

Flowering plants under global pollinator decline

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There is now compelling evidence of a reduction of pollinator richness and density at a global scale. In this opinion article, we argue that such pollinator decline intensifies pollen limitation and reduces plant reproductive success, threatening natural populations of extinction. We use genetic architecture and selection experiments on floral traits and evaluate the potential for plant reproductive strategies to adapt rapidly to new pollination environments. We propose that plant reproductive strategies could adapt to the current pollinator decline by decreasing or increasing their reliance to pollinators, for example, increasing autonomous selfing or reinforcing interactions with pollinators. We further discuss if and how adaptation of plant reproductive strategies can buffer the demographic consequences of pollinator decline, and possibly rescue plant populations from extinction.

Plant–pollinator interactions under pollinator decline

Insect pollination is a prevalent ecological process: more than 80% of wild plant species [1] and almost 75% of cultivated plant species [2] rely on insects, particularly wild bees, for fruit and seed production.

As a facet of global changes, the recent decline of insect pollinator communities is currently a major concern [3], because of its impact on ecological and agricultural systems. Changes in anthropogenic land use and agricultural intensification are considered as the main causes of current pollinator decline [1]. Bees have experienced worldwide reduction in species richness [4,5], functional composition [6], and population density [7,8], a pattern that has increased since the 1950s [9]. This global trend nevertheless hides discrepancies among functional groups of bees, because species with medium or long proboscis are the most impacted [8].

The alteration of pollinator communities is likely to have cascading effects on plant population dynamics and thus on population persistence. Reduction of population densities of the endemic New Zealand shrub *Rhabdothamnus solandri* was shown to be linked to the rarefaction of its most efficient pollinators (birds in this case) [10]. Other studies have shown a parallel decline of entomophilous plants and their pollinators [4,11], suggesting that pollinator decline can

lead to changes at the plant community level [12] through ‘species sorting’ that excludes the most pollinator-dependent species. Beyond plant community changes, we hypothesise that short-term adaptation of plant populations can take place and mitigate the impact of pollinator decline on plant demography, possibly rescuing them from extinction.

In this opinion article, we investigate the potential for plant reproductive strategies (including mating system and floral traits) to adapt to the current decline of their main pollinators. We use data describing (i) the effect of pollinator abundance on seed set, (ii) the genetic architecture, (iii) phenotypic selection on floral traits in natural populations, and (iv) the demographic effects of pollinator abundance. Confronting these scattered elements with theory of plant mating systems helps evaluate the potential for contemporary evolution of plant reproductive strategies and determine whether it can buffer the detrimental effects of pollinator decline on plant demography.

Effect of pollinator decline on plant reproductive success

Pollinator decline potentially has a major effect on plant reproductive success. Studies of pollination and plant seed set along fragmentation gradients provide indirect evidence that pollinator decline can exacerbate existing levels of pollen limitation (see Glossary) in natural populations [13,14]. A meta-analysis comparing fragmented with unfragmented habitats found that seed set reduction, due to fragmentation, is higher for self-incompatible species than for self-compatible species [15], a pattern that can be explained by reduced pollinator abundance rather than increased mate limitation. Moreover, decreased pollinator richness and density, and associated reduced number of

Glossary

Autonomous selfing: within flower spontaneous selfing, that is, not necessitating pollinator vectors.

Evolutionary rescue: the recovering of sustainable population growth rate via adaptive changes.

Geitonogamy: among flower selfing resulting from pollinator foraging behaviour within individual plants.

Inbreeding depression: the reduced fitness of offspring from related individuals. In hermaphroditic individuals, inbreeding depression is classically estimated as the fitness reduction of selfed progeny relative to outcrossed progeny.

Pollen limitation: the reduction of fruit or seed set due to limited pollen receipt.

Reproductive assurance: the increase of seed set by selfing when outcrossed success is pollen limited.

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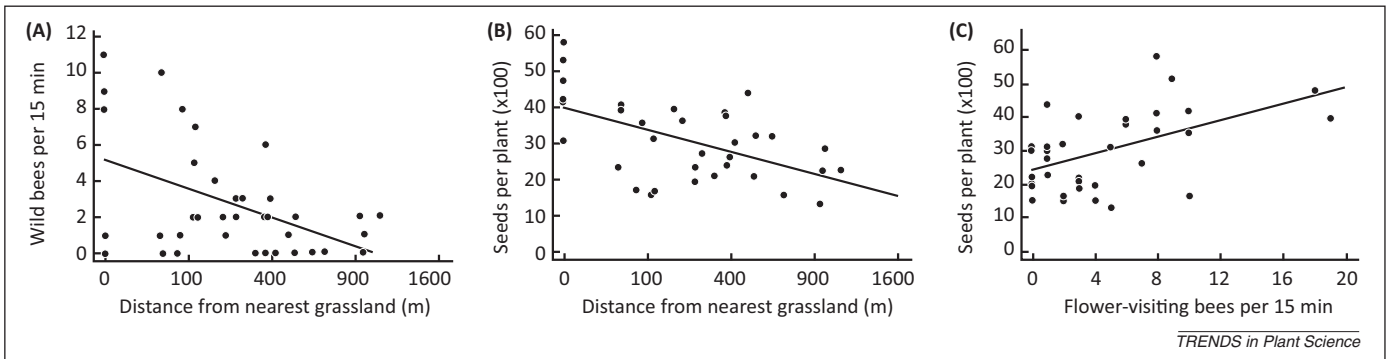


Figure 1. Reduction of seed set associated with a reduction of pollinator visits along gradients of habitat isolation. Such spatial patterns provide surrogates for the effect of pollinator decline on plant seed set [1]. Increasing distance from natural habitats (i.e., increasing isolation) decreases the number of bees visiting the mustard plant, *Sinapis arvensis* (A), and results in a substantial decrease in plant seed set (B, C). Reproduced from [16].

pollinator visits, quantity of pollen receipt and seed set, are frequently observed with increasing isolation in fragmented landscapes [16–18] (Figure 1), even for generalist self-compatible plant species [19]. Similarly, populations of anthropogenically disturbed habitats exhibit higher selfing rates than those in undisturbed habitats, probably because of a reduction of outcrossed pollen receipt [20]. Disentangling the effect of pollinator limitation from mate limitation is however difficult without additional information, for example, on plant and pollinator densities.

Pollinator decline can magnify selection on floral traits involved in pollen transfer (Box 1), because the relationship between pollen receipt and seed set is usually saturating

[21,22]. Therefore, we expect variation in pollen receipt to translate into larger variance in fitness among plants when pollen limitation is stronger, for example, induced by pollinator decline.

Two putative directions for plant reproductive strategies adaptation

Pollen limitation is a major ecological factor promoting the evolution of plant reproductive strategies [23]. At a contemporary time scale, we hypothesise two main evolutionary scenarios under pollinator decline for plants whose reproductive success is mainly ensured by pollinators: (i) evolution towards less reliance on pollinators by

Box 1. Plant reproductive traits in two scenarios of adaptation

Evolution towards autonomous selfing

Highly selfing species often share a suite of traits that constitute a selfing syndrome. Specifically, traits associated with high autonomous selfing are low herkogamy (i.e., anther-stigma distance) and low dichogamy (i.e., temporal separation between mature anthers and mature stigmas, Figure 1A). Small flowers are also often associated with autonomous selfing. Similarly, shorter flower longevity, lower pollen:ovule ratio, and smaller rewards could be selected along with the evolution of higher selfing rates.

Evolution towards reinforced interactions with pollinators

Numerous traits are correlated to pollinator visitation rates and efficiency of pollen transfer. Floral traits associated with high

visitation rates comprise large corolla size (Figure 1B), large floral display (i.e., numerous flowers open simultaneously, Figure 1C), strong scent, and large rewards. When pollination is low and unpredictable, a longer individual flowering period is also expected. Less predictable adaptive changes could also include all traits involved in attraction cues for pollinators (including floral colour), pollen placement on pollinators body (positioning of fertile organs and floral design), and the adjustment of individual flowering time (mean and variance) with the activity of pollinators.

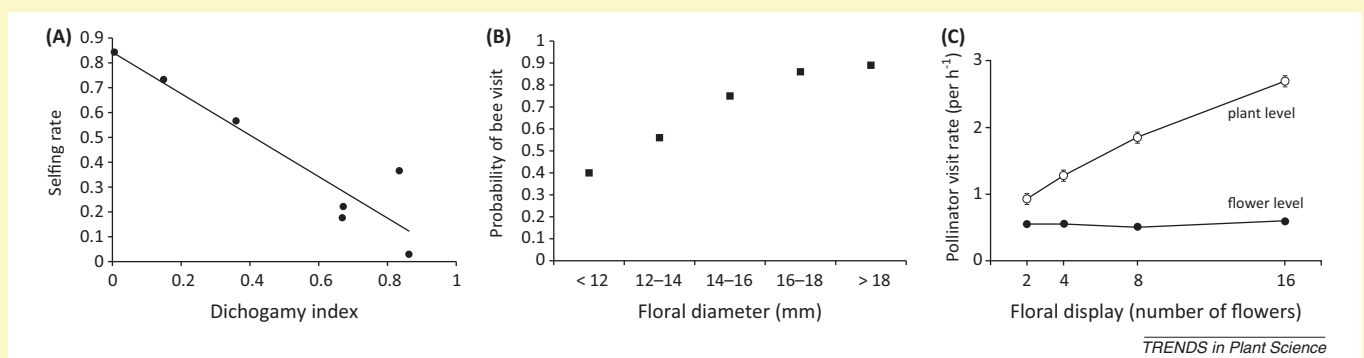


Figure 1. Examples of relationships between several floral traits and plant reproductive strategies. (A) Lower dichogamy (here protandry, with anthers being mature before stigmas) in *Gilia achilleifolia* (adapted from [76]; dots represent population averages) increases autonomous selfing. Plants with (B) larger flowers in *Polemonium viscosum* (adapted from [77]) and (C) larger floral displays in *Mimulus ringens* (adapted from [78]; least squares means \pm standard errors) are both more visited by bees. However, note that increased floral display does not always translate into more visits per flower (C).

increasing autonomous selfing, and (ii) evolution towards reinforced interactions with pollinators, thus maintaining the production of outcrossed seeds [13,20].

The first scenario emerges from the abundant theory analysing the evolution of self-fertilisation [23]. This theory predicts that evolution towards selfing results from a balance between the 50% transmission advantage of genes for selfing individuals [24], reproductive assurance under pollen limitation, and inbreeding depression that counteracts these latter two advantages [25]. In the absence of pollen limitation, complete selfing (respectively complete outcrossing) is expected to evolve when inbreeding depression is lower than 0.5 (respectively greater than 0.5) [26]. Because the production of selfed seeds increases plant fitness under pollen limitation (i.e., reproductive assurance), pollinator decline is expected to increase the inbreeding depression threshold below which selfing is selected through the evolution of floral traits (Box 1). The selective advantage of selfing under pollen limitation is however modified by the relative timing of outcrossing and selfing events during reproduction [25]. Mechanisms that allow selfing after any opportunity for outcrossing (i.e., delayed selfing) should always be selected, but those that allow selfing prior to outcrossing are less advantageous as they pre-empt ovules potentially devoted to outcrossing.

In the second scenario, reinforced interactions with pollinators could evolve to compensate for their decline, and thus maintain outcrossing strategies, via increased pollinator visitation rates and efficiency of pollen transfer (Box 1). Greater investment in attraction is thought to be more beneficial to the male than the female component of fitness because pollen export keeps increasing with further pollinator visits when most ovules have already been fertilised [27,28]. However, selection on attractive floral traits via the female fitness is also expected to be stronger when pollinators are scarcer [29]. Adjusting individual flowering phenology to pollinator availability also contributes to increase visitation rates [30,31]. Nevertheless, increasing pollinator attraction, for example, by opening additional flowers on the same plant on a given day (i.e., floral display), can increase pollinator-mediated selfing (here geitonogamy) [25], and thus does not necessarily allow the maintenance of outcrossing.

Spatial associations of the lack of pollinators with higher autonomous selfing in *Centaureum erythraea* [32,33] and with enhanced pollinator attraction in *Alkanna orientalis* [34] are consistent with these two evolutionary scenarios.

Most trait values involved in the two proposed scenarios are *a priori* opposite (Box 1, but see [35]); therefore, we expect the scenarios to be mutually exclusive. The evolutionary trajectory of plant populations will be determined by the interplay of multiple ecological, demographic, and genetic factors. Evolution towards less reliance on pollinators by increased selfing is expected to be more frequent for plants specialised to a few pollinators. Evolution towards reinforced interactions with pollinators could be easier for more generalist plants, as they can maintain reproductive success via (i) altered proportions of visits from several pollinator species and (ii) attraction of new pollinators (shift or diversification), for example, simply by changing their flowering phenology. Population

demography is also likely to affect which of the two scenarios can evolve. Low plant density that limits pollinator attraction (pollen quantity, [36]) and potentially increases the amount of heterospecific pollen receipt (pollen quality, [37]) is expected to impede evolution towards reinforced interactions with pollinators, especially for generalist plant species. By contrast, models show that rare species can evolve towards specialised pollination and avoid heterospecific pollen receipt [38]. Regarding genetic factors, we expect self-compatibility and low inbreeding depression to facilitate evolution towards autonomous selfing. By contrast, self-incompatibility (~40–50% of plants species, [39]) should be associated with evolution towards reinforced interactions with pollinators, because it strongly constrains short-term evolution towards selfing (but see [40,41] for a rapid breakdown of self-incompatibility) and cancels the genetic costs of pollinator-mediated selfing. High inbreeding depression can also hamper evolution towards higher selfing if purging of deleterious mutations is inefficient [42].

Potential for rapid adaptation of plant reproductive strategies

The potential for rapid adaptation of plant reproductive strategies in the context of pollinator decline requires at least (i) genetic variance of mating and floral traits and (ii) selection driven by pollinator decline.

Floral traits commonly exhibit coefficient of variation between ~15% and ~30%, up to ~55% for reward traits [43]. Estimates of heritabilities for 41 hermaphroditic species reveal substantial heritability for floral traits involved in mating systems (e.g., average $h^2 \approx 0.40$ for anther-stigma separation and positioning), pollinator attraction at the flower level (e.g., average $h^2 \approx 0.45$ for corolla size; average $h^2 \approx 0.20$ for nectar production), or at the plant level (e.g., average $h^2 \approx 0.35$ for floral display) [44]. Overall, these data suggest that adaptation of reproductive strategies is not expected to be constrained by a lack of genetic variance. Nevertheless, the evolution of floral traits can be slowed down by genetic correlations [45,46], which are commonly found among floral traits [44], but the effects of correlations on multivariate evolution is an open question [47].

Selection mediated by pollinators is frequently detected in natural populations, for reproductive traits such as flowering phenology, number of open flowers, corolla size, anther-stigma distance or position, floral morphology, and floral colour patterns (see [48] for a review). Note that most studies estimate individual fitness with the number of seeds produced and thus neglect the male component of fitness (but see [49,50]). Estimates of selection on floral traits for contrasted abundances of pollinators are still rare but particularly valuable for investigating the potential for rapid adaptation under pollinator decline. In the wild radish, *Raphanus sativus*, large corolla were favoured when pollinators were scarce (as they increased pollen export, i.e., male fitness component), but selection was not detected on corolla size when pollinators were abundant [51]. Likewise, selection on attractive traits via the female component of fitness increased with pollen limitation intensity [52]. These two studies suggest that

pollinator decline can drive short-term evolution towards increased attraction through both male and female components of fitness. In contrast to this, selection favoured plants with reduced anther-stigma distances in populations of the monkey flowers *Mimulus guttatus* [53] and *Mimulus luteus* [54] when pollinators were experimentally excluded, a pattern that was not found when pollinators visited flowers.

Quantifying the short-term evolution of reproductive strategies requires a quantitative genetics framework. Selection differentials (*sensu* [45]) can be inferred from estimated regressions of floral traits on fitness in natural or experimental populations [55]. For example, an increase of 20% to 40% in pollinator limitation, consistent with empirical estimates [16], may induce a selective differential of selfing rate of $\sim 1\%$ per generation (Box 2). Predicting

Box 2. A quantitative framework to analyse selection on mating system traits

Here, we propose to evaluate the intensity of selection on a floral trait determining selfing rates (e.g., herkogamy or dichogamy) after a sudden increase in pollen limitation. We consider a quantitative trait z characterised by a normal distribution $D(z)$ of mean \bar{z} and variance σ_z^2 affecting individual selfing rate s .

Individual fitness

Following [25], the fitness of a hermaphroditic plant $w(z)$ results from the contribution of (i) selfed seeds, (ii) outcrossed seeds, and (iii) pollen export to other plants. Whereas selfed progeny suffers from inbreeding depression (δ), outcrossed contributions to fitness (ii and iii) depend on pollinator activity captured by parameter e .

$$w(z) = \underbrace{2s_z(1-\delta)}_i + \underbrace{[(1-s_z)]}_{ii} + \underbrace{(1-\bar{s}_z)}_{iii} e,$$

Selection

Starting from a balance between costs and benefits of selfing ($1-\delta = e/2$, see [25]), we evaluate how relative changes in pollinator activity e affect the mean floral trait \bar{z} and hence the selfing rate s . After selection, the distribution of trait z is given by $D(z)$ weighted by individual fitness $w(z)$:

$$\frac{w(z) \times D(z)}{\bar{w}}, \text{ with } \bar{w} = \int w(z) D(z) dz.$$

The selection differential scaled by the trait mean is thus:

$$\left(\frac{w(z) \times D(z)}{\bar{w}} - \bar{z} \right) / \bar{z}$$

Using the empirical data of anther-stigma distance for z ($s(z) = 0.78 - 0.1z$) adjusted from [79], we compute the selection differential of z by varying the reduction in relative pollinator activity $1 - e'/e$ (i.e., the intensity of selection) (Figure I).

Example of shift in herkogamy in experimental populations of *Mimulus guttatus*

In the only study available of experimental evolution on the plant mating system [35], populations of *Mimulus guttatus* grown without pollinators during five generations in a greenhouse evolved reduced anther-stigma distance and became more able to self autonomously than populations grown with pollinators (Figure II).

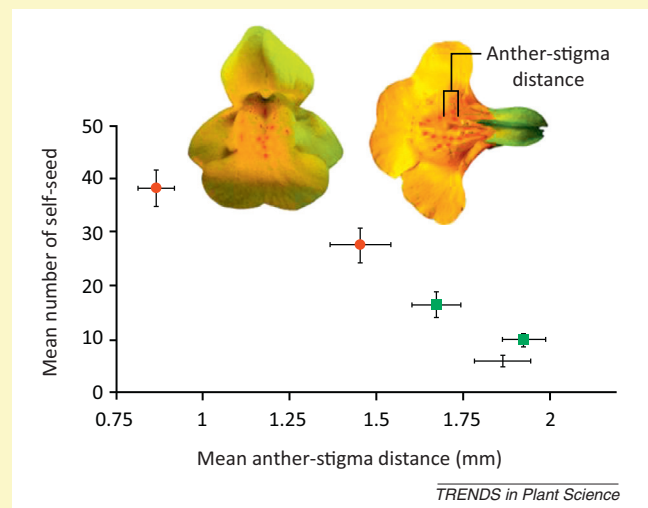


Figure II. Herkogamy shifts in four experimental populations of *Mimulus guttatus* evolving with pollinators (green square) or without pollinators (red circle) during five generations from initially equivalent populations (black). Evolved reduced herkogamy increases the production of selfed seeds. Reproduced and adapted from [35]. Error bars are standard errors.

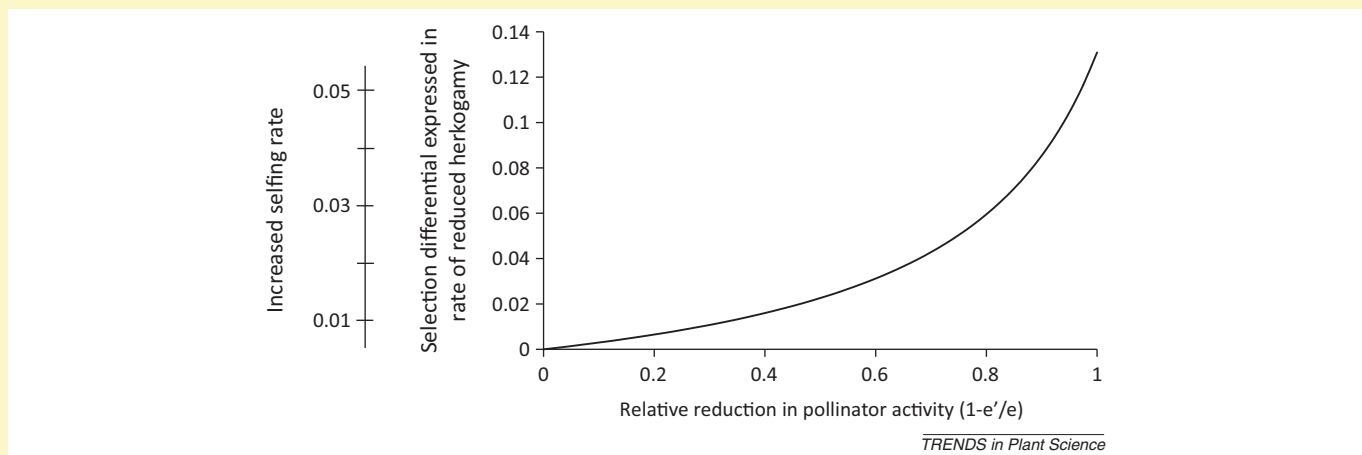


Figure I. Selection differential after one generation plotted as a rate of reduced herkogamy (and associated increased selfing) depending on the relative reduction in pollinator activity $1 - e'/e$, where e and e' represent pollination activity before and after pollinator decline, respectively. Anther-stigma distance of the ancestral plant population is $4.35 \text{ mm} \pm 1.40 \text{ mm}$ (SD).

a per generation rate of evolution is however not straightforward in partial self-fertilising plants because, among other things, the evolution of a trait related to selfing rate (e.g., herkogamy or floral size) modifies its genetic architecture and thus its own evolution, potentially leading to complex evolutionary dynamics [56]. A selection experiment manipulating pollinator abundance in a greenhouse [35] showed that after five generations with no pollinators, *M. guttatus* populations increased their ability to self autonomously (Box 2), thus providing the first demonstration of short-term evolution towards increased selfing. Interestingly, the authors also showed that the evolution of selfing was accompanied by a higher heritability on anther-stigma distance, and independently of inbreeding, such that short-term evolution did not erode but instead increased adaptive potential.

Consequences of reproductive strategies on population demography

The impact of pollen limitation on plant population demography and persistence depend on the sensitivity of population growth rate to seed production. For example in *Lathyrus vernus*, seed production but not population growth rate was pollen limited [13]. Conversely, in *Cytisus scoparius*, increased seed production through pollen supplementation increased population growth rate by 50% [13]. Pollen limitation can further increase extinction risk because of reproductive failure, as shown for the lovely clarkia (*Clarkia concinna*) [36]. These examples show that for seed limited populations demography is expected to be affected by pollinator decline. For such seed limited populations, adaptation of reproductive strategies increasing seed set may buffer the impact of pollinator decline and

further act as an evolutionary rescue. Although higher selfing can increase seed set under pollen limitation, its net effect on the population growth rate is not straightforward because several life history traits (e.g., germination, size at reproduction, or survival) can suffer from inbreeding depression.

To what extent adaptation can mitigate the negative impacts of environmental changes on plant demography depends on the interplay between population size and genetic variation [57], and on the rate and intensity of the environmental changes [58] (see [59] for inferring these parameters in natural populations). Adaptation has to be fast enough to both prevent deterministic extinction and prevent populations from reaching critical densities below which demographic stochasticity threatens population persistence [60] (Box 3). For example, under selection, the rate of evolution is increased by the contribution of several major genes to the genetic variation [61].

Changes in mating systems *per se* can have a major effect on population dynamics and hence on the evolutionary rescue of populations. A comparative study of gentian populations (*Gentianella campestris*) in a fragmented landscape showed that population seed set and viability were insensitive to pollinator abundance for selfing populations but instead increased with increased pollinator abundance for outcrossing populations. Further, under low pollinator abundance selfing populations had a higher population viability than outcrossing populations, and the opposite pattern was found under higher pollinator abundance, probably because inbreeding depression lowered the growth rate of selfing populations [62]. Most theories on mating system evolution consider relative fitness of plant traits and cannot address population demography, which

Box 3. Putative effects of plant reproductive strategy evolution on population size following change in pollination regime

As a heuristic tool, we propose a conceptual eco-evolutionary framework of plant populations after pollinator decline, depending on whether plants evolve increased selfing (Figure 1A) or reinforced interaction with pollinators (Figure 1B).

Following [60] and [68], N_c represents the critical population size above which demographic stochasticity can be neglected as a factor of extinction.

Scenario A

(A): (a) Reduced pollination leads to a population growth rate below one. Without evolution, populations become extinct. In the other two trajectories, evolution is fast enough to rescue populations, but the probability of going below N_c is increased and the population size at equilibrium is decreased in the absence of purging (b) compared to efficient purging of inbreeding depression, δ (c). Because the evolution of selfing reduces the dependence on pollinators, such trajectories should however reduce environmental stochasticity due to pollinators.

Scenario B

(B): (a) Reduced pollination leads to a population growth rate below one. Without evolution, populations become extinct. In the other two trajectories, evolution can rescue populations but high costs associated with the evolution of reinforced interactions with pollinators (i.e., building and maintenance of attractive structures) are expected to increase the probability of going below N_c and decrease the population size at equilibrium (b and c). Populations evolving reinforced interactions should still suffer from environmental stochasticity due to pollinators, but evolution may eventually buffer such fluctuations (e.g., evolution towards generalised pollination).

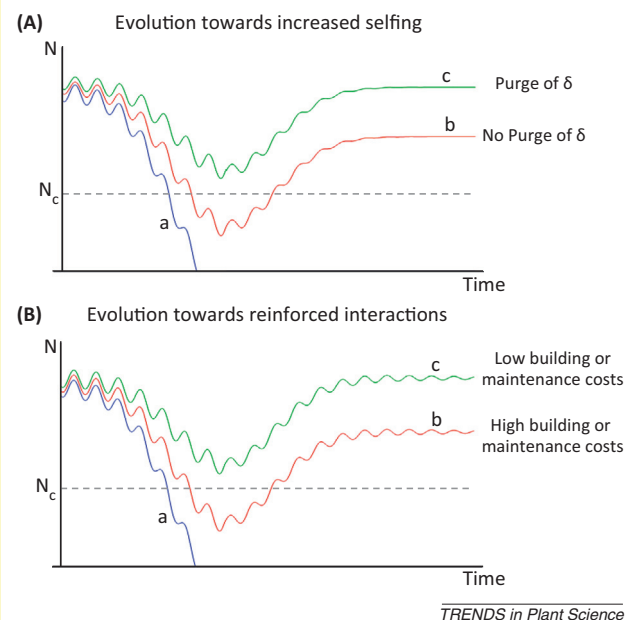


Figure 1. Schematic illustration of plant population sizes during the course of evolution.

relies on absolute fitness. The few theoretical studies linking demography and mating system evolution (e.g., [63,64]) have shown that a mating system shift does influence population demography and growth rate.

Although this theory only deals with population demography at evolutionary equilibrium, it can help identify demographical processes during transitions of plant reproductive strategies under pollinator decline (Box 3). Because inbreeding depression lowers absolute fitness [65], evolution towards increased selfing would be associated with reduced population sizes if the genetic load is not purged (Box 3). However, the effect of variations in local pollinator abundance on plant population sizes (i.e., environmental stochasticity; see [66]) is expected to be lower for populations that self-fertilise more and rely less on pollinators for seed production. Evolution towards reinforced interactions with pollinators should not change plant population sizes, unless costs are associated with the evolution of floral traits (e.g., increased nectar production; Box 3).

Concluding remarks

After 30 years of abundant theories on plant reproductive strategies (e.g., [23,26,67]) and recent calls to go beyond models of evolutionary rescue [59,68], pollinator decline provides a unique opportunity to test theoretical predictions on a broad scale and in natural populations. Until now, only a few empirical and experimental studies investigated the evolutionary consequences of pollinator decline (e.g., [33,35,53]) (Box 2), and no direct evidence of rapid evolution of plant reproductive strategies under pollinator decline has yet been reported *in natura*.

Taking advantage of long-term studies in natural populations (e.g., [69]) should allow comparison of current and past plant reproductive strategies (e.g., selfing rate, floral traits). However, disentangling genetic evolution from phenotypic plasticity is usually neither straightforward nor possible. In this context, growing stored seeds from past and current populations in similar conditions allows estimating genetic differentiations of traits (e.g., [70,71]). The establishment of seedbank collections for future experiments (e.g., Baseline Project; see [72]) is a promising avenue for analysing rapid evolution of plants under pollinator decline.

Theoretical developments that predict evolutionary changes of plant reproductive strategies and their association with population persistence are also lacking. The evolution of mating system traits fundamentally departs from other traits because of the feedback on their genetic architecture and populations inbreeding [56]. Although classical genetics tools such as the breeder's equation provide useful approximations [73], they need to be amended to account specifically for the evolution of mating system traits. Similarly, the explicit modelling of demography (population size, growth rate, sensitivity to stochasticity) during transitory dynamics [59] will help understand eco-evolutionary processes involved in mating system changes.

Although persistence of threatened populations appears plausible through short-term evolution, it does not necessarily translate into long-term persistence. Evolution of reinforced interactions with pollinators could eventually

be an evolutionary trap if pollinators keep declining. Evolution towards increased selfing when associated with reduced pollinator attraction and reduced genetic load could initiate an evolutionary trajectory towards even more selfing and could constrain reversal evolution towards outcrossing [74]. Further, recurrent evolution towards selfing has been shown to correlate with increased extinction of selfing lineages ('dead end hypothesis', [75]). Evolutionary rescue of flowering plants under pollinator decline through short-term response of reproductive strategies questions the future of population persistence and more generally of ecosystems functioning.

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References

- Potts, S.G. *et al.* (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353
- Klein, A.M. *et al.* (2007) Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* 274, 303–313
- Winfree, R. *et al.* (2011) Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Evol. Syst.* 42, 1–22
- Biesmeijer, J.C. *et al.* (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351–354
- Grixti, J.C. *et al.* (2009) Decline of bumble bees (*Bombus*) in the North American Midwest. *Biol. Conserv.* 142, 75–84
- Bommarco, R. *et al.* (2012) Drastic historic shifts in bumble-bee community composition in Sweden. *Proc. R. Soc. B* 279, 309–315
- Cameron, S.A. *et al.* (2011) Patterns of widespread decline in North American bumble bees. *Proc. Natl. Acad. Sci. U.S.A.* 108, 662–667
- Rasmont, P. *et al.* (1993) The faunistic drift of Apoidea in Belgium. In *Bees for Pollination* (Bruneau, E., ed.), pp. 65–87, Commission of the European Communities
- Kosior, A. *et al.* (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. *Oryx* 41, 79–88
- Anderson, S.H. *et al.* (2011) Cascading effects of bird functional extinction reduce pollination and plant density. *Science* 331, 1068–1071
- Pauw, A. and Hawkins, J.A. (2011) Reconstruction of historical pollination rates reveals linked declines of pollinators and plants. *Oikos* 120, 344–349
- Pauw, A. and Bond, W.J. (2011) Mutualisms matter: pollination rate limits the distribution of oil-secreting orchids. *Oikos* 120, 1531–1538
- Ashman, T.L. *et al.* (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85, 2408–2421
- Knight, T.M. *et al.* (2005) Pollen limitation of plant reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.* 36, 467–497
- Aguilar, R. *et al.* (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* 9, 968–980
- Steffan-Dewenter, I. and Tschamntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121, 432–440
- Garibaldi, L.A. *et al.* (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062–1072
- Winfree, R. *et al.* (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90, 2068–2076
- Gomez, J.M. *et al.* (2010) Changes in pollinator fauna cause spatial variation in pollen limitation. *J. Ecol.* 98, 1243–1252
- Eckert, C.G. *et al.* (2010) Plant mating systems in a changing world. *Trends Ecol. Evol.* 25, 35–43

- 21 Waser, N.M. and Price, M.V. (1991) Outcrossing distance effects in *Delphinium nelsonii* – pollen loads, pollen tubes, and seed set. *Ecology* 72, 171–179
- 22 Mitchell, R.J. (1997) Effects of pollination intensity on *Lesquerella fendleri* seed set: variation among plants. *Oecologia* 109, 382–388
- 23 Lloyd, D.G. (1979) Some reproductive factors affecting the selection of self-fertilization in plants. *Am. Nat.* 113, 67–79
- 24 Fisher, R.A. (1941) Average excess and average effect of a gene substitution. *Ann. Eugen.* 11, 53–63
- 25 Lloyd, D.G. (1992) Self-fertilization and cross-fertilization in plants. 2. The selection of self-fertilization. *Int. J. Plant Sci.* 153, 370–380
- 26 Lande, R. and Schemske, D.W. (1985) The evolution of self-fertilization and inbreeding depression in plants. 1. Genetic models. *Evolution* 39, 24–40
- 27 Bell, G. (1985) On the function of flowers. *Proc. R. Soc. B* 224, 223–265
- 28 Vamossi, J.C. and Otto, S.P. (2002) When looks can kill: the evolution of sexually dimorphic floral display and the extinction of dioecious plants. *Proc. R. Soc. B* 269, 1187–1194
- 29 Haig, D. and Westoby, M. (1988) On limits to seed production. *Am. Nat.* 131, 757–759
- 30 Elzinga, J.A. *et al.* (2007) Time after time: flowering phenology and biotic interactions. *Trends Ecol. Evol.* 22, 432–439
- 31 Devaux, C. and Lande, R. (2010) Selection on variance in flowering time within and among individuals. *Evolution* 64, 1311–1320
- 32 Brys, R. *et al.* (2011) Importance of autonomous selfing is inversely related to population size and pollinator availability in a monocarpic plant. *Am. J. Bot.* 98, 1834–1840
- 33 Brys, R. and Jacquemyn, H. (2012) Effects of human-mediated pollinator impoverishment on floral traits and mating patterns in a short-lived herb: an experimental approach. *Funct. Ecol.* 26, 189–197
- 34 Gilbert, F. *et al.* (1996) Spatial variation in selection in a plant–pollinator system in the wadis of Sinai, Egypt. *Oecologia* 108, 479–487
- 35 Bodbyl Roels, S.A. and Kelly, J.K. (2011) Rapid evolution caused by pollinator loss in *Mimulus guttatus*. *Evolution* 65, 2541–2552
- 36 Groom, M.J. (1998) Allele effects limit population viability of an annual plant. *Am. Nat.* 151, 487–496
- 37 Arceo-Gomez, G. and Ashman, T.L. (2011) Heterospecific pollen deposition: does diversity alter the consequences? *New Phytol.* 192, 738–746
- 38 Sargent, R.D. and Otto, S.P. (2006) The role of local species abundance in the evolution of pollinator attraction in flowering plants. *Am. Nat.* 167, 67–80
- 39 Iqbal, B. and Kohn, J.R. (2006) The distribution of plant mating systems: study bias against obligately outcrossing species. *Evolution* 60, 1098–1103
- 40 Reinartz, J.A. and Les, D.H. (1994) Bottleneck-induced dissolution of self-incompatibility and breeding system consequences in *Aster furcatus* (Asteraceae). *Am. J. Bot.* 81, 446–455
- 41 Willi, Y. (2009) Evolution towards self-compatibility when mates are limited. *J. Evol. Biol.* 22, 1967–1973
- 42 Winn, A.A. *et al.* (2011) Analysis of inbreeding depression in mixed-mating plants provides evidence for selective interference and stable mixed mating. *Evolution* 65, 3339–3359
- 43 Cresswell, J.E. (1998) Stabilizing selection and the structural variability of flowers within species. *Ann. Bot.* 81, 463–473
- 44 Ashman, T.L. and Majetic, C.J. (2006) Genetic constraints on floral evolution: a review and evaluation of patterns. *Heredity* 96, 343–352
- 45 Falconer, D.S. (1981) *Introduction to Quantitative Genetics*, Longman Inc.
- 46 Walsh, B. and Blows, M.W. (2009) Abundant genetic variation plus strong selection = multivariate genetic constraints: a geometric view of adaptation. *Annu. Rev. Ecol. Syst.* 40, 41–59
- 47 Agrawal, A.F. and Stinchcombe, J.R. (2009) How much do genetic covariances alter the rate of adaptation? *Proc. R. Soc. B* 276, 1183–1191
- 48 Harder, L.D. and Johnson, S.D. (2009) Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. *New Phytol.* 183, 530–545
- 49 van Kleunen, M. and Burczyk, J. (2008) Selection on floral traits through male fertility in a natural plant population. *Evol. Ecol.* 22, 39–54
- 50 Kulbaba, M.W. and Worley, A.C. (2012) Selection on floral design in *Polemonium brandegeei* (polemoniaceae): female and male fitness under hawkmoth pollination. *Evolution* 66, 1344–1359
- 51 Young, H.J. and Stanton, M.L. (1990) Influences of floral variation on pollen removal and seed production in wild radish. *Ecology* 71, 536–547
- 52 Ashman, T.L. and Morgan, M.T. (2004) Explaining phenotypic selection on plant attractive characters: male function, gender balance or ecological context? *Proc. R. Soc. B* 271, 553–559
- 53 Fishman, L. and Willis, J.H. (2008) Pollen limitation and natural selection on floral characters in the yellow monkeyflower, *Mimulus guttatus*. *New Phytol.* 177, 802–810
- 54 Carvallo, G.O. and Medel, R. (2010) Effects of herkogamy and inbreeding on the mating system of *Mimulus luteus* in the absence of pollinators. *Evol. Ecol.* 24, 509–522
- 55 Lande, R. and Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution* 37, 1210–1226
- 56 Kelly, J.K. and Arathi, H.S. (2003) Inbreeding and the genetic variance in floral traits of *Mimulus guttatus*. *Heredity* 90, 77–83
- 57 Bell, G. and Gonzalez, A. (2009) Evolutionary rescue can prevent extinction following environmental change. *Ecol. Lett.* 12, 942–948
- 58 Bell, G. and Gonzalez, A. (2011) Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science* 332, 1327–1330
- 59 Gomulkiewicz, R. and Shaw, R.G. (2013) Evolutionary rescue beyond the models. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 368, 20120404
- 60 Gomulkiewicz, R. and Holt, R.D. (1995) When does evolution by natural-selection prevent extinction. *Evolution* 49, 201–207
- 61 Gomulkiewicz, R. *et al.* (2010) Genetics, adaptation, and invasion in harsh environments. *Evol. Appl.* 3, 97–108
- 62 Lennartsson, T. (2002) Extinction thresholds and disrupted plant–pollinator interactions in fragmented plant populations. *Ecology* 83, 3060–3072
- 63 Cheptou, P.O. (2004) Allele effect and self-fertilization in hermaphrodites: reproductive assurance in demographically stable populations. *Evolution* 58, 2613–2621
- 64 Morgan, M.T. *et al.* (2005) Plant population dynamics, pollinator foraging, and the selection of self-fertilization. *Am. Nat.* 166, 169–183
- 65 Hedrick, P.W. and Kalinowski, S.T. (2000) Inbreeding depression in conservation biology. *Annu. Rev. Ecol. Syst.* 31, 139–162
- 66 Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142, 911–927
- 67 Barrett, S.C.H. and Harder, L.D. (1996) Ecology and evolution of plant mating. *Trends Ecol. Evol.* 11, A73–A79
- 68 Kinnison, M.T. and Hairston, N.G. (2007) Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Funct. Ecol.* 21, 444–454
- 69 Thompson, J. *et al.* (2013) Evolution of a genetic polymorphism with climate change in a Mediterranean landscape. *Proc. Natl. Acad. Sci. U.S.A.* 110, 2893–2897
- 70 Franks, S.J. *et al.* (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl. Acad. Sci. U.S.A.* 104, 1278–1282
- 71 Sultan, S.E. *et al.* (2013) A resurrection study reveals rapid adaptive evolution within populations of an invasive plant. *Evol. Appl.* 6, 266–278
- 72 Shaw, R.G. and Etterson, J.R. (2012) Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *New Phytol.* 195, 752–765
- 73 Kelly, J.K. and Williamson, S. (2000) Predicting response to selection on a quantitative trait: a comparison between models for mixed-mating populations. *J. Theor. Biol.* 207, 37–56
- 74 Iqbal, B. and Busch, J.W. (2013) Is self-fertilization an evolutionary dead end? *New Phytol.* 198, 386–397
- 75 Goldberg, E.E. *et al.* (2010) Species selection maintains self-incompatibility. *Science* 330, 493–495
- 76 Schoen, D.J. (1982) The breeding system of *Gilia achilleifolia* – variation in floral characteristics and outcrossing rate. *Evolution* 36, 352–360
- 77 Galen, C. and Newport, M.E.A. (1987) Bumble bee behavior and selection on flower size in the sky pilot, *Polemonium viscosum*. *Oecologia* 74, 20–23
- 78 Mitchell, R.J. *et al.* (2004) The influence of *Mimulus ringens* floral display size on pollinator visitation patterns. *Funct. Ecol.* 18, 116–124
- 79 Holtsford, T.P. and Ellstrand, N.C. (1992) Genetic and environmental variation in floral traits affecting outcrossing rate in *Clarkia tembloriensis* (Onagraceae). *Evolution* 46, 216–225