

Ecosystem services of pollinator diversity: a review of the relationship with pollen limitation of plant reproduction¹

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Abstract: Recent work on the ecosystem service of biodiversity suggests that higher pollinator diversity could lower pollen limitation, but these two aspects of plant–pollinator communities have only rarely been causally connected. Here we present a review of studies that produced quantitative assessments of both pollinator diversity and evenness as well as pollen limitation of focal plant species. Although pollen limitation is expected to be lower when pollinator diversity is high, our analysis suggests this relationship is weak. The relationship may be obscured when features of the plant species (e.g., average level of specialization) are confounded with features of the plant communities (e.g., habitat). We encourage researchers investigating pollen limitation to consider including measures of diversity of the floral visitors, and their effectiveness. These data would permit a more powerful test of the relationships among these variables and improve our understanding of the critical elements of stable plant–pollinator networks.

Key words: ecosystem services, pollination, pollen, insects, flowering plants, pollinator diversity.

Résumé : Un travail récent sur les services rendus aux écosystèmes par la biodiversité suggère qu'une plus grande diversité de pollinisateurs pourrait réduire la limitation par le pollen, mais on a rarement établi la relation de cause à effet de ces deux aspects de la relation plantes–pollinisateurs communautés. Les auteurs présentent une revue des études ayant produit des évaluations quantitatives à la fois de la diversité des pollinisateurs et l'uniformité et de la limitation par le pollen d'espèces végétales déterminées. Bien que l'on s'attende à ce que la limitation par le pollen soit plus faible en présence d'une forte diversité de pollinisateurs, les auteurs constatent que cette relation est faible. La relation est possiblement masquée lorsque les particularités de l'espèce végétale (p. ex., degré moyen de spécialisation) se confondent avec les particularités des communautés végétales (p. ex., habitat). On encourage les chercheurs sur la limitation par le pollen à considérer des mesures inclusives de la diversité des visiteurs floraux, et leur efficacité. Ces données fourniraient une évaluation plus forte des relations entre ces variables et amélioreraient notre compréhension des éléments critiques des réseaux stables plante–pollinisateur.

Mots-clés : services aux écosystèmes, pollinisation, pollen, insectes, plantes à fleurs, diversité des pollinisateurs.

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Introduction

Pollen limitation (PL), the reduction in plant reproductive success as a result of inadequate quantity or quality of pollen deposition, is widespread among flowering plants. Previous reviews have calculated that between 60% and 73% of populations studied suffer significant PL (Ashman et al. 2004; Burd 1994; Knight et al. 2005). Although close to 90% of flowering plant species rely on animals for pollination (Ollerton et al. 2011), suboptimal pollinator activity is frequently invoked as the cause of PL (Knight et al. 2005), and the degree to which PL is due to low abundance, diversity, or efficacy of flower visitors is unknown. A logical first step is thus to examine the literature to date on this particular aspect of PL to determine whether or not existing evidence supports the general hypothesis that pollinator diversity is directly related to PL.

Inadequate quantity and quality of pollen deposition can result from visitation limitation (too few pollinator visits, pollen vector rare owing to competition or variation in pollinator abundance), low pollen availability (e.g., pollen theft), and inefficient pollen transfer (transport loss, interspecific transfer by pollinators, inadequate cross-pollen transfer), although self-compatible species may be more immune to these sources of declines in pollen delivery (Knight et al. 2005) because of the relative ease of delivery of self-pollen (in autogamous species, especially). Global-scale comparisons indicate that sharing pollinators increases PL because plants in highly diverse floral communities suffer a greater magnitude of PL (Vamosi et al. 2006). However, there is only rudimentary information on whether the magnitude of PL is related to the diversity or abundance of pollinators. A meta-analysis indicated that plants visited by many pollinators (>5 species) are less pollen limited than those visited by one or few (2–5) species (Knight et al. 2005), although no distinction regarding whether pollinators were from the same or different genera, families, and (or) orders was made. In contrast, recent research found no effect of pollinator diversity (measured as species richness or family richness) on the magnitude of PL in a study of 11 temperate plant species (Hegland and Totland 2008). Aguilar et al. (2006) conducted a meta-analysis showing that habitat fragmentation reduced both pollination services (pollinator visits, pollen deposition, pollen tube growth) and plant reproductive success. However, species with generalized (>1 order) and specialized (1 order) pollination suffered similar reproductive declines (Aguilar et al. 2006). A broader analysis of the literature would thus provide a useful insight into whether pollinator diversity has the capacity to explain PL.

Other traits that affect pollinator attraction and pollen placement may also modify PL through their influence on pollinators. Several possibilities have been posed with respect to floral symmetry. Knight et al. (2005) suggest that plants with specialized flowers (i.e., zygomorphic flowers) may have lower PL than those with actinomorphic flowers, because zygomorphic flowers encourage more precise placement of pollen and generally attract more specialized pollinators. In contrast, Larson and Barrett (2000) hypothesized that plant species with unspecialized floral morphology (open flowers) would have lower levels of PL than species with specialized floral morphology (tubular flowers), because open flowers receive more visits than tubular flowers (McCall and Primack 1992). Neither study showed a differ-

ence in the magnitude of PL between plants with specialized and unspecialized floral morphologies, but neither included the intervening link: pollinator diversity. Similarly, although self-incompatibility is expected to increase PL through mate limitation (Larson and Barrett 2000), an examination of how self-incompatibility, floral morphology, PL, and the pollinator community co-vary has not been done. Furthermore, if traits that are intrinsic to the plant species in question (e.g., floral symmetry and self-compatibility) determine the magnitude of PL, then an examination of phylogenetic autocorrelation (the degree to which closely related species are more similar in PL than expected by chance) should accompany investigations of the effect of these traits on PL.

If pollinator diversity is a key factor determining the level of PL, then unrelated species living in the same habitats may exhibit correlations in PL (i.e., we should observe spatial autocorrelation in PL). Spatial variation in pollinator assemblages has been linked to PL in two plant species (Cosacov et al. 2008; Gómez et al. 2010), but comparisons of spatial autocorrelation in PL across species have, to our knowledge, never been performed. Similar studies using pollen deposition levels do indicate that habitat (e.g., open versus closed) can affect PL of a number of plant species within a community (Potts et al. 2006), but whether similarities in pollinator diversity or activity are critical factors determining mean reproductive success amongst coexisting plant species is not clear. The degree to which plant communities depend upon pollinator diversity (Ricketts et al. 2008), as well as determining the most meaningful metric of pollinator diversity (e.g., species richness, diversity indices, evenness) for healthy plant communities, requires careful study. Here we use the term diversity in a general sense to encompass the various measures of diversity considered in different studies, while specifically referring to other metrics (e.g., Simpson's diversity) where appropriate.

Here, we review published pollen supplementation studies that have quantitatively measured aspects of the pollinating community experienced by a given species, and we test the hypothesis that diversity of pollinators is related to PL. To estimate the relative degree to which biome- versus species-specific traits influence PL, we examine PL in terms of both spatial and phylogenetic autocorrelation and investigate PL and pollinator diversity patterns while taking into account relevant floral traits (floral symmetry and self-incompatibility).

Methods

Database search

We searched ISI Web of Knowledge (which includes Web of Science, BIOSIS Previews, Zoological Record, MEDLINE) for publications up to the end of 2010 using the following keyword combinations: ((pollen limit*) or (poll* and supplement*)) and (pollinator diversity or pollinator richness or pollinator assemblage or floral visitor). Only studies that provided the following data were included (i) a test of PL using a supplementation experiment, where reproductive output from control (naturally pollinated) flowers was compared with output from treated flowers (i.e., flowers receiving natural pollination plus manually-applied supplemental outcross pollen); (ii) a survey of floral visitors in the same population and season that PL was measured. Although floral visitors

can vary in effectiveness, the number and identity of visitors is assessed more frequently than whether each visiting species effectively transfers pollen (Pellmyr 2002). We therefore follow Sahli and Conner (2006) whose analysis suggests that visit frequency is a reasonable surrogate for effectiveness and assume that floral visitors are indeed pollinators.

We found 15 studies representing 51 populations from 26 plant species in 19 families (Supplementary data,¹ Table S1). Seed set was more commonly measured than fruit set to estimate PL (20 species vs. 6 species), and only four studies involved supplementation to all of the flowers on the plant. We pooled all studies as previous studies have suggested that the differences between varying response variables and levels of treatment are strongly correlated (Knight et al. 2006). Where more than one population was studied for a given species, each population was treated as independent. Populations that were studied in more than one year were treated as replicates.

Comparison of experimental procedures for determining PL of plant reproduction

In addition to the 15 published articles utilizing pollen supplementation experiments to determine PL, an additional 12 articles (17 populations, Table S2) fit our criteria but utilized a bagged outcross pollination experiment. In these studies, pollinators were excluded with bags of fine mesh, preventing natural pollen delivery, and supplemental outcross pollen was added by hand. Although these studies do not test whether pollen supplementation above natural levels increases fruit or seed production, results are often interpreted in terms of PL and results from such studies have been included in previous reviews (Knight et al. 2005). However, bagged outcross experiments may have on average higher quality pollen deposited because pollen applied by hand is normally outcrossed, but pollen delivered by pollinators may include a mixture of outcross and self-pollen. In addition, bagging flowers and fruits may alter the micro-environment in which pollen grains germinate tubes and fruit develop, and this could affect the overall success rate of fruit or seed set (Aizen and Harder 2007; Harder and Aizen 2010). Because the data violated assumptions of homogeneity of variances and normal distributions, we tested the hypothesis that the two experimental methods produce different values of PL using a Mann–Whitney U nonparametric test.

Phylogenetic and spatial autocorrelation

A phylogenetic tree for the species included in our dataset was obtained using the angiosperm APGIII consensus tree (R20091110) from Phylomatic (Webb and Donoghue 2005). Branch lengths were calibrated from the minimum age of clade divergence from Wikström et al. (2001) using the BLADJ function. We then mapped PL and pollinator species richness onto this phylogeny to examine the degree of phylogenetic autocorrelation (or phylogenetic signal (Blomberg et al. 2003)) between populations and species in the dataset. The phylogenetic signals for PL and pollinator species richness were estimated via maximum likelihood (Freckleton et al. 2002) with a subroutine (generously provided by R. Freckleton) in the ape package (Paradis et al. 2004) in the R environment. A phylogenetic signal value (λ) of 0 can be

interpreted to mean that there is no phylogenetic autocorrelation, whereas a value of 1 indicates maximum phylogenetic autocorrelation.

A sparse dataset that extends over vast geographical areas is unlikely to detect spatial autocorrelation if it exists. However, the inclusion of several spatially clustered populations and species in our dataset provides a cursory test of the effect of similarities in pollinator communities. We calculated Moran's I using the software ROOKCASE (Sawada 1999) over distances of ~ 110 km, over 220 km, and finally over a very large distance (~ 1000 km) to evaluate whether spatial autocorrelation plausibly influenced PL.

PL and pollinator richness, diversity, and evenness

The measurements of reproductive output varied among studies and included fruit set (%), seed set (%), seed:ovule ratio, seeds per capsule, seeds per flower, and seeds per fruit per plant. The values were taken from publications directly when reported in text or tables, or extracted from figures using digital imaging software Fiji (Schindelin 2008). The magnitude of PL was calculated using the log response ratio (following Knight et al. 2005) as follows: $\ln R = \ln(\text{mean output from supplementation} / \text{mean output from control})$.

A value of 0 reflects no difference in reproductive success between pollen-supplemented and control plants, a positive value indicates higher reproductive success with pollen supplementation, and a negative value indicates higher reproductive success in the control treatment (i.e., pollen limited).

Species richness of pollinators was determined from species lists, figures, or text. While richness provides some understanding of generalization in pollination systems, it is not as accurate as diversity, which integrates richness and evenness (e.g., Sahli and Conner 2006). We used a subset of the data to calculate two diversity indices, including only those plant populations for which data on pollinator visits per unit time were reported (33 plant populations, Table S1). Simpson's reciprocal diversity index ($1/D$) (Jost 2006; Magurran 2004) was calculated as follows: $1/D = 1/(\sum p_i^2)$ where p_i equals the proportion of pollinator visits by the i th species.

The maximum value occurs when all species are equally abundant with the greatest species richness.

Simpson's measure of evenness ($E_{1/D}$) (Magurran 2004; Sahli and Conner 2006) was calculated as follows: $E_{1/D} = (1/D)/S$ where S equals species richness.

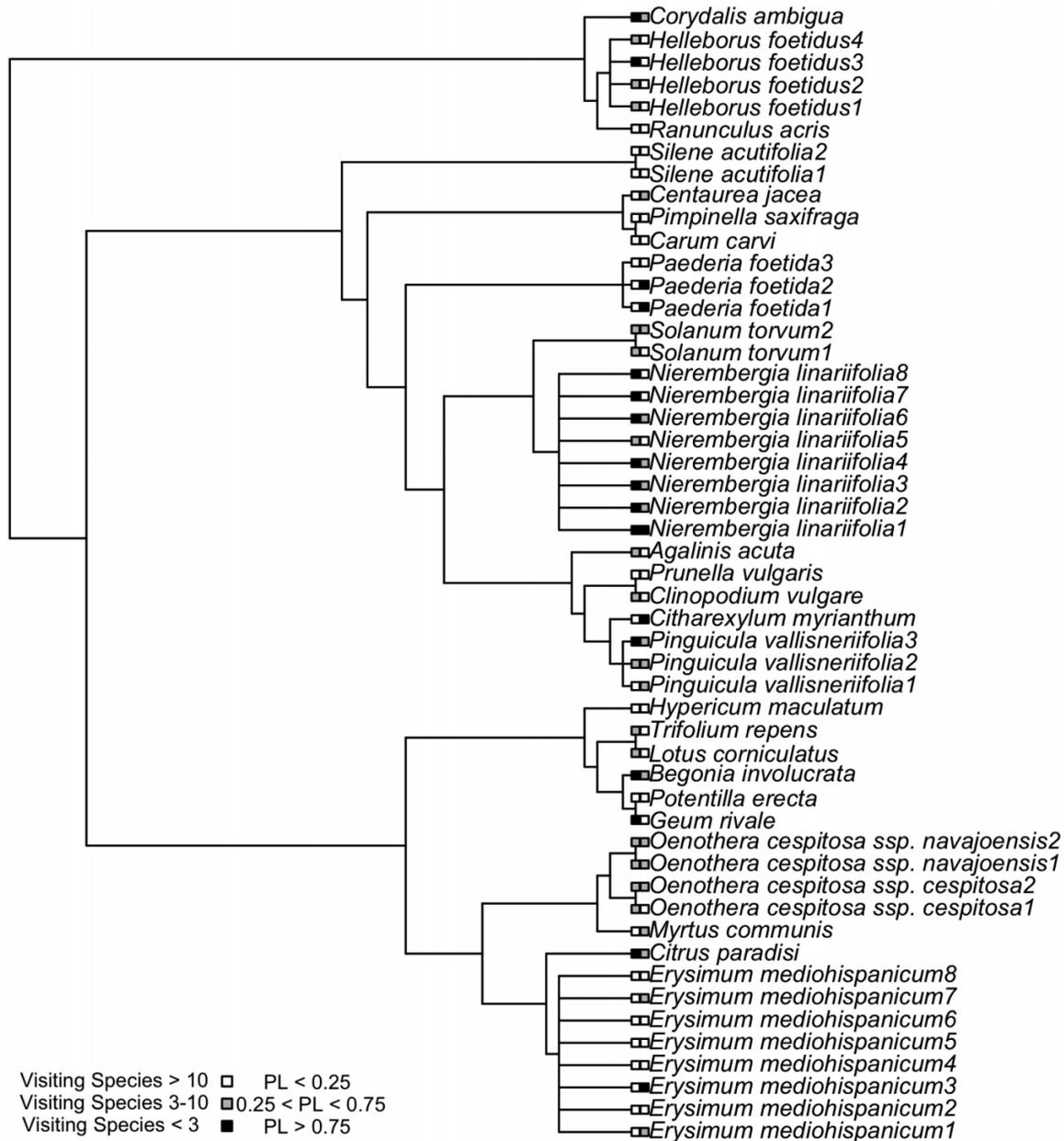
The maximum value (1) occurs when all species are equally abundant. Linear regression was used to investigate relationships between magnitude of PL ($\ln R$) and pollinator species richness, family richness, Simpson's diversity, and evenness.

PL, self-compatibility, and floral symmetry

Because pollinator visit rates are expected to vary with specialization of flowers and potentially affect PL in plants, we performed three additional analyses. First, we asked whether PL ($\ln R$) differed between self-compatible and self-incompatible plant species and whether pollinator species richness varied with compatibility, using Mann–Whitney U tests. For one species (*Pimpinella saxifraga*) no information

¹Supplementary data are available with the article through the journal Web site (<http://nrcresearchpress.com/doi/suppl/10.1139/b2012-017>).

Fig. 1. Hypothesized phylogeny of populations examined for comparisons. Despite the inclusion of numerous populations of the same species (e.g., *Helleborus*), no phylogenetic signal was detected in pollen limitation (PL). Squares indicate categories of the number of visiting species (first square) and PL (as $\ln R$; second square).



regarding self-compatibility was available (Hegland and Totland 2008), and so this species was not included in the analysis. Second, we used Mann–Whitney U tests to ask whether PL or pollinator species richness varied with floral symmetry (actinomorphic vs. zygomorphic). One species (*Erysimum mediohispanicum*) exhibits highly variable floral symmetry (Gómez et al. 2007), so it was excluded from this analysis. Finally, we performed an analysis of covariance (ANCOVA) to determine whether the slopes between PL and pollinator diversity were influenced by factors such as self-incompatibility or floral symmetry. As a secondary statistical test and check on the relative sensitivity of these analyses, a formal meta-analysis was also conducted to test for differences in breeding system, floral symmetry, and experimental method

of testing for PL (please see Supplementary Appendix for full details of methodology).

Results

Twenty-seven out of the 51 populations (53%; Fig. 1) were reported by original authors to exhibit significant PL, 23 populations showed no significant PL, and 1 population was not analysed by the original study. The prevalence of PL in the current review is much lower than has been reported in previous reviews (e.g., 63% Knight et al. 2005; 62% Burd 1994; 73% Ashman et al. 2004). The mean \pm SE $\ln R$ was 0.288 ± 0.074 ($n = 51$); however, most plant populations recorded low magnitudes of PL (median = 0.174, Fig. 2). The mean \pm

SE lnR for bagged outcross experiments was 0.900 ± 0.223 ($n = 17$), but the values were highly skewed (Fig. 2). The magnitudes of PL did not differ significantly between supplementation and bagged outcross studies (Mann–Whitney $U = 565$, $z = -1.86$, $P = 0.063$ two-tailed), with a trend for bagged outcross experiments to exhibit higher PL. In our meta-analysis, the bagged hand-cross and supplementation methodologies both detected PL (i.e., effects were significantly different from no effect at $P < 0.05$), yet we found that bagged hand-cross studies have significantly larger effect sizes associated with PL (see Supplementary Appendix).

Phylogenetic and spatial autocorrelation

We found that lnR did not show a phylogenetic signal and λ was not significantly different from zero ($\lambda = 0.09$; $P = 0.44$), whereas pollinator species richness did show a slight phylogenetic signal ($\lambda = 0.44$; $P = 0.03$). This indicates that closely related species (or populations) are not more similar in PL than expected by chance, allowing for each population to be treated as an independent data point in our analyses, but also suggests that pollinator specialization is likely affected by plant traits that exhibit a phylogenetic signal, such as floral symmetry.

Spatial autocorrelation is undetectable in these data, regardless of the lag distance employed (Moran's I, lag distance of 1 degree (~ 110 km) = -0.0181 , $P = 0.519$; Moran's I, lag distance of 2 degrees (~ 220 km) = -0.0255 , $P = 0.464$). When Moran's I statistic was calculated for a lag distance that was the mean distance between data points (~ 9.95 degrees), spatial autocorrelation was still very weak (Moran's I = -0.00947 , $P = 0.42$).

PL and pollinator richness, diversity, and evenness

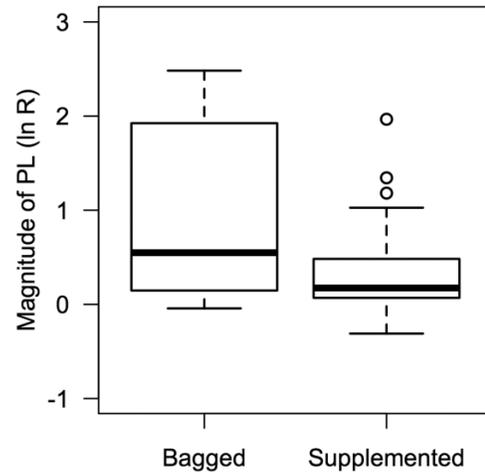
The plants in this review were rarely specialists, with many hosting greater than 15 species or families of floral visitors. The mean \pm SE number of pollinator species per plant population was 12.4 ± 1.8 (range: 1 to 49). The mean \pm SE number of floral visitor families per plant population was 6.9 ± 1.0 (range: 1 to 27). However, there was no linear relationship between floral visitor species richness and PL ($r^2 = -0.020$, $F_{[1,49]} = 0.017$, $P = 0.898$; Fig. 3a) nor was there any relationship between visitor family richness and PL ($r^2 = -0.016$, $F_{[1,49]} = 0.209$, $P = 0.650$; Fig. 3b).

There was no linear relationship between lnR and Simpson's index of pollinator diversity ($r^2 = -0.034$, $F_{[1,31]} = 2.136$, $P = 0.154$; Fig. 3c) or between lnR and floral visitor evenness ($r^2 = -0.028$, $F_{[1,31]} = 0.124$, $P = 0.728$; Fig. 3d); however, we note that there is a lack of PL studies of plants with high visitor diversity that include both abundance and richness data.

PL, self-compatibility, and floral symmetry

There is a significant difference in lnR between self-incompatible ($n = 17$) and self-compatible ($n = 33$) plant populations (Mann–Whitney U test, $z = -2.21$, $P = 0.027$ two-tailed, Fig. 4a and Supplementary Appendix). Self-compatible plant species did not, however, have more pollinator species than self-incompatible plant species (Fig. 3b; Mann–Whitney U test, $z = 1.47$, $P = 0.142$ two-tailed). In addition, the relationship between lnR and pollinator richness was not significantly influenced by self-compatibility as de-

Fig. 2. Variation in magnitude of pollen limitation (PL; calculated as lnR) from studies using bagged hand-cross and supplementation experiments. Boxplot indicates quartiles with the median marked as the thick horizontal line; circles are outliers.



termined with ANCOVA (visitor species richness \times self-incompatibility, $t_{1,48} = 0.136$, $P = 0.893$).

There was no significant difference in lnR between actinomorphic ($n = 25$) and zygomorphic ($n = 18$) plants (Mann–Whitney U test, $z = -0.92$, $P = 0.3576$ two-tailed, Fig. 5a and Supplementary Appendix). Zygomorphic plants have significantly fewer floral visitor species than actinomorphic plants (Mann–Whitney U test, $z = 3.05$, $P = 0.002$ two-tailed, Fig. 5b). However, the relationship between lnR and floral visitor richness were equivalent in both actinomorphic and zygomorphic plants in an ANCOVA (visitor species richness \times zygomorphy interaction, $t_{1,42} = -0.640$, $P = 0.526$).

Discussion

While detailed examinations of particular species reveal that the ecosystem service of pollination is influenced by pollinator diversity (Hoehn et al. 2008; Klein et al. 2003), our across-species analysis does not support this general hypothesis. While there are hundreds of studies on PL (Knight et al. 2005), previous studies have used different methodologies and few studies have measured both PL and pollinator abundance and diversity. Perhaps in some part owing to our limited sample sizes, we find little evidence that pollinator diversity is a strong determinant of PL. Yet, if pollinator diversity were a critical factor in plant reproductive success, we should have detected a relationship between PL and our measures of pollinator diversity. Thus, the practise of inferring that PL results from limited pollinator diversity may invoke an assumption that has little empirical support (Aizen and Harder 2007). We hope that more researchers include data on pollinator observations, so that future estimates of this component of plant–pollinator ecosystems can be robustly generated.

Phylogenetic and spatial autocorrelation

The variation in PL is surprisingly high over spatial gradients and between populations of the same species. On the one hand, the lack of phylogenetic or spatial autocorrelation improved our sample size by allowing us to treat populations

Fig. 3. Relationship between magnitude of pollen limitation (PL; $\ln R$) and (a) visitor species richness, (b) visitor family richness, (c) visitor diversity ($1/D$), and (d) visitor evenness (E).

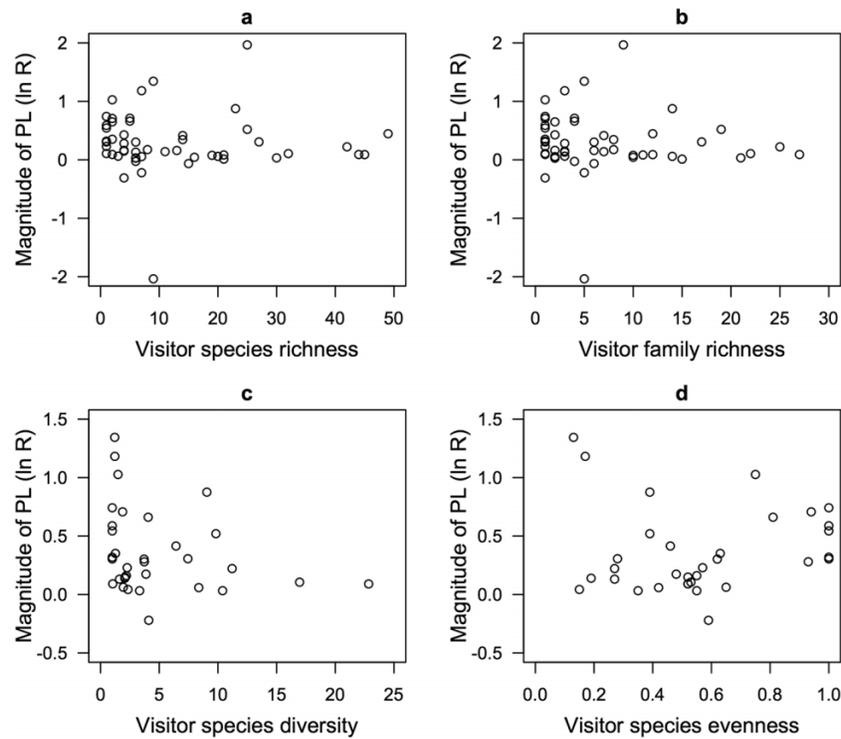
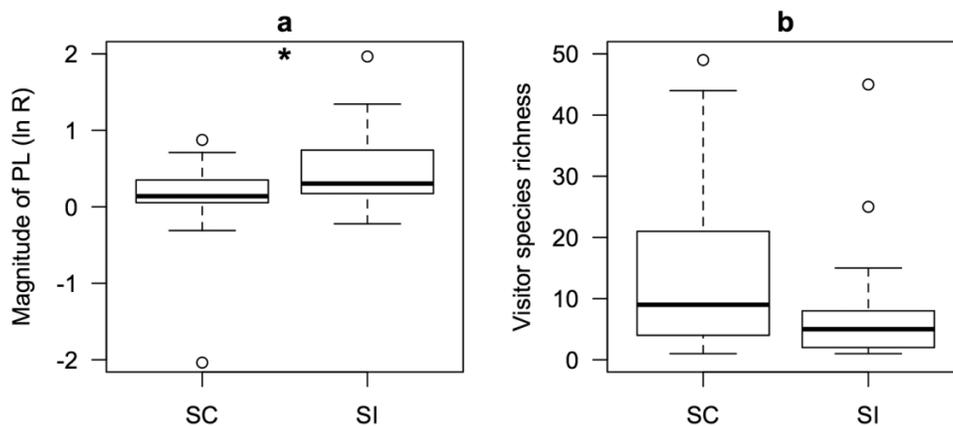


Fig. 4. Differences in (a) magnitude of pollen limitation (PL; $\ln R$) and (b) visitor species richness between plants with different mating systems (SC, self-compatible; SI, self-incompatible). Boxplots indicate quartiles with the median marked as the thick horizontal line; circles are outliers. * indicates $P < 0.05$, Mann–Whitney U test.



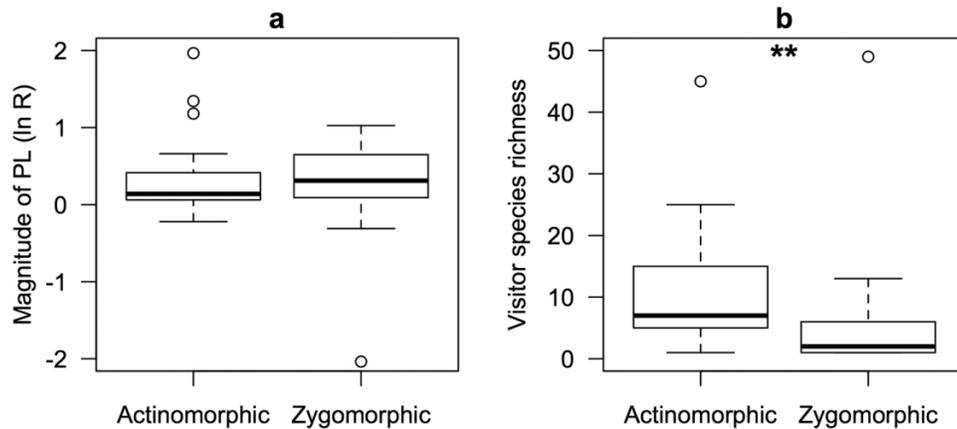
as independent data points, yet several previous studies have found autocorrelation at broad scales (Larson and Barrett 2000; Vamosi et al. 2006), indicating that some aspects of the species themselves or their habitats can influence PL. The high variability in PL observed within-species (Gómez et al. 2010) might be a result of beta diversity in pollinator communities. The strong autocorrelation between species observed in other studies, on the other hand, may result from calculating an average level of PL per species and then observing the variation determined by species-specific traits such as self-incompatibility and zygomorphy. This approach may be why studies that examine the association between PL and pollinator diversity between species have found little effect (Hegland and Totland 2008). Further examination of

within- and between-species comparisons will require larger datasets but is a research gap worthy of attention.

PL and pollinator richness, Simpson's diversity, and evenness

Despite the expectation that the richness or diversity of floral visitors should affect measured PL, we found no relationship between these variables. We included a substantial range of pollinator richness values in our analysis, but we had to limit our dataset for analysis of Simpson's diversity and evenness. In the latter dataset, there was high variability in the magnitude of PL for plants with low pollinator diversity and limited sample size at high pollinator diversity, which could have reduced our power. However, the expecta-

Fig. 5. Differences in (a) magnitude of pollen limitation (PL; $\ln R$) and (b) visitor species richness in plants with different floral symmetry. Boxplots indicate quartiles with the median marked as the thick horizontal line; circles are outliers. ** indicates $P < 0.01$, Mann–Whitney U test.



tion that high pollinator diversity and evenness should improve the ecosystem function of pollination was not supported by our analysis. Previous studies have shown that generalized and specialized species suffer similar reproductive declines as a result of habitat fragmentation (Aizen et al. 2002; Aguilar et al. 2006). Although PL was not examined directly, Aguilar et al. (2006) also showed a clear link between pollination (pollinator visits, pollen tube numbers, pollen load) and reproductive success.

These counter-intuitive results may reflect the asymmetrical nature of plant–pollinator interactions (Ashworth et al. 2004). Network analyses of plant–pollinator communities indicate that specialists interact with subsets of the species with which generalists interact, such that specialized plants tend to rely on more generalized insects and vice versa (Bascompte et al. 2003; Bascompte and Jordano 2007; Vázquez et al. 2009). A nested structure can provide a buffer against fluctuations and loss of specialist pollinators (Tylianakis et al. 2010); therefore, specialized plants may be less susceptible to PL when they are visited by generalized pollinators. Conversely, generalized plants may lose reproductive output if their specialized pollinators are scarce in some sites or years. This logic has been confirmed by a mathematical model (Abramson et al. 2011), but this logic does rely on the assumption that observed asymmetries in pollination networks reflect true network properties and not sampling bias (see cautions in Blüthgen et al. 2008).

Clearly, the above logic does not apply to situations where both plants and their pollinators are specialized (see PL, self-compatibility, and floral symmetry). However, such reciprocal specialization should result in highly efficient pollination when the appropriate pollinator is present. Thus, reciprocal specialization may lead to greater spatial variability in PL owing to the presence/absence of specialist pollinators (e.g., Martín-Rodríguez and Fenster 2010), rather than consistently higher PL. However, the distribution of our data did not allow us to test this possibility directly.

PL, self-compatibility, and floral symmetry

Our findings on mating systems are consistent with previous studies in that self-incompatible species exhibit higher degrees of PL than do self-compatible species (Larson and

Barrett 2000; Knight et al. 2005). While this may appear to contradict the pollen quality arguments of Harder and Aizen (2010), one would expect greater PL in self-compatible species if low pollen quality is the main cause of PL. However, low pollen quality may also reflect delivery of heterospecific or incompatible pollen.

Selection for selfing may occur in pollinator-variable or pollinator-poor environments, which would result in a correlation between self-compatibility and low pollinator diversity. Surprisingly, self-compatible species were not more or less generalized in their pollination systems than self-incompatible species (consistent with Ollerton et al. (2006)). There was a nonsignificant trend for greater pollinator richness for self-compatible plants, and it would be interesting to explore this trend more generally (i.e., in plant species for which visitor assemblage was measured, even if PL was not). Self-incompatibility often co-occurs with floral traits to improve pollen placement or reduce interference between stigmas and anthers (Dai and Galloway 2010), such traits may co-vary with the visitor assemblage (see below). However, the generalization level of the pollinators themselves (e.g., the average level of pollinator sharing between self-compatible versus self-incompatible species) will require additional network approaches (Elle et al. in press; Moeller 2004). Furthermore, grouping self-compatible species as having uniform selfing rates is clearly an oversimplification that may be masking important patterns (Goodwillie et al. 2005; Moeller and Geber 2005).

Also similar to previous reviews (Larson and Barrett 2000; Knight et al. 2005), we found no difference in PL between specialized and unspecialized flowers using either conventional or meta-analytical statistics. We found that pollinator richness was indeed lower for zygomorphic species, indicating that floral structure can be important for excluding pollinators. This result supports the view that zygomorphy provides a rough approximation of specialization versus generalization (Sargent 2004). However, the evolution of specialization does not appear to have large advantages in terms of reducing PL. This result was somewhat in contrast with similar studies that have found that species with few pollinators may have higher PL (Knight et al. 2005; Martín-Rodríguez

and Fenster 2010). To our knowledge, no experimental comparisons of the variation in PL with floral symmetry have been performed. This would be an interesting line of future inquiry as it would help resolve why pollinator specialization so commonly evolves (Sargent and Otto 2006; Waser et al. 1996), despite the theory that it can be a risky strategy.

Future research

While we clearly need more information regarding floral visitor abundance and diversity paired with examinations of plant reproductive success, the ecosystem service putatively provided by increasing pollinator diversity does not appear to directly reduce PL. A number of caveats remain for future investigation. First, some studies show that the most common visitor is not always a pollinator, or at the very least, not a dependable pollinator (Mayfield et al. 2001). Second, the degree to which high pollinator diversity can buffer communities from disturbance may also be dependent on the plant composition of the community in question (Sargent et al. 2011). Third, we note that our estimates of the average degree of PL are lower than previous estimates, which may be due to our exclusion of bagged experiments (Harder and Aizen 2010). Our analysis of the bagged versus supplementation methods provided some support (albeit only with meta-analysis) that bagged experiments are exaggerating the level of PL. The lower PL observed using supplementation indicate that additional pollinator visits after sufficient pollen delivery has taken place may actually reduce plant reproductive success. Four, the experiments that did meet our criteria have been performed mostly in environments that have been previously found to experience the least PL (e.g., temperate, open communities (Larson and Barrett 2000)). To provide more robust examinations of the ecosystem service provided by pollinator diversity, we will need more PL estimates from communities where pollinator activity is reduced (e.g., shaded environments), or in anthropogenically modified environments where outcrossing rates are known to be compromised (Eckert et al. 2010).

The lack of a close relationship between the pollinator community and PL is surprising and anti-intuitive (Hegland and Totland 2008). While more data are sorely needed, a lack of power is certainly not the only explanation. We need to reassess our assumption that PL gives much insight into the degree that plants are pollinator limited (Wilcock and Neiland 2002). The ecosystem service provided by pollinator diversity (Fontaine et al. 2006) is likely stronger for some species than others and an understanding of the critical factors underlying these patterns will help focus conservation efforts.

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