of specialization in plant-pollinator
649 interactions. *Ecology* 84: 2493–2501.

650 WANG, G., S. G. COMPTON, AND J. CHEN. 2013. The mechanism of pollinator specificity between
651 two sympatric fig varieties: a combination of olfactory signals and contact cues. *Annals of*
652 *Botany* 111:173-181.

653 WASER, N. M. 1983. The adaptive value of floral traits. In: Real, L. (ed.), Pollination biology, pp.
654 241-277. Academic Press, New York, USA.

655 WASER, N. M. 1986. Flower constancy: definition, cause, and measurement. *The American*
656 *Naturalist* 127: 593–603.

657 WASER, N. M., L. CHITTKA, M. V. PRICE, N. M. WILLIAMS, AND J. OLLERTON. 1996.
658 Generalization in pollination systems, and why it matters. *Ecology* 77: 1043–1060.

659 WEIBLEN, G. D. 2004. Correlated evolution in fig pollination. *Systematic Biology* 53: 128–139.

660 WILCOCK, C., AND R. NEILAND. 2002. Pollination failure in plants: why it happens and when it
661 matters. *Trends in Plant Science* 7: 270–277.

662 ZAMORA, R. 2000. Functional equivalence in plant-animal interactions: ecological and
663 evolutionary consequences. *Oikos* 88: 442-447.

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Table 1. Location**,** community type (code), flowering period, number of focal species, total co-flowering species richness, flower visitor functional groups observed and number of pollen morphotypes identified at each location.

Location	Community	Flowering period sampled	Number of focal species	Number of insect pollinated co-flowering species	Number of flower visitor functional groups	Number of pollen morphotypes
California	Serpentine seeps (SS)	June-July 2010	6	50	11	20
Andalusia	Dolomite outcrops (DO)	May-June 2010	9	67	11	32
Yucatan	Dry scrublands (DS)	July-September 2011	4	38	10	16

Table 2. Nineteen study species (species code used in Fig 2; for complete taxonomic names see Appendix 1), plant family (family codes), community type and sample size (*N*). For each, the evenness of flower visiting fauna, within-species variance (CV) in HP load size (pollen grains), and mean number of HP morphotypes receive is given, as well as the type of CP-HP relationship (described in Fig. 1) observed. For each CP-HP regression the coefficient (*b*) and its significance are given. '.' denotes data not available.

Community type	Family (code)	Species code	*N*	Pollinator evenness	CV of HP load size	Mean number of HP types	HP-CP pattern	*b*	*P*
SS	Plantaginaceae (Pl)	Anc	150	0.51	220.9	1.2	Increasing linearly	0.04	0.0007
SS	Ranunculaceae (Ra)	Deu	150	0.68	102.9	2.7	Increasing linearly	0.32	0.0001
SS	Phyrmaceae (Ph)	Mig	151	0.19	237.2	2.09	Decreasing exponential	-0.0015	0.0001
SS	Phyrmaceae (Ph)	Min	151	0.35	318.8	1.3	Decreasing exponential	-0.002	0.0004
SS	Liliaceae (Li)	Trp	115	0.53	137.4	3.8	Increasing linearly	0.99	0.0001
SS	Liliaceae (Li)	Ziv	151	0.52	156.5	1.8	Increasing linearly	0.032	0.03
DO	Cistaceae (Ci)	Fub	113	.	187.9	1.2	Decreasing exponential	-0.0009	0.0001
DO	Cistaceae (Ci)	Fup	63	0.6	260.4	1.5	Decreasing exponential	-0.004	0.008
DO	Cistaceae (Ci)	Hcr	90	0.23	395.8	1.4	Decreasing exponential	-0.006	0.003
DO	Cistaceae (Ci)	Hci	129	.	612.1	0.27	Decreasing exponential	-0.005	0.001
DO	Lamiaceae (La)	Sii	123	0.37	580.6	0.03	No pattern	0.0001	0.86
DO	Caryophyllaceae (Ca)	Sco	133	.	349.2	2.3	Increasing exponential	0.005	0.002
DO	Caryophyllaceae (Ca)	Spl	200	.	338.8	3.1	Increasing linearly	0.09	0.01
DO	Lamiaceae (La)	Tpo	222	0.31	285.7	0.29	Decreasing exponential	-0.004	0.0001
DO	Lamiaceae (La)	Tho	118	0.23	349.7	0.14	Decreasing exponential	-3.6	0.0001
DS	Plantaginaceae (Pl)	Ang	52	0.31	413.4	0.28	Increasing linearly	0.17	0.0004
DS	Malvaceae (Ma)	Cie	212	0.19	300.4	0.77	Increasing linearly	0.05	0.0001
DS	Lythraceae (Ly)	Cup	97	0.4	256.2	0.27	Increasing exponential	0.01	0.002
DS	Malvaceae (Ma)	Sid	148	0.43	246.3	0.25	Increasing exponential	0.01	0.001

Table 3. Multiple regressions for the effects of: flower biomass, longevity, floral visitor diversity and conspecific flower density on mean and variance (CV) of HP load size (number of grains) and diversity (number of morphotypes) (N =14 species). The coefficient of determination (R^2) and significance is given for each model along with the standardized regression coefficients (β) for each independent variable. Significant models and regression coefficients ($P< 0.05$) are denoted in bold face.

Variables				**Model**	
Dependent	**Independent**	***β***	***P***	***R²***	***P***
A. Mean HP load size	Flower biomass	0.44	**0.05**	0.78	**0.005**
	Flower longevity	0.01	>0.9		
	Flower visitor diversity	0.54	**0.02**		
	Conspecific density	-0.01	>0.9		
B. Mean HP diversity	Flower biomass	0.29	0.12	0.84	**0.001**
	Flower longevity	-0.23	0.14		
	Flower visitor diversity	0.53	**0.01**		
	Conspecific density	-0.23	0.2		
C. CV of HP load size	Flower biomass	0.11	>0.7	0.42	0.24
	Flower longevity	0.24	>0.4		
	Flower visitor diversity	-0.64	0.07		
	Conspecific density	0.02	>0.9		
D. CV of HP diversity	Flower biomass	-0.14	>0.6	0.57	0.07
	Flower longevity	0.56	0.04		
	Flower visitor diversity	-0.16	>0.5		
	Conspecific density	0.1	>0.4		

Appendix 1 Description of study plant species in each community (com.) serpentine seeps (SS), dry scrubland (DS) and dolomite outcrops (DO). Family (Fam.) and species (Sp.) codes. Information on floral characters (mean flower size [biomass], flower shape (actinomorphic [A], zygomorphic [Z]), mean flower longevity[days]) and ecological characters (mean conspecific flower density [flowers/m^2], floral visitor diversity [1/*D*]) and heterospecific pollen (HP) receipt (mean and CV of load size and diversity per flower). '.' denotes data not available.

				Floral characters			**Ecological characters**		**HP load size**		**HP load diversity**	
Com.	**Fam. code**	**Species**	**Sp. code**	**Flower biomass (g)**	**Floral shape**	**Flower longevity**	**Flower density**	**Floral visitor diversity**	**Mean**	**CV**	**Mean**	**CV**
DO	Ca	*Sideritis incana*	Sii	0.00418	Z	12	25.9	1.1	0.04	580.6	0.03	547.6
DO	Ca	*Silene lasiostyla*	Spl	0.00966	A	4.5	0.6	.	18.5	338.8	3.13	75.2
DO	Ci	*Fumana baetica*	Fub	0.00887	A	0.5	1.7	.	9.1	187.9	1.2	94.7
DO	Ci	*Fumana paradoxa*	Fup	0.00924	A	0.5	3.4	2.4	9.4	260.4	1.5	61.9
DO	Ci	*Helianthemum cinereum*	Hcr	0.0026	A	2.3	1.9	.	2	612.1	0.27	182.8
DO	Ci	*Helianthemum appeninum*	Hci	0.01614	A	1	7.6	1.8	14.3	395.8	1.4	129.4
DO	La	*Silene colorata*	Sco	0.00788	A	.	1.3	.	11.6	349.2	2.3	88.9
DO	La	*Thymus orospedanus*	Tpo	0.00069	Z	4	217.2	1.8	0.3	349.7	0.14	279
DO	La	*Teucrium polium*	Tho	0.00253	Z	10	19.5	1.3	0.75	285.7	0.29	197.7
SS	Li	*Triteleia peduncularis*	Trp	0.0149	A	4.4	3.6	4.2	191.5	137.4	3.8	42.1
SS	Li	*Zigadenus venenosus*	Ziv	0.004	A	2.8	5.8	2.5	10.6	156.5	1.8	71.3
DS	Ly	*Cuphea gaumeri*	Cup	0.002	Z	5	12	2.4	0.59	256.2	0.27	161.8
DS	Ma	*Cienfuegosia yucatanensis*	Cie	0.02	A	1	2.9	1.3	4.09	300.4	0.77	102.3
DS	Ma	*Sida acuta*	Sid	0.003	A	0.5	3.5	2.1	0.81	246.3	0.25	187.9
SS	Ph	*Mimulus guttatus*	Mig	0.00638	Z	3.1	14.5	1.6	22.1	237.2	2.09	74.7
SS	Ph	*Mimulus nudatus*	Min	0.0022	Z	2.2	11.8	1.1	17.1	318.8	1.3	82.9

SS	Pl	*Antirrhinum cornutum*	Anc	0.0033	Z	6.2	6	1.5	16.09	220.9	1.2	45.4
DS	Pl	*Angelonia angustifolia*	Ang	.	Z	1	41.4	1.2	8.5	413.4	0.28	198.2
SS	Ra	*Delphinium uliginosum*	Deu	0.02975	Z	8.2	10.3	4.1	133.2	102.9	2.7	48.5

Appendix 2 Description of floral visitor functional groups (adapted from Koski et al., 2015) observed visiting plants in the three studied communites, serpentine seeps (California), dolomite outcrops (Andalusia) and dry scrublands (Yucatan).

Flower visitor functional group	Description
Large solitary bees	Bees with large bodies (≥ 10 mm), solitary, forage on pollen and nectar, pollen carried on hind legs or the underside of abdomen, includes members of Andrenidae and Megachilidae
Small solitary bees	Bees of very small body size (≤ 5 mm), ectothermic, narrow temperature range of activity, fast flyer, solitary, pollen carried on hind legs, includes members of Halictidae and Apidae
Large social bees	Bees with large bodies (~ 15 mm), social, efficient forager of pollen and nectar, efficient recruiter, pollen carried on hind legs, includes members of Apidae
Beetles	Pollen eaters, inefficient, mostly ectothermic, narrow daily activity range, short flying range, pollen not carried in specific location on body, includes members of Cleridae and Buprestidae (Coleoptera)
Bee flies	Flies in the family Bombyliidae, fast feeder, narrow thermal range, territorial, narrow spectrum of flowers, long mouth parts, pollen not carried on specific location on body
Large syrphid flies	Large flies in the family Syrphidae (≥ 10 mm), hoverflies, forage on pollen and nectar, fast flying, specialized digestive system for processing pollen, long foraging time, pollen not carried on specific location on body
Small syrphid flies	Small flies in the family Syrphidae (≤ 10 mm), hoverflies, forage on pollen and nectar, fast flying, specialized digestive system for processing pollen, long foraging season, pollen not carried on specific location on body
Other flies	Other flies different from bomblyiid and syrphid flies, incidental visitors, small, inefficient, pollen not carried on specific location on body, includes members of Muscidae and Callophoridae
Butterflies	Nectar foragers, long foraging times, visit few flowers per plant, fly long distances, narrow thermal requirements, forage on low concentrated nectar, pollen not carried on specific location on body, includes members of Lepidoptera
Wasp	Carnivorous, secondary flower visitors, some groups visit for nectar, pollen not carried on specific location on body, includes members of Vespidae
Walking insects	Walking insects, pollen not carried on specific location on body, includes members of Formicidae

Fig 1. Predicted intraspecific relationships between conspecific (CP) and heterospecific pollen (HP) receipt per flower derived from variation in the evenness and quality of the floral visitor assamblage (see text). Four relationships are hypothesized: 1) HP receipt increases linearly with CP receipt (solid line); 2) HP varies independently of CP receipt and thus no relationship exists between HP and CP receipt (dotted line); 3A) HP decreases or 3B) increases exponetially with increasing CP receipt (dashed lines). Note that curve 2 is shown below curves 3A and 3B for visual clarity and not because HP is predicted to be lower.

Fig. 2 Mean (± SE) (A and B) and coefficient of variation (CV) (C and D) for heterospecific pollen (HP) load size (number of grains per flower) and HP diversity (number of HP morphotypes per flower) for each of the 19 studied plant species. Species were sampled in three plant communities: serpentine seeps (open bars), dry scrubland (solid bars) and dolomite outcrops (dashed bars; Table 1). Species codes follow names in table 2. Note the broken axis in pane A.

Fig. 3 Examples of the four types of relationships between the amount of conspecific (CP) and heterospecific pollen (HP) received on stigmas (described in Figure 1). A) type 1: HP linearly increases with CP in *Delphinium uliginosum*, B) type 2: HP varies independently with CP in *Silene colorata*; C) type 3A: HP exponentially decreases with CP in *Mimulus guttatus*; D) type 3B: HP exponentially increases with CP in *Sida acuta*. Note the broken axis in pane C.

Figure
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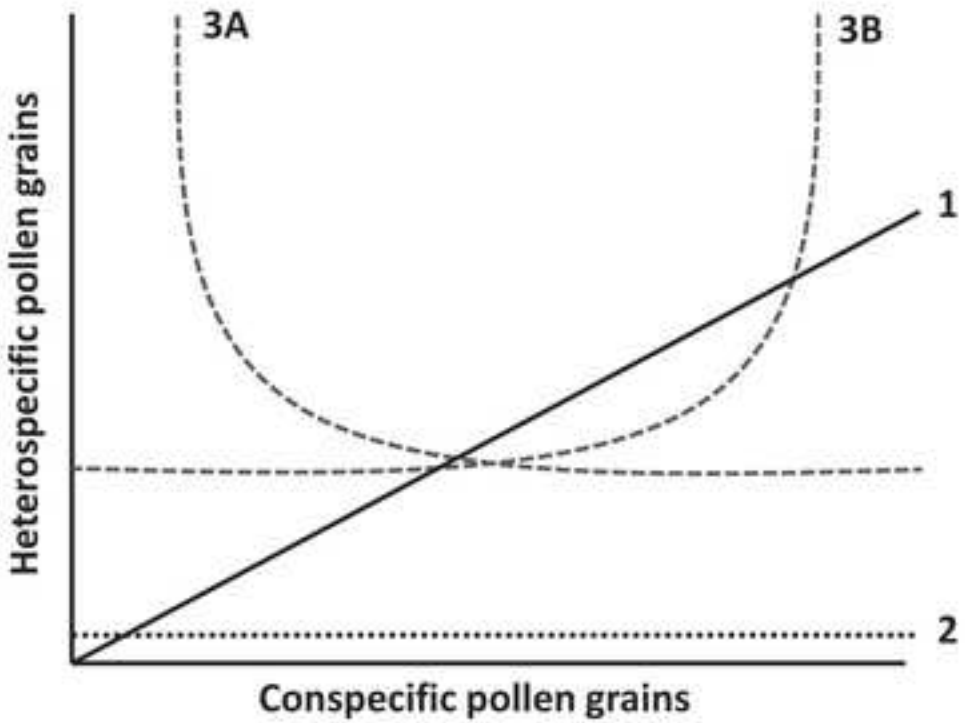

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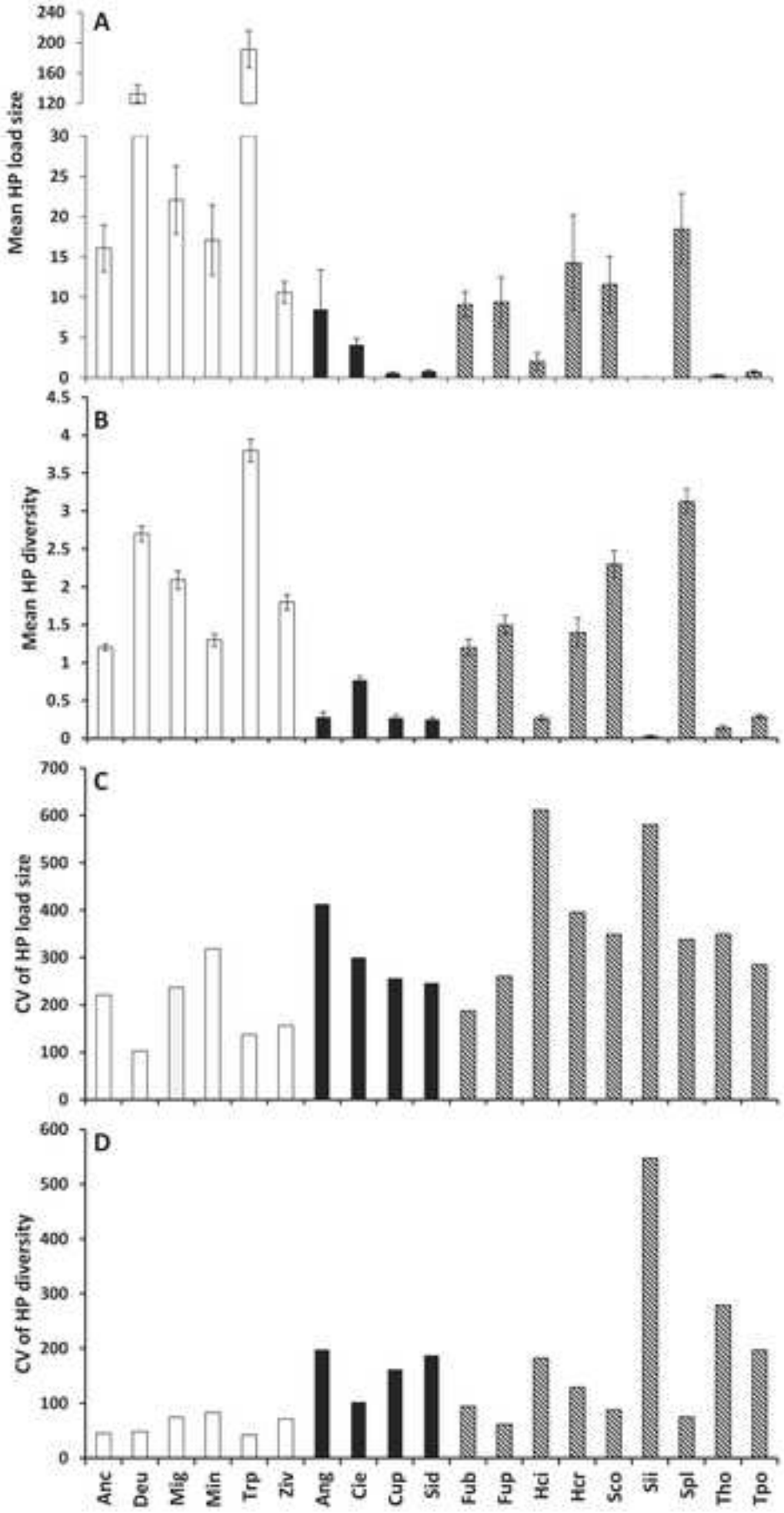
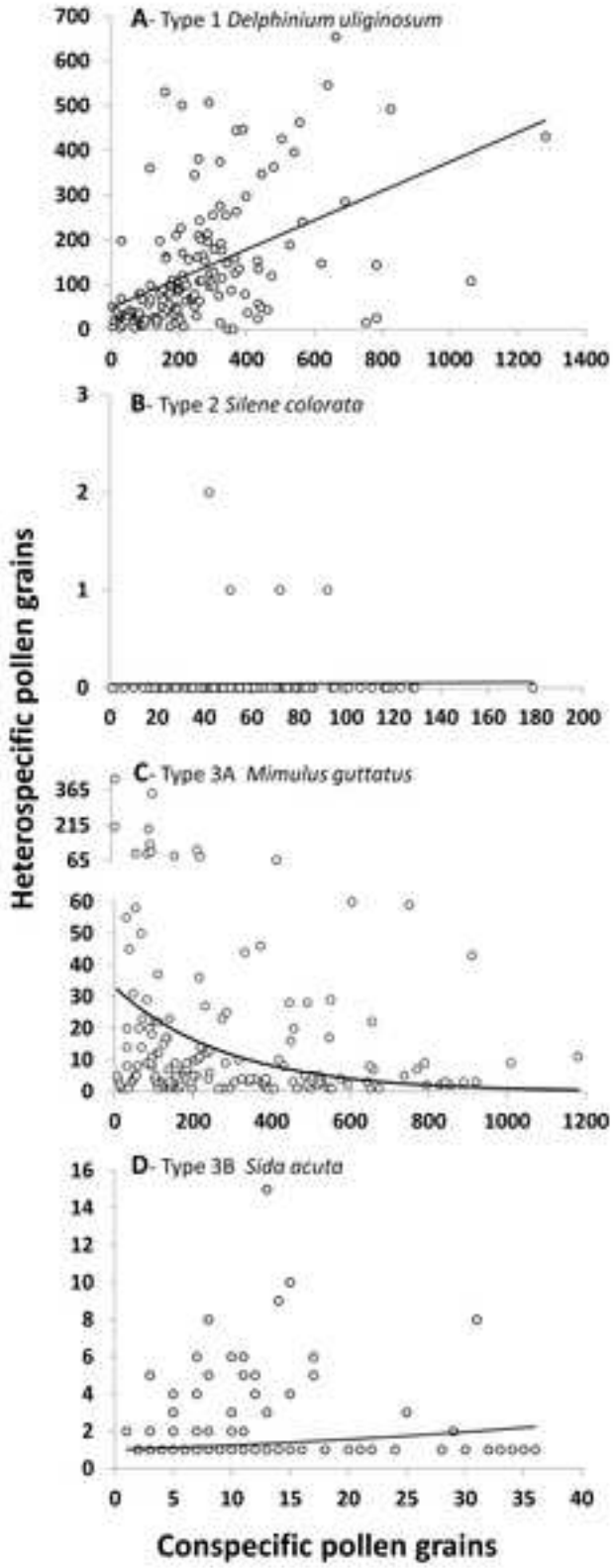
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