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Inter-annual facilitation via pollinator support arises with species-specific germination rates in a model of plant–pollinator communities

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Facilitation is likely important for understanding community diversity dynamics, but its myriad potential mechanisms are under-investigated. Studies of pollinator-mediated facilitation in plants, for example, are typically focused on how co-flowering species facilitate each other's pollination within a season. However, pollinator-mediated facilitation could also arise in the form of inter-annual pollination support, where co-occurring plant populations mutually facilitate each other by providing dynamic stability to support a pollinator population through time. In this work, I test this hypothesis with simulation models of annual flowering plant and bee pollinator populations to determine if and how inter-annual pollination support affects the persistence and/or stability of simulated communities. Two-species plant communities persisted at higher rates than single-species communities, and facilitation was strongest in communities with low mean germination rates and highly species-specific responses to environmental variation. Single-species communities were often more stable than their counterparts, likely because of survivorship—persistent single-species communities were necessarily more stable through time to support pollinators. This work shows that competition and facilitation can simultaneously affect plant population dynamics. It also importantly identifies key features of annual plant communities that might exhibit inter-annual pollination support- those with low germination rates and species-specific responses to variation.

1. Introduction

The diversity of life on Earth is undergirded by species interactions, the dynamics of which are critical to understanding the maintenance of individual populations as well as community diversity. Though interactions between organisms can range from mutually negative, competitive interactions to mutually positive, facilitative interactions, studies of diversity maintenance within trophic levels tend to focus on how competitive interactions can be leveraged to understand population dynamics [1,2]. Plant diversity maintenance in particular is classically understood through the lens of competitive coexistence theory [3–5]; as a result, investigations of community diversity maintenance framed explicitly in terms of facilitation and its effects on population dynamics are comparatively rare. That being said, there is a substantial and growing body of empirical evidence showing that positive interactions between plants are not only common in biological communities but integral to understanding plant community assembly and coexistence, though mechanisms are sometimes unclear [1,6–11].

One mechanism of plant–plant facilitation is through sharing pollinators, or pollinator-mediated plant interactions [1,7,8,12–14]; reviewed by [15]. The bulk of pollinator-mediated plant interaction studies focus on how pollinator foraging behaviours respond to variation in the abundance or diversity of co-flowering plants in communities [16–22]. These studies have shown that plants can facilitate each other's reproductive success due to pollinator attraction to increased floral diversity or abundance, where patches of co-flowering plants that are denser, more diverse, or both have higher visitation rates, lower pollen limitation, or higher seed production [12,23–26]. Less well-studied are interactions where plants that do not necessarily co-flower may support more pollinators through time if pollinator populations exhibit a numerical response to increasing floral diversity or abundance [12–15,24,26–28]. The idea behind numerical pollinator support (which has been called 'facilitation by pollinator support' [12] or more recently 'apparent pollination support' [15]) is that diverse communities of plants should be better able to support pollinator populations both within and between years, because in years when certain plant species perform poorly (or have low abundance) there are other species in the community that perform well, providing dynamic stability [14,29]. In species-rich plant communities, this means that pollinator populations should not suffer losses when one plant population fails to provide enough resources for pollinators in a given year. Instead, pollinators can rely on the other plants for necessary floral resources, and plant assemblages support large, stable pollinator populations. As a result, the whole community of plants and pollinators is sustained by plant diversity and plants' mutual support of pollinator populations through time [12,14,–26].

Though not infrequently referenced as a potential means for plant facilitation, strong empirical evidence for apparent pollination support is hard to come by [15]. This is not only because facilitation is under-investigated in plant communities, but because long-term datasets of pollinator populations are virtually nonexistent—especially for multiple communities with well-documented flowering plant diversity [16]. A valid workaround that allows us to test the pollinator support hypothesis, however, is simulation modelling. Proof-of-concept models offer a way to test verbal hypotheses, verify their predictions, and potentially provide new, more precise direction to empirical work [30]. In the case of pollinator support, modelling is necessary to understand if and under what conditions the pollinator support hypothesis yields the facilitative interactions that we expect between pollinator-sharing plants.

The verbal model of pollination support suggests that sharing pollinators is a mechanism for interspecific facilitation and diversity maintenance in plant communities. Facilitation from co-occurrence could be a result of (1) preventing bee population crashes, which then prevents plant community crashes, or (2) providing lower variation in pollinators' food resources between years, which dynamically provides for more stable plant communities through time. In the following work, I build a simulation model of pollinator-sharing annual plants to ask if and how plants can facilitate each other via pollinator support. To do so, I model communities of two plant species and one pollinator species and compare their plant/pollinator persistence and stability to communities with one plant species. In two-species communities, I manipulate plants' species-specific responses to the environment to explore the assumption that pollinator support occurs when plant species respond differentially to variation in the environment [12]. I vary species' germination correlations from –1 (the highest level of species specificity- when one species' germination rate is high in response to the environment, the other is low) to 1 (the lowest level of species specificity—both species have the exact same germination rates in response to the environment). I then compare plant/pollinator persistence and stability in two-species model outputs under different germination correlations with single-species plant communities.

I predict that both plants and pollinators will have higher rates of persistence (fewer population crashes) in two-species plant communities than in single-species plant communities. I expect this to depend on values of germination correlation, which determine the specificity of species' responses to environmental variation (figure 1*a*). As germination correlation becomes more positive, two-species plant communities should crash as frequently as single-species plant communities through time, causing pollinator communities to crash (figure 1*g*). If two-species communities with more positive germination correlation persist, I expect them to be more variable in population size than those with negative germination correlation (figure 1*b*,*e*,*g*). Plant and pollinator abundance should also be most stable (exhibit the lowest variation through time) in two-species plant communities with species-specific responses to the environment (figure 1). However, I expect that single-species communities will be more stable than two-species communities with positive germination correlation, because single-species communities should have lower plant community abundances and therefore lower interannual variation (figure 1*c*,*h*).

2. Methods

The following equations represent a system of annual plant communities where the plant species share pollinators. The pollinators (I use the life history of solitary bees as a model) are also 'annual,' dying after they produce their eggs. Adult bees emerge from eggs in the following growing season. In the model, the plant species provide substitutable resources for the bees.

(a) Model description

(i) Plant equations

The annual plant population model proceeds in four stages: germination, competition, pollination, and seed survival (electronic supplementary material, figure S1). Plants of species i (P_i) germinate at species-specific rates (g_i) from seeds (S_i) produced in the last time-step t:

$$P_i(t) = g_i S_i(t). \tag{2.1}$$

Seeds that do not germinate survive to the next time-step at the rate s_i. The number of un-fertilized ovules O_i a plant produces is a function of how 'large' the plant is, as determined by the competition it experiences and the maximum potential ovule production of the species λ_i. The number of ovules produced by species i at time t is:

$$O_i(t) = \frac{\lambda_i P_i(t)}{1 + \sum_j \alpha_{ij} P_j(t)}. \tag{2.2}$$

The maximum number of ovules, λ_i, is scaled by competition with competition coefficients α_{ij}, which measure the *per-capita* effects of competition of species j on i.

Finally, the number of seeds produced for the next time-step depends on the pollinators in the system. I model limitation to seed production introduced by pollinators with the bee-to-ovule ratio

$$x = \frac{B(t)}{\sum_{O_i\ (t)}}. \tag{2.3}$$

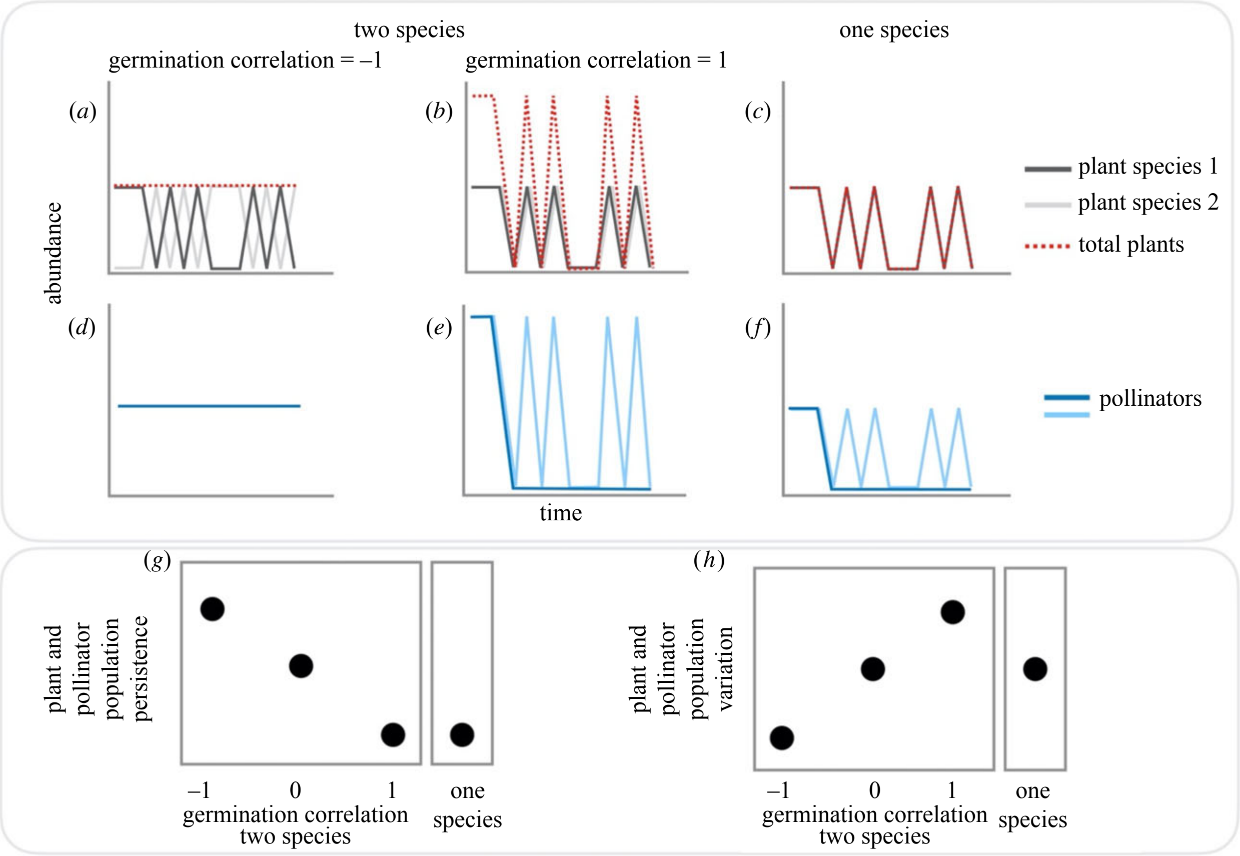

Figure 1. The predictions of facilitation via pollinator support. (*a*) two-species plant communities with negative germination correlation are stable (less variable) through time and (*d*) support stable pollinator populations. (*b*) Two-species plant communities with positive germination correlation are less stable (more variable if the community does not crash); (*e*) bee populations in two-species plant communities with highly positive germination correlation will either crash due to low resources in a given year (dark line) or be more unstable through time (light line). (*c*) Single-species plant communities and (*f*) their pollinators should crash as much as two-species positive germination correlation communities (dark line) and be unstable when they persist (light line). (*g*) two-species, negative correlation treatments will have higher rates of persistence and (*h*) exhibit lower variation through time (higher stability).

I include a constant L that represents the pollination to seed conversion penalty, which can also be thought of as pollinator efficiency. The seed production coefficient $1/L$ modifies x, so that as L increases, seed production decreases (as in electronic supplementary material, figure S2). Together, pollen limitation to seed production at time t and the survival of seeds from the previous time step determine the total number of seeds $S_i(t)$ in the following equation:

$$S_i(t+1) = O_i(t)\,(1 - e^{-x/L}) + S_i(t)_{S_i}(1 - g_i). \tag{2.4}$$

The contribution of pollinator visitation to seed production operates on available ovules, and the seed production coefficient is close to one either when x is high (the ratio of bees to ovules is high), or when L is low (the ovule to seed conversion penalty is low, electronic supplementary material, figure S2).

(ii) Bee equations

The bee population model assumes there is only one species of bee pollinator and is similar in structure to the plant population model. Here the bees are semelparous and use floral resources to produce eggs in their adult phase before dying. The eggs emerge as adults in the next season (time step). Egg production is a function of the number of floral resources in a year.

The number of bees produced in a growing season, $B(t)$ is the product of the number of eggs $E(t)$, and the per-egg rate of an egg becoming an adult, *p:* (electronic supplementary material, figure S1)

$$B(t) = pE(t). \tag{2.5}$$

Eggs produced by bees in $B(t)$ are a function of floral resources available to bees to produce eggs, and maximum *per--capita* egg production λ_B. I assume $\sum O_i(t)$, the sum of all plant ovules in the community, is proportional to the total amount of floral resources available to bees in the community. To model the relationship of resource limitation to bees' egg production, I again use x, the ratio of bees to ovules, to modify egg production:

$$E(t+1) = \lambda_B B(t)\,(1 - e^{-M/x}). \tag{2.6}$$

Here, the effect of the bee-to-ovule ratio on egg production is modified by M, or the pollen to egg conversion efficiency. The value M is a constant that controls the rate of saturation of x. As M increases, the egg production coefficient approaches one, and bees produce eggs at their maximum *per-capita* growth rate (electronic supplementary material, figure S2).

(b) Simulations and analysis

Using the difference equations from above, I built simulation models of communities with one bee pollinator species and one or two plant species in R v. 3.5.2 [31]. To ensure I was searching over a broad range of parameter space, I parameterized the models using 1000 different parameter sets, each replicated at five different mean germination rates. In two-species communities, I manipulated plant species' germination correlation to be more species-specific (negative correlation) to less species specific (positive correlation). I simulated the model of one- and two-species plant communities in these different scenarios and measured plant and pollinator persistence, mean abundance, and the

Table 1. Parameter values used in the model. Range denotes the range of values I used in searching parameter space.

symbol	meaning	units	range
p	rate of bee egg developing into adult bee	per-egg rate of maturation	1.0×10^{-4}, 1
λ_B	maximum number of eggs per bee	eggs per bee	0, 5
s_i	survival rate of seeds in species *i*	survival per seed	0.0001, 1
λ_i	maximum ovule production of plant species *i*	ovules per plant	0, 1000
L	pollen to seed conversion penalty (see electronic supplementary material, figure S2)	N/A	1.0×10^{-4}, 1.0×10^{4}
M	saturation constant for floral resource limitation to bee reproduction (see electronic supplementary material, figure S2)	N/A	1.0×10^{-4}, 1
α_{ii}, α_{ij}	interspecific and intraspecific competition coefficients	N/A	1

coefficient of variation (stability) of plant and pollinator populations through time.

(i) Parameter sets

I built a matrix of 1000 parameter sets. Each row in the matrix represented a complete parameter set except for germination mean and correlation structure, which were stored in separate arrays. Each column vector in the matrix contained all values of one parameter (a set of 1000 unique values because there were 1000 parameter sets). The range of values for each parameter varied (table 1 shows the minimum and maximum values for each parameter). To assemble the parameter set matrix, I first generated 1000 values in a regular sequence with prescribed minimum and maximum values for each parameter. Then, to ensure that values were uncorrelated across parameters within parameter sets, I randomized the order of each column. This ensured that, for example, the first (last) parameter set in the matrix did not contain the lowest (highest) possible value for each parameter. This technique, known as Latin hypercube sampling, allowed me to search for patterns evenly over a wide parameter space without a full-factorial simulation design [32].

I simulated the model with all parameter sets through six community types (treatments) of either one- or two-plant species scenarios. Two-species communities were simulated with five different germination correlation levels: –1, –0.5, 0, 0.5 and 1. Single-species scenarios, the sixth and final community type, were run using the same parameter sets, but only using parameters for species 1.

(ii) Germination arrays

Species-specific responses to the environment are incorporated into the model with variable germination rates. Negative correlation corresponds to highly species-specific responses to the environment, and positive correlation corresponds to general, shared responses (figure 1). Correlation in germination was incorporated using a copula (*sensu* [33]; modelled closely after [34], see their appendix A for details). In this approach, germination values were generated for each species, in each parameter set, at each timestep, for each mean germination rate, at each germination correlation level. To do so, I generated random draws from a multivariate normal distribution with prescribed mean and correlation structure of interest (command mvrnorm in the MASS package, [35]; see code for this paper stored in the Dryad Digital Repository). Each draw produced two values (one for each species) according to the prescribed mean germination ($g = 0.02$, 0.16, 0.5, 0.84 or 0.98), and germination correlation (–1, –0.5, 0, 0.5 or 1). These raw values were *z*-scores. I converted z-score values to germination values by integrating the normal pdf from $-\infty$ to the *z*-scores. This process converts z-score values to be between zero and one (the range of values germination rates can possibly take) while retaining the correlation structure of interest generated by the mvrnorm function. Germination values were stored in three-dimensional arrays: 5 correlation levels × 1000 parameter sets × 5000 timesteps. There was a germination array for each mean germination rate.

(iii) Model analysis

I simulated both one-species and two-species plant community models using the described parameter sets and germination arrays (electronic supplementary material, figure S3). To ensure that outputs were comparable across species diversity treatments, I used the same parameter sets and germination arrays for simulations. In the single-species models, I only used one set of plant parameter values (i.e. λ_1, s_1) and the germination arrays for species 1.

I measured the average number of bees or plants in the final 1000 timesteps of simulations. Mean bee population and plant community abundance < 1 were assigned a value of zero after the simulations were run. In persisting populations, I calculated the coefficient of variation (CV) of abundances in the final 1000 timesteps of simulations. I calculated germination covariance for each mean germination rate × prescribed germination correlation to understand the relationship of germination correlation to realized germination covariance, which is a measure of the realized relationship of species' germination rates in the simulations.

To understand the sensitivity of model outputs to variation in parameters, I calculated the partial Pearson correlation coefficients (Pearson's *r*) of model parameters in table 2 for (1) the log of abundance and (2) the coefficient of variation of both plant communities and bee populations. I log-transformed abundances because a linear relationship (correlation) should be most apparent as population abundances increase geometrically. I did not include λ_2 or s_2 because these parameters only existed for some of the simulation runs (those with two species). Because mean germination rate was not a continuous variable, I did not include it in the correlative analysis.

I measured population persistence by counting successful populations in each scenario × germination rate scenario. I defined successful persistence of a population as having a mean greater than one in the final 1000 timesteps of the model. To compare population persistence among these scenarios, I calculated the risk ratio. Here, the risk ratio is the number of persisting populations in two-species scenarios with germination correlation = –1, divided by the number of persisting populations for each scenario. I compared plant and bee persistence in all scenarios to scenarios with two plant species and germination correlation = –1, because I predicted that such simulations would have highest population persistence. Risk ratios of one indicate the scenario has the same

Table 2. Values of partial Pearson's correlations. I calculated Pearson's *r* for population abundance and parameters, and for population stability CV. Bolded values are above 0.2, which I interpret as a strong relationship between variables.

parameter	log(bees)	log(plants)	CV bees	CV plants
p	0.18	−0.01	0.01	0.02
M	0.17	−0.10	−0.01	0.02
s_1	0.01	0.01	−0.01	0.02
λ_1	0.07	−0.02	−0.01	0.05
λ_B	**0.21**	−0.04	0.01	0.01
L	0.02	−0.03	0.02	−0.01
log(bees)	1.00	**0.94**	N/A	N/A
log(plants)	**0.94**	1.00	N/A	N/A
CV bees	N/A	N/A	1.00	0.08
CV plants	N/A	N/A	0.08	1.00

rate of persistence as these communities. Values above two indicate much lower success rates in a scenario compared to the two-species, −1 germination correlation scenario [36].

I used the coefficient of variation in persisting populations-populations with a non-zero mean in the final 1000 timesteps-as a measure of population stability. Higher coefficients of variation are interpreted as lower stability. As before, I used germination rate × scenario groupings to understand the effects of species diversity and increasing germination correlation on stability. I calculated the average coefficient of variation in all germination rate × scenario groups. Then, I computed Cohen's *d* by comparing the difference in the CV of each germination rate × scenario group and the CV of the two-species, −1 germination correlation scenario. I made this comparison because I predicted the simulations with more species-specific responses would exhibit the lowest population variation. Values for Cohen's *d* can be positive or negative. Here, positive values indicate that a scenario has on average higher variation than the scenario with −1 germination correlation, and negative values indicate that a scenario has lower variation than those simulations. Absolute values of $d = 0.2$ or larger are conventionally considered meaningful differences in group means [36].

3. Results

I simulated $n = 30\,000$ plant and bee communities (5 mean germination rates × 1000 parameter sets × 6 germination correlation treatments). Because I used Latin hypercube sampling, results represent model responses across an evenly sampled swath of parameter space.

In two-species communities, realized germination covariance increased with prescribed germination correlation (electronic supplementary material, figure S4). Realized germination covariance was smaller in magnitude than prescribed germination correlation, though the signs were the same - negative correlations yielded negative germination covariance. This confirms that the manipulation of germination correlation resulted in a corresponding change in realized germination covariance. The two-species communities with germination correlation = −1 had the most species-specific (negative) germination covariance.

Partial correlation coefficients of model parameters with plant community or bee population abundance were generally low (table 2). Of these relationships, all values of Pearson's *r* were below 0.2 except for the positive relationship between bee abundance and λ_B, the maximum number of eggs per bee. Plant and bee abundances were the only variables that were highly correlated. Log-transformed abundances of plants and bees had a Pearson's $r = 0.94$, suggesting strong interdependence. Generally, bee and plant stability did not vary with model parameters, and Pearson's *r* values ranged from −0.01 to 0.05. The strongest relationship in terms of stability was between the CVs of bees and plants, but this was still quite negligible ($r = 0.08$, table 2).

Population persistence was almost exactly the same between bee populations and plant communities, where the number of successful, persisting communities declined with increasing germination correlation in two plant species communities (figure 2). All communities with two plant species had higher rates of persistence than single-species communities, irrespective of germination correlation. Of the 30000 simulation runs, 32% of both plant and bee populations persisted. In 165 simulations, bees or plants seemed to persist without their counterparts. In the case of plants persisting without bees, the seed bank likely maintained plant populations above one even after bee populations crashed. In both cases, the manner in which I calculated success/persistence also probably played a role; in some scenarios, a population average of plants was above zero but below one, and as such was assigned a 'zero' value for persistence despite continuing to support its bee counterpart. The outputs of these simulations do not qualitatively affect the following results.

Persistence of both bees and plants varied according to mean germination rate and scenario. In general, plant–plant facilitation via pollinator support was strongest in communities with low mean germination rates (mean $g = 0.02$ or 0.16; figure 2). In communities with the lowest plant germination rates (mean $g = 0.02$), persistence declined as germination correlation increased (figure 4), and bees and plants did not persist in single-species scenarios or two-species scenarios with germination correlation of 1 (that is, when the two species respond to the environment in the same way; figure 1). The risk ratios in communities with mean germination rates of 0.02 or 0.16 increased with the germination correlation treatment—as plant germination correlation becomes positive, risk ratios increase. At germination correlation of 0 and above, the populations with $g = 0.02$ and $g = 0.16$ exhibited significantly lower persistence as compared to the −1 germination correlation treatment (risk ratios above 2; figure 2).

Both plant and bees in the remaining scenarios—those with mean $g > 0.16$—generally persisted at lower rates with increasing germination correlation (figure 2). However, as germination rate increased, population persistence increased on average and risk ratios became negligible (figure 3). As population persistence increased with mean germination rate, it also became more similar between germination correlation treatments (figure 2). For example, in simulations with the highest mean germination rate, $g = 0.98$, persistence became nearly equivalent among scenarios. Risk ratios in high-germination scenarios were close to 1 across all germination correlation treatments, as well as single-species scenarios.

Plant community stability depended on mean germination rate and germination correlation treatment (figure 4). Stability (mean coefficients of variation) generally increased with

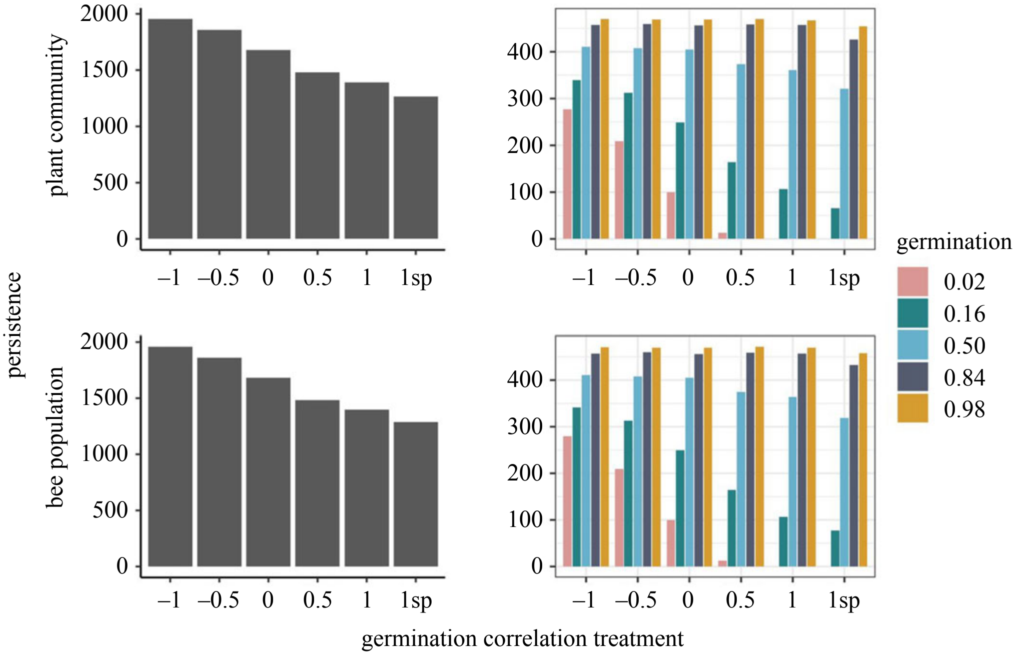

Figure 2. Population persistence in terms of number of successful populations. In the left two panels, populations of plants and bees have higher rates of persistence in two-species plant communities than single-species plant communities. The benefit of two-species plant communities on persistence is highest in communities with the lowest germination correlation. In the right two panels, overall trends in persistence are grouped by mean germination rate.

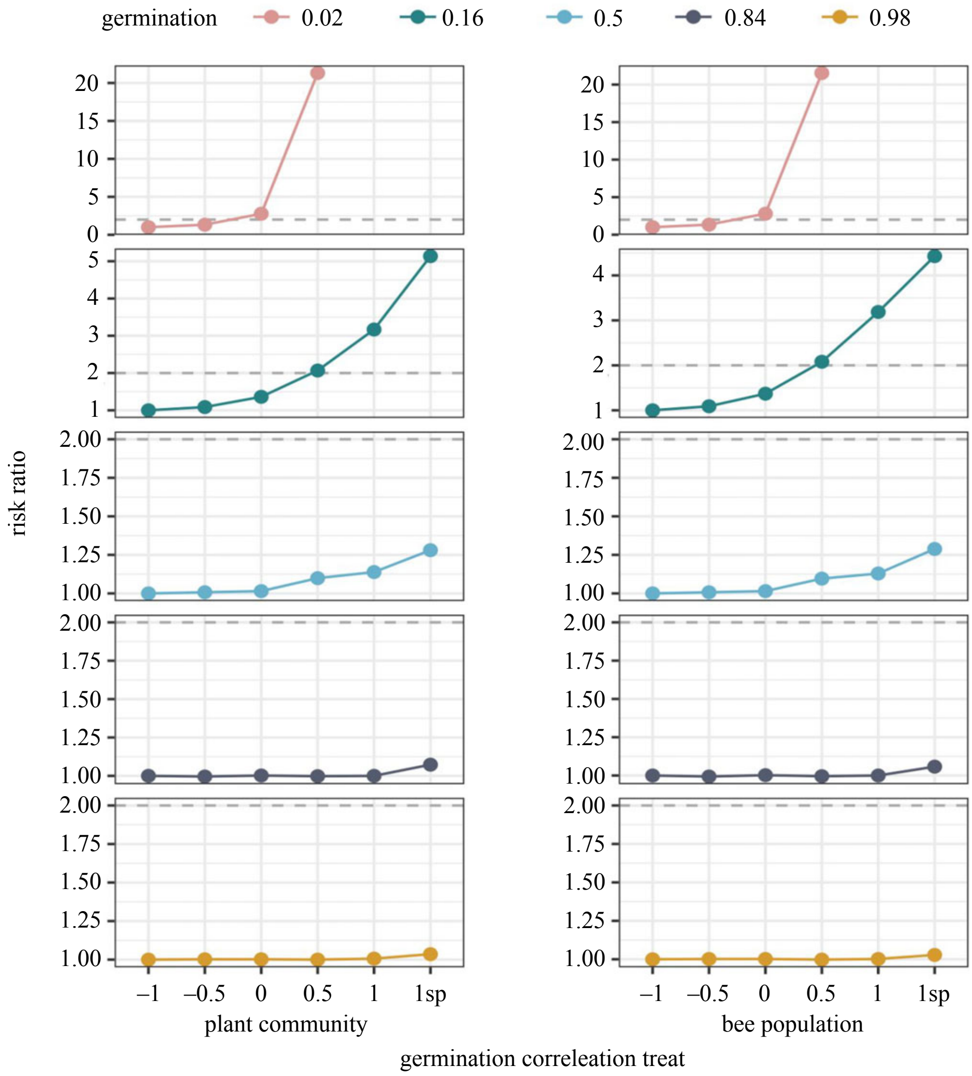

Figure 3. The risk ratios of each plant community treatment grouped by mean germination rate. Higher risk ratios indicate higher risk of the population crashing as compared to the reference group, which in this case was the treatment of two plant species with germination correlation = –1. In the case that no populations survived in a treatment group, the risk ratio is not depicted. Risk ratio values greater than or equal to 2 (dotted lines) indicate a meaningful difference in risk/persistence.

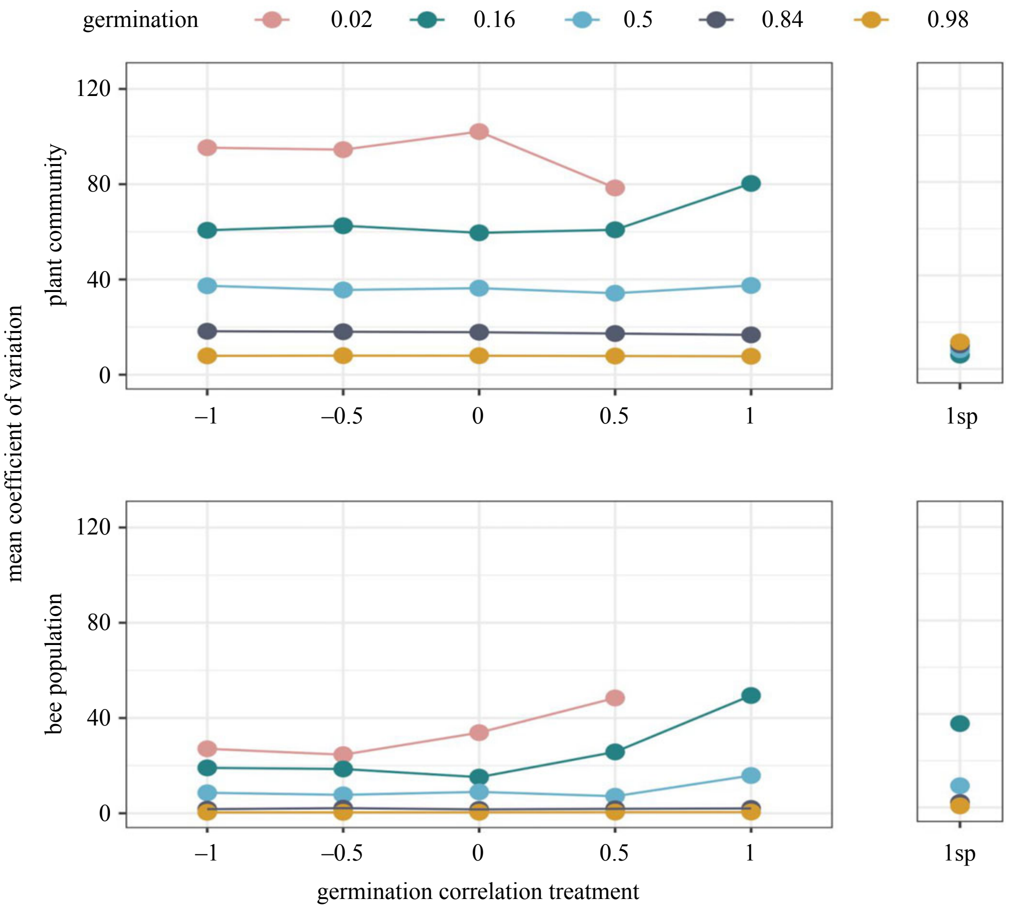

Figure 4. Mean coefficients of variation in successful (*a*) plant and (*b*) bee populations. Coefficients of variation (CVs) were calculated for all persisting populations using population size from the final 1000 timesteps in simulation runs. A lower mean CV indicates higher stability, on average.

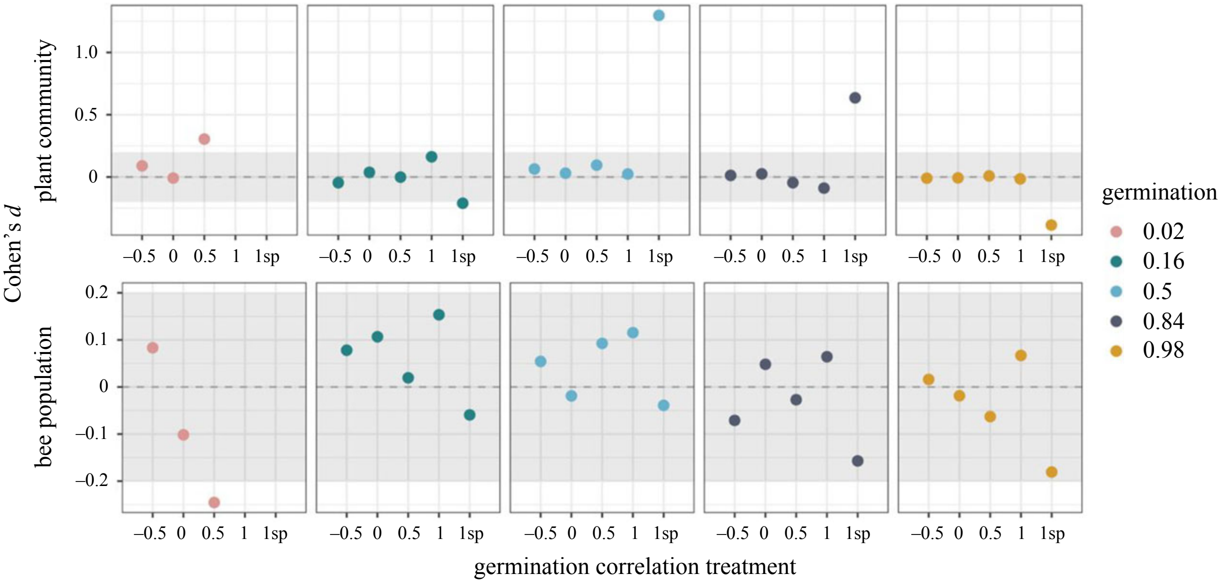

Figure 5. Cohen's *d* values comparing the difference in stability (mean coefficients of variation) between model treatments. Each point is the comparison of the germination correlation treatment with the reference treatment (two-species, −1 germination correlation). Values are grouped by mean germination rate. Negative values (values below the dashed line) indicate lower stability (higher variation) than the reference treatment. Values below 0.2 in magnitude are negligible differences in stability (grey areas).

increasing mean germination rates. Unexpectedly, single-species plant communities were often more stable than two-species communities across germination rates (figure 4); significantly so in communities with germination rates $g = 0.5$ and $g = 0.84$. In the lowest germination plant communities ($g = 0.02$), stability initially declined with increasing germination correlation in two species communities but increased abruptly (and significantly; figure 5) when germination correlation was zero. In the next-lowest germination communities ($g = 0.16$), stability declined with increasing germination correlation in two-species communities. Simulations with $g = 0.16$ were the only group of simulations to fully match the predictions regarding stability: more positive germination correlation communities trended towards lower stability compared to those with negative germination correlation (figure 4). With higher germination rates ($g = 0.5$, $g = 0.84$ and $g = 0.98$), this trend disappeared, and coefficients of variation became more similar across ass scenarios. As such, in most cases, two-species plant community stability did not change with germination correlation (figure 4). Cohen's d values reflect this: most values fell between –0.2 and 0.2, and were therefore negligible across all scenarios (figure 5).

Trends in bee population stability were slightly different than in plant communities. First, bee populations were more stable than plant communities: whereas plant communities' mean coefficients of variation reached values higher than 100, the mean coefficients of variation in bee communities did not surpass 60 (figure 4). Second, the stability of bee populations declined with increasing germination correlation in both low-germination two-species scenarios ($g = 0.02$ and $g = 0.16$; figure 4). Bee population stability did not vary among community scenarios where mean germination was greater than 0.5 (figure 4). As in the plant communities, bee population stability increased with mean germination rate: as mean germination increased, coefficients of variation generally declined irrespective of the community type (figure 4).

4. Discussion

Though empirical evidence of facilitation in natural communities is common and growing, we are still in the early stages of incorporating it into our theories of how plant interactions give rise to plant diversity maintenance. Pollinator sharing presents one avenue of investigation: not only is it a common way for plants to interact with each other, but a way for plants to potentially facilitate each other [12,15,26]. In this study, I have built a model to determine the potential for interspecific plant facilitation via inter-annual pollinator support. Despite being straightforward, this hypothesis is difficult to test empirically due to the paucity of longitudinal datasets of plant–pollinator communities across a range of plant community diversity. What I have shown is that pollinator-sharing plants mutually support pollinator populations through time, and as a result, diverse communities persist at higher rates than depauperate communities. As such, this work corroborates a specific mechanism of plant facilitation and diversity maintenance. Importantly, the work has also put a finer point on the conditions under which we might expect facilitation to occur as a result of inter-annual pollinator support: when plants exhibit strong species-specific responses to environmental variation and low germination fractions.

In the analysis, there were different ways that plants could potentially facilitate each other, where plant diversity could either increase population persistence, stability, or both. I observed a facilitative effect of plant species co-occurrence in community persistence, but not stability. Specifically, plant–pollinator communities persisted at higher rates in two-species plant communities compared to single-species plant communities. This effect declined with increasing mean germination rate in the simulations– i.e. community persistence became more similar among germination correlation and species diversity treatments with increasing germination rate. This is because when mean germination rate was high, the probability of bees having little or no resources available to them in a given year was low, irrespective of the number of species in the community. As a result, even single-species communities had similar rates of persistence to two-species communities in high-germination scenarios.

I found no evidence of interspecific facilitation in terms of stability, probably due to survivorship bias. Single-species communities persisted at lower rates than two-species communities, but tended to have greater stability than two-species communities in both plants and bees. Therefore, single-species communities likely did not persist unless they were more stable through time than their two-species counterparts. Survivorship bias also explains the discrepancy in results between the lowest-germination scenarios ($g = 0.02$) versus higher-germination scenarios ($g > 0.02$). In the lowest-germination scenarios, plant community stability initially declined with germination correlation treatment, but abruptly increased at germination correlation = 0.5 before communities crashed altogether (no persistence) at germination correlation = 1. Conversely, stability declined with increasing germination correlation at higher germination fractions. Together, these patterns suggest that extremely low germination fractions, paired with the year-to-year variability characterizing either high germination correlations or single-species plant communities, make for plant–pollinator systems that are too unstable to persist. Interestingly, this implies that to persist, plant communities can exhibit either high germination correlations or low germination fractions, but if they exhibit both, persistence is not viable—a plant community with both features cannot support a corresponding pollinator population through time. Further research into this result, especially in quantifying the way in which these two features trade off, would illuminate how stability varies according to these two distinct demographic responses to the environment.

The results presented in this work suggest that facilitation via pollinator support may occur anywhere three conditions are met: (1) plants exhibit species-specific responses to environmental variation and (2) low mean germination rates and (3) pollinator populations cannot persist through periods of low resource availability (e.g. a season where few flowers are produced). Though many systems may meet these criteria, arid environments might be the first place to look for evidence of pollinator support for a few reasons. First, high rates of seed dormancy (low rates of germination) are typical of unpredictable, arid environments, such as chaparral, Mediterranean, or desert ecosystems—environments often populated by annual flowering plants, as I have modelled [37–41]. Second, in arid environments, there is well-documented evidence of plant species-specific responses to variation in the amount and/or timing of seasonal rainfall, and variation in temperature [39,42–44]. Finally, and perhaps most importantly, arid environments consistently play host to the highest diversity of bees on Earth [45,46]. The vast majority of these are solitary bees that emerge as adults during flowering, build and provision nest cells with pollen, and then die—that is, exhibiting the demographic structure modelled in this study [46].

Testing the ideas explored in this paper might be most tractable in systems of pollinators that exhibit plant specialization along some axis—for example, by selecting a pollinator that is specialized on a family or genus, or floral phenotype (e.g. long-tongued bees). Focusing on a specialist pollinator and its plant hosts would make measuring the inter-annual abundance of plant and pollinator species a more manageable task. This is because a study designed to explore the ideas in this work would have to include multiple locations that vary in plant host diversity. The important data to gather would be the floral abundance of the relevant species, the covariance in plant species abundance through time, and pollinator population abundance, through multiple years or growing seasons. In systems of plants with relatively low germination rates, the results of this model would suggest that the effects of plant diversity and covariation in floral abundance will dictate the persistence of the pollinator species of interest.

The benefit of multi-species plant assemblages was maximized in communities with negative germination correlation (i.e. species-specific responses to variation in the environment). These results, therefore, have implications for how pollinator support can be explicitly tied into plant coexistence theory. In coexistence theory, the storage effect can enhance coexistence in variable environments when: (1) competing species have species-specific responses to environmental variation, (2) there is positive covariance between the environment and the amount of competition a species experiences and (3) populations have buffered population growth, or the ability to 'save up' the benefits of a good environment for later (e.g. through seed survival in a seed bank), which then mediates the negative effects of bad years [47,48]. Though this study was not an explicit test of the storage effect, the model did have necessary components for the storage effect to contribute to coexistence. Model results suggest that if the storage effect operates in communities of flowering plants, it may yield the added benefit of facilitation via pollinator support. To disentangle the extent to which the storage effect is related to pollinator support, follow-up simulation modelling could quantify the storage effect and its relationship to community persistence in pollinator-sharing plant communities (e.g. [11]).

Finally, while conceding that this is a very simple model, this study demonstrates an important idea: that competition and facilitation can both simultaneously be at play in a system, and are likely both relevant for plant diversity maintenance. Facilitation has been classically overlooked in studies of diversity maintenance in part because it results in unwieldy, runaway dynamics in the simple Lotka-Volterra models that are standard fare in coexistence theory [49,50]. In the model, I separated competitive interactions and interactions with pollinators into two different ontogenetic stages—growth and pollination—and found that interactions with pollinators determined in large part the maintenance of the entire community due to inter-annual plant–plant facilitation, despite the existence of intra-annual plant–plant competition during vegetative growth. That being said, competitive interactions may occur over pollination due to interspecific pollen transfer or pollinator niche partitioning [16–19,51,52], which was not included in the model. Furthermore, I did not vary the strength of interspecific competitive interactions in the simulations; as such, the relative importance of facilitation versus competition in the results remains unexplored. Future iterations of this model might elucidate how competition over pollination, or competitive hierarchies, might affect plant diversity maintenance when pollination support is at play.

We are in large part still in the nascent period of understanding the full scope of how facilitation might affect plant diversity maintenance. However, given the urgency of maintaining species diversity in the face of ongoing climate disaster [53], it is imperative to explore all types of interspecific interactions and how they might contribute to community diversity and persistence. Here, I have provided evidence with a proof-of-concept simulation model that facilitative interactions between plants can be integral in maintaining species diversity, and that plant and pollinator population dynamics should be studied together to understand plant community diversity. With this study I hope to add to a line of inquiry that incorporates a rich diversity of interactions into population models, which can illuminate the multifarious ways in which plant diversity is maintained in natural communities.

Data accessibility. Code generates data, all of which can be accessed on the author's GitHub at https://github.com/slaubrie/apparent-facilitation.git.

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.866t1g1tq [57].

Additional data are provided in electronic supplementary material [58].

Authors' contributions. A.R.M.J.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing.

Conflict of interest declaration. I declare I have no competing interests.

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