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SPECIAL FEATURE: EMPIRICAL PERSPECTIVES FROM MATHEMATICAL ECOLOGY

Pollinator declines and the stability of plant–pollinator networks

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Abstract. Population declines of pollinators constitute a major concern for the fate of biodiversity and associated ecosystem services in a context of global change. Massive declines of pollinator populations driven by habitat loss, pollution, and climate change have been reported, whose consequences at community and ecosystem levels remain elusive. We conducted a mathematical modeling and computer simulation study to assess the dynamic consequences of pollinator declines for the biodiversity of plants and pollinators. Specifically, we evaluated the effects of increased mortality and decreased carrying capacity of specialist vs. generalist and effective vs. ineffective pollinators visiting specialist vs. generalist plants on long-term community biomass and species persistence. Our results reveal that increased larval mortality and increased competition for space among larvae had the greatest impacts on the decline of pollinator diversity. In contrast, the largest sustained decreases in pollinator biomass were driven by increased adult mortality in spite of a small increase in pollinator species persistence. Decreased pollinator diversity led in turn to decreased plant diversity. Attacking pollinators with high degree and connected mostly to low-degree plants produced the greatest losses of plant diversity. Pollinator effectiveness had no noticeable effect on persistence. Our results illuminate our understanding of the consequences of pollinator declines for the maintenance of biodiversity.

Key words: dynamic models; plant–pollinator networks; pollination; pollinator decline; Special Feature: Empirical Perspectives From Mathematical Ecology.

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INTRODUCTION

Many plant species depend on pollinators for reproduction. A large proportion of plants in natural ecosystems worldwide are pollinated by animals, mostly insects, and would not be able to reproduce without them (Kearns et al. 1998, Ollerton et al. 2011). The yield and the quality of many crop species also depend on animal pollinators (Aizen et al. 2009, Garibaldi et al. 2013, Potts et al. 2016). In turn, many animal species depend partially or completely during their life cycle on floral resources (Kearns et al. 1998).

There is increasing evidence that many pollinator species are declining, becoming geographically restricted, and, in some cases, going extinct

(Kearns et al. 1998, Vanbergen 2013, Sánchez-Bayo and Wyckhuys 2019). These declines constitute a major concern for the fate of biodiversity in a context of global change. The drivers of these declines include agricultural intensification and other forms of land use change, pesticides, pathogen transmission, alien species, and climate change (Bommarco et al. 2012, Bartomeus et al. 2013, González-Varo et al. 2013, Morales et al. 2013, Vanbergen 2013, Goulson et al. 2015, Potts et al. 2016, Sánchez-Bayo and Wyckhuys 2019). Given the high dependence of many plant species on animal pollination, these declines are expected to affect the pollination and reproduction of many plant species in both natural and agro-ecosystems (Kearns et al. 1998, Vanbergen 2013, Potts et al. 2016).

Yet, in spite of the potential importance of pollinator declines for the maintenance of biodiversity and the world's agriculture, the community-level consequences of such declines are poorly understood. Model-based studies suggest that some topological features of plant–pollinator networks make them particularly robust to perturbations. Key network attributes favoring robustness include nestedness (Memmott et al. 2004, Thébault and Fontaine 2010) and asymmetric interaction strength (Bascompte et al. 2006). However, the conclusions of ecological studies based on mathematical models may depend heavily on the assumptions being made. For example, debates, such as Kondoh (2003) vs. Brose et al. (2003) with respect to food web structure, Mougi and Kondoh (2012) vs. Suweis et al. (2014) with respect to functional responses, and Arditi et al. (2016) vs. Ramos-Jiliberto and Moisset de Espanés (2017) with respect to migration functions, show that slightly modifying assumptions can lead to different results. In the field of plant–pollinator networks, several alternative dynamic models have been proposed (Vázquez et al. 2015, Valdovinos 2019), which suggests that some of the conclusions of past studies might change if the same questions were re-examined with different modeling approaches. Arguably, mechanistic models of plant–animal mutualistic interactions are more appropriate to describe the dynamics of such communities than simpler, phenomenological models (Valdovinos 2019). Therefore, for this study we used a modified version of a model we developed previously (Ramos-Jiliberto et al. 2018) that accounts for key mechanisms involved in the mutualistic interaction between plants and their pollinators. These mechanisms include consumption of floral resources, development and latency of plants and pollinators, and phenology of insect recruitment and flowering. This approach contrasts sharply with the more phenomenological models commonly used for representing plant–pollinator interactions (reviewed in Vázquez et al. 2015), in which the mechanisms of the mutualistic interaction are hidden in favor of model simplicity.

Here, we present the results of a computer simulation study aimed at assessing the dynamic consequences of pollinator declines for the biodiversity of plants and pollinators. Specifically, through the use of a dynamic model for mutualistic interactions applied to an empirical plant–pollinator network, we evaluate the effects of increased mortality and decreased carrying capacity of specialist vs. generalist and effective vs. ineffective pollinators visiting specialist vs. generalists plants on the long-term community biomass and species persistence. Our results illuminate our understanding of the consequences of pollinator declines for the maintenance of biodiversity.

METHODS

Population dynamics

We built a dynamic model as a set of coupled ODEs. This system is a particular case of a more general integro-differential model published in Ramos-Jiliberto et al. (2018). Our model is of a semi-discrete type (Pachepsky et al. 2008, Mailleret and Lemesle 2009), which is suitable to account for phenological and synchrony effects in host–parasitoid interactions (Godfray et al. 1994), consumer–resource modules (Revilla et al. 2014), and life history (Zonneveld 1992). Each plant species is described by five state variables: adult reproductive plants (V), immature seeds (I), mature seeds (S), flowers (F), and floral resources (N). For simplicity, pollinators are assumed to be composed only by insect species and are described by three state variables: active adult pollinators (A), immature larvae (E), and mature larvae (L). The transitions between the state variables are depicted in Fig. 1.

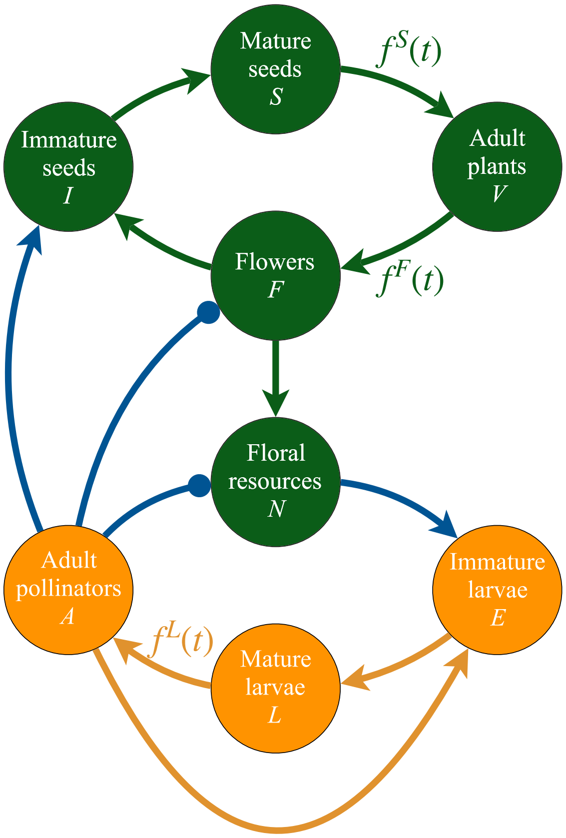

Fig. 1. Graphical representation of the basic structure of our dynamic model. Circles represent state variables (name and symbol used in formulae are shown). Lines ended in arrows/circles indicate a positive/negative effect of one variable on another. Green/orange lines indicate life cycle transitions within plant–pollinator species. Blue lines represent interactions between plants and their visiting pollinators. Self-effects are not shown for simplicity. Those transitions labeled with $f(t)$ are governed by time-dependent functions. In these functions, superscripts S, F, and L indicate germination, flowering, and pollinator recruitment, respectively.

All state variables are measured in biomass density, and their values vary over chronological time t. We define t as a continuous variable measured in weeks. Thus, $0 \leq t \leq Y$, where parameter Y is the length of the year measured in weeks. We also use integer superindex T to indicate the year each state variable corresponds to. Throughout the model description, we will use i and j to indicate plant and pollinator species, respectively.

Mature seeds and larvae transit to adult states when they match the appropriate subseason where environmental conditions are favorable for germination/recruitment. In our model, adult plants can produce flowers and flowers produce floral resources only during certain period of the year. Adult pollinators visit flowers and consume floral resources. After visitation, fertilized flowers are not available to pollinators anymore and immature seeds and larvae are produced (Fig. 1). Environmental favorability for germination, flowering, and pollinator recruitment is described by time-dependent functions named here as "phenology functions," $f(t)$, which govern timing and intensity of occurrence of phenological events: $f(t)^S$ for germination, $f(t)^F$ for flowering, and $f(t)^L$ for pollinator recruitment. Phenophase dates for plant flowering and pollinator recruitment were taken from our field records (see *Model parameterization and simulation* below), whereas dates for germination phenophases were assumed. We will first describe the dynamics of the system during year T, and later on, we will define the inter-annual transitions. In Appendix S1: Tables S1, S2, we give definitions of state variables and model parameters. Temporal dynamics of immature seed biomass is given by:

$$\frac{dI_i^T}{dt} = \sum_j \pi_{ij}\varphi_{ij} - \mu_i^S I_i^T. \tag{1}$$

Seed production is proportional to visitation rate (φ) of pollinators with biomass A_j^T to flowers with biomass F_i^T. Pollination effectiveness (π) represents the conversion rate of visits into seed biomass. The second term represents immature seed mortality, where μ_i^S is the mortality rate per unit seed biomass. Mature seed dynamics is given by

$$\frac{dS_i^T}{dt} = -\sigma_i f_i^S(t) S_i^T - \mu_i^S S_i^T. \tag{2}$$

Germination phenology is governed by function $f_i^S(t)$, which is a smoothed rectangular pulse with height equal to 1 and width equal to 30 weeks. We assume all plant species have the same germination phenology. These are qualitatively consistent with our empirical observations at the study site. The beginning of germination, that is, the rising edge of the pulse, is located 12 weeks before the latest flowering season end among all species. The second term represents mature seed mortality. For simplicity, we assume the mortality rate for mature and immature seeds is the same. Biomass density growth rate of adult plants is given by:

$$\frac{dV_i^T(t)}{dt} = \left(1 - \alpha_{ii}V_i^T - \sum_{k\neq i}\alpha_{ik}V_k^T\right) v_i \sigma_i f_i^S(t) S_i^T - \mu_i^V V_i^T, \tag{3}$$

where plant biomass production due to seed germination is limited by competition for space, represented by the factor within parenthesis. This factor is the same as the one used in the classic competitive Lotka-Volterra equations. The $\alpha_{ii}V_i^T$ term represents the strength of intraspecific competition, while the summation term over all plant species *k* other than *i* is the interspecific competition. The last term of the equation is plant mortality rate. Dynamics of flower biomass density is given by:

$$\frac{dF_i^T(t)}{dt} = r_i^F \cdot \left(\kappa_i V_i^T - F_i^T\right) f_i^F(t) - \sum_j \gamma_{ij}\varphi_{ij} - \hat{\mu}_i F_i^T, \tag{4}$$

with mortality rate $\hat{\mu}_i = \left(\mu_i^F + \rho_i^F \left(1 - f_i^F(t)\right)^2\right)$, composed by basal mortality μ_i^F and added seasonal mortality related to *f*(*t*). This added mortality impedes flowers to persist beyond the flowering season. The first term of the equation represents the increase in flower biomass, limited by plant biomass. The second term is the removal of fertile flowers due to fertilization. The third term is mortality rate, explained above. Biomass dynamics of floral resources is given by:

$$\frac{dN_i^T(t)}{dt} = r_i^N \cdot \left(q_i F_i^T - N_i^T\right) - \sum_j \delta_{ij}\varphi_{ij} \cdot \left(\frac{\frac{N_i^T}{F_i^T}}{\varepsilon_{ij} + \frac{N_i^T}{F_i^T}}\right), \tag{5}$$

where the first term represents the increase in floral resources, which is limited by flower biomass. The second term represents resource consumption by pollinators. Resource consumption is determined by visitation rate φ and the amount of resources extracted by pollinators in each visit. Resource extraction per visit is a saturating function of resources per unit flower. Biomass growth rate of immature larval pollinators is given by the equation:

$$\frac{dE_j^T}{dt} = \left(1 - \omega_{jj}\left(E_j^T + L_j^T\right) - \sum_{k\neq j}\omega_{jk}\left(E_k^T + L_k^T\right)\right)$$
$$\sum_i \eta_{ij}\delta_{ij}\varphi_{ij} \cdot \left(\frac{\frac{N_i^T}{F_i^T}}{\varepsilon_{ij} + \frac{N_i^T}{F_i^T}}\right) - \mu_j^L E_i^T,$$

that has the same structure as Eq. 1 for seeds, plus a factor representing competition for space within and among species. We assume space limitation among pollinator larvae given that, unlike adults, they are usually sessile and long-lived stages. These processes are regulated by parameters ω_{ii} and ω_{ij}.

Mature larvae follow the equation

$$\frac{dL_j^T}{dt} = -\chi_j L_j^T f_j^L(t) - \mu_j^L L_i^T. \tag{7}$$

The first term represents insect larval maturation into adults. χ_j is the recruitment rate. The second term models mortality. Biomass density dynamics of adult insects is governed by:

$$\frac{dA_j^T}{dt} = y_j \chi_j L_j^T f_j^L(t) - \hat{\mu}_j^A A_j^T, \tag{8}$$

where y_j is the conversion factor from larvae to adult biomass. Mortality rate $\hat{\mu}_j^A = (\mu_j^A + \rho_j^A (1 - f_j^L(t))^2)$ is similar to the one used in Eq. 3. However, for adult insects, there is no competition for space and there is seasonal mortality. Visitation rate of flowers by pollinators was modeled as a Beddington-DeAngelis-like functional response (Fishman and Hadany 2010):

$$\varphi_{ij} = \frac{\tau_{ij} A_j^T F_i^T}{\beta_{ij} + a_{ij} \sum_{k \in R(j)} F_k^T + b_{ij} \sum_{l \in C(i)} A_l^T} \Pi_{ij}^T(F), \tag{9}$$

where $R(j)$ is the set of plant species visited by pollinator j, and $C(i)$ is the set of pollinator species that visit plant i. Here, we added a factor $\Pi_{ij}^T(F) = F_i^T / \sum_{k \in R(j)} F_k^T$, which represents the fraction of time pollinators allocate to each resource species. Finally, the between-years dynamics of seeds is governed by

$$S_i^T(0) = I_i^{T-1}(Y) + S_i^{T-1}(Y), \tag{10}$$

$$I_i^T(0) = 0. \tag{11}$$

The equations above simply mean that the mature seed biomass at the beginning of year T is the sum of the mature and immature seed biomasses at the end of year $T-1$. This assumes that all immature seeds mature during the transition from one year to the following one. Equivalently, inter-annual dynamics for larvae is

$$L_i^T(0) = E_i^{T-1}(Y) + L_i^{T-1}(Y), \tag{12}$$

$$E_i^T(0) = 0. \tag{13}$$

Parameter values were drawn from random uniform distributions. The center of these distributions was based on values taken from available studies on some species (Brian 1952, Cruden and Lyon 1985, Waser and Price 1994, Tilman et al. 1996, Ishii and Harder 2012). The width of the distributions was set to 50% of their means.

Numerical experiments

We consider two causes for pollinator population decline. The first one is loss of habitat, which corresponds to increasing the strength of space competition among pollinators ω_{ij}. The second one is an increase in mortality rates (Sánchez-Bayo and Wyckhuys 2019). In our model, this corresponds to increasing mortality μ_A of adults and/or mortality μ_L of latent stages. Let n be the number of pollinator species. Given a sequence $(S_i)_{i=1}^n$ of pollinator species, we apply pressure with increasing magnitude to the chosen target. This magnitude ranges linearly from real parameter $P \geq 1$ (maximum for S_1) to 1 representing no pressure being exerted on S_n. More formally, to apply a pressure on a parameter $\text{par} \in \{\omega_{ij}, \mu_A, \mu_L\}$ corresponding to species S_k, the adjusted value is computed as $\text{par}^* = \text{par} \cdot (1 + (n-k)(P-1)/(n-1))$. We conducted 10 treatments (see Table 1). For treatments 0–7 (selective pressure), the order of species in S depends on the combination of three attributes of pollinators. The first one is pollinator effectiveness (parameter π), the second one is pollinator degree (number of interacting plant species, deg), and the third attribute is mean neighbor degree, degN. For treatment 8, S is a random permutation of the pollinator species. This represents non-selective penalization. For treatment 9, $P = 1$, which implies no species is penalized (control).

Treatments 0–7 can be viewed as a 3-factorial experiment. In each treatment, we apply higher pressure to pollinator species exhibiting a combination of attributes, which is closer to a specified profile (see Table 1). For example, in treatment 1, we apply higher pressure to species with lower values for degree, lower average neighbor degree, and higher values for π. For this purpose,

Table 1. Description of treatments used in our experimental design: degN, mean degree of neighbors; deg, degree of target species; π, pollinator effectiveness.

Treatment	degN	deg	π
0	Low	Low	Low
1	Low	Low	High
2	Low	High	Low
3	Low	High	High
4	High	Low	Low
5	High	Low	High
6	High	High	Low
7	High	High	High
8	NSP	NSP	NSP
9	Control	Control	Control

NSP, non-selective pressure treatments.

we model the 3D attribute space as a unit cube. Each axis represents the 0–1 normalized value of each attribute of pollinator species. Each vertex corresponds to a different treatment, that is, a combination of high/low value for each attribute. Given a treatment, we define S by sorting the pollinator species by their Euclidean distance to the appropriate vertex. In summary, we induce pollinator population decline by applying pressure on three different target parameters (individually). We select the target species according to alternative criteria: completely random selection and proximity to each of the eight vertices of the cube representing the attribute space. Finally, there is a control treatment that involves no pressure. For each one of the ten treatments, we run 30 replicates. Each replicate consists of a single time series generated by integrating the ODE model described in Subsection *Population dynamics*.

Model parameterization and simulation

We obtained numerical solutions for the equations using the *ode23* function of MATLAB R2018b limiting the maximum step to one week and with tolerances specified in Appendix S1: Table S1. We run every instance for 5000 weeks of simulated time. We used an empirical network structure described in Chacoff et al. (2018) for the year 2011 as a base for our dynamic system. This network consists of 112 pollinator and 46 plant species. Its connectance is 0.097. Initial values of biomass densities were obtained randomly from uniform distributions, centered at specific values for each state variable (Appendix S1: Table S1). State variables were forced to zero whenever their biomass density decreased below certain threshold (Appendix S1: Table S1). At the same time, a species was considered extinct when all their state variables fell down to zero. For each replicate, the parameter values were randomly drawn from uniform distributions, centered in values taken from biologically plausible estimates or based on available literature. These values are shown in Appendix S1: Table S2. For each replicate, a transient simulation was run until the system reached an asymptotic oscillatory behavior, which can be considered analogous to the steady behavior in classical autonomous dynamic models. The number of species persisting at the end of this transient dynamics was recorded and used as the initial species richness for the post-transient phase. When using biomass as response variable, we show the average value over all species and over the last 52 weeks of the simulation. We conducted sensitivity analysis for both model parameter values and network structure. For the first one, we increased the variability of parameter values around their mean: 10%, 25%, 50%, and 75%. Sensitivity to network structure was conducted by running the same experiments for two additional networks from the same location but sampled at different years: 2009 and 2010 (Vázquez et al. 2009, Chacoff et al. 2018). The first one has 103 pollinator and 37 plant species with a connectance of 0.085, while the second one has 65 pollinator and 36 plant species with a connectance of 0.095.

RESULTS

Species persistence

When increasing adult pollinator mortality, μ^A, species persistence (for both plants and pollinators) remained mostly unaffected with respect to the control. For plants, the response was stronger than for pollinators. Plant persistence in treatments 2 and 3 decreased by 0.14 with respect to control, while pollinators even increased their persistence (Fig. 2, top row). When increasing larval mortality μ^L and space competition ω (Fig. 2, middle and bottom rows), species persistence dropped for both plants and pollinators. However, for plants, the attributes of the pollinators being attacked determine the levels of persistence decrease. For the three target parameters, the most affected plant persistence was that corresponding to generalist species with specialist pollinators (treatments 2 and 3), followed by generalist species with generalist pollinators (treatments 6 and 7) and specialist species with specialist pollinators (treatments 0 and 1). The least affected were specialist species with generalist pollinators (treatments 4 and 5). The effect of applying pressure to randomly selected species (treatment 8) resulted in an intermediate-level effect similar to that observed for treatments 0 and 1. Pollinator effectiveness π had negligible effects on the persistence of plant and pollinator species. The strongest effect on pollinator persistence was obtained by increasing space competition ω.

Adult plant and pollinator biomasses

Adult plant biomasses were largely insensitive to both treatments and the choice of target parameters (Fig. 3). The greatest effects were observed when increasing space competition ω. Regarding the different treatments, their respective effects exhibited a reverse rank as compared to their effects on species persistence. When increasing adult mortality μ^A, pollinator biomass decreased almost linearly, with little differences among treatments. When increasing larval mortality μ^L, pollinator biomass became U-shaped with a minimum around $P = 10$. Here, we obtained the highest biomass values for treatments 4, 5, and 8. There were not noticeable differences among the rest of the treatments. Increasing ω yielded an almost linear increase in pollinator biomass. The rank of effects by treatment followed the same pattern as that obtained when increasing larval mortality μ^L.

Seed and larval biomasses

As shown in Fig. 4, seed biomass was only slightly sensitive to increases in adult mortality μ^A, exhibiting a small decrease for stronger pressures. There were minimal differences among all

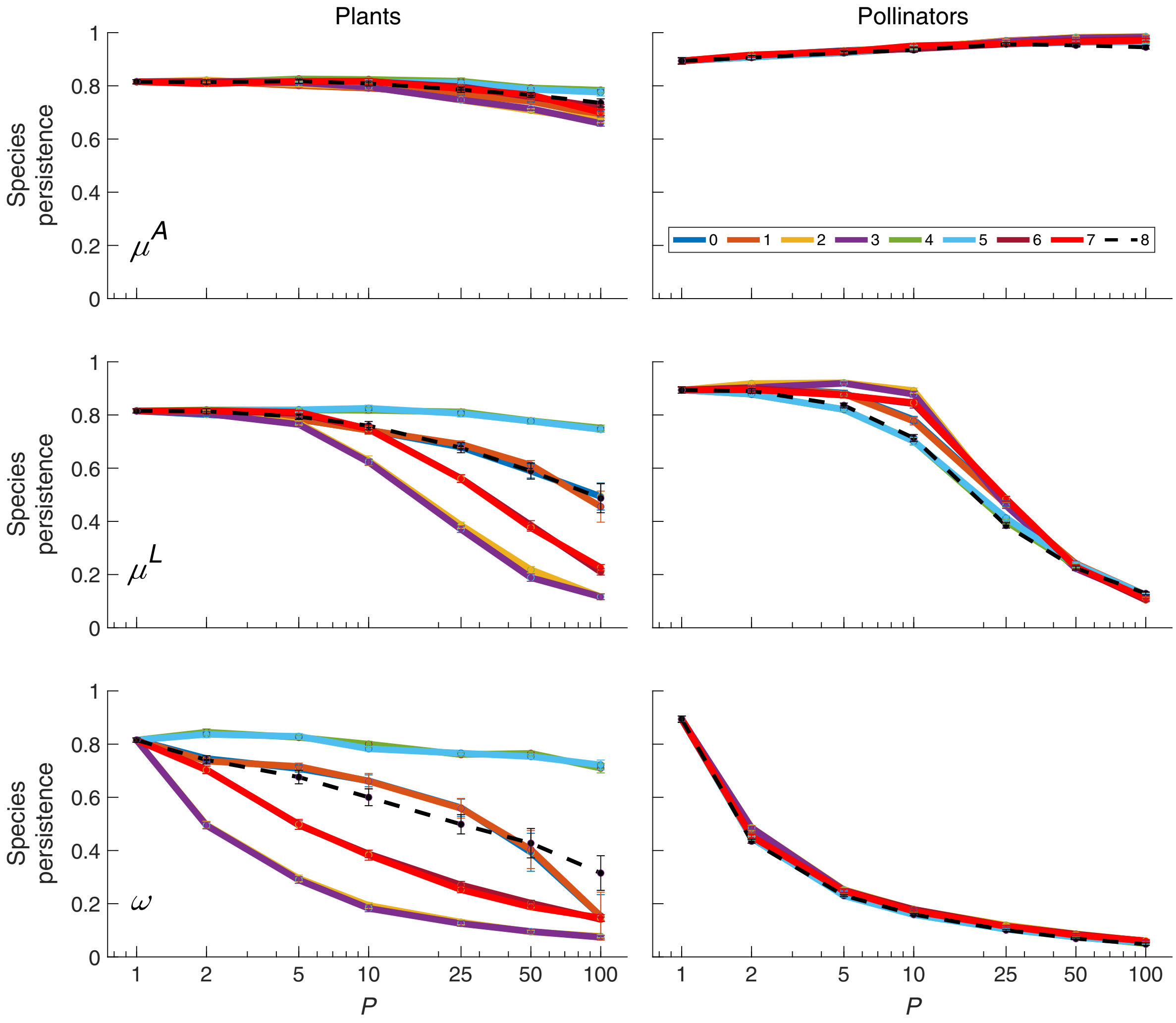

Fig. 2. Species persistence of plants and pollinators as a function of maximal pressure intensity P on pollinator species. Pollinator parameters experimentally affected were as follows: adult mortality μ^A, larval mortality μ^L, and space competition ω. Line colors show treatments 0–8.

treatments. Similarly, seed biomass was not very sensitive to increasing larval mortality μ^L. Only for high pressure intensities, we observed differences among treatments. The highest values for seed biomass corresponded to treatments 2, 3, and then 8. When increasing space competition ω, we observed a slight increase in seed biomass for treatments 2, 3, and 8. For the other treatments, seed biomass exhibited a U-shaped response. Larval biomass was insensitive to μ^A but increased with μ^L and ω. For the three target parameters, we observed little differences among treatments.

Sensitivity analysis

Our results were robust to random changes in the parameter values. The results displayed in Appendix S2: Fig. S1–S3 show consistent trends in mean values with moderate increases in 95% confidence intervals after raising the range of random variation in parameter values and initial conditions. Moreover, after repeating the simulations for the two additional networks, we obtained essentially the same results. This can be seen by comparing Appendix S3: Figs. S1–S6 against Figs. 2, 3, and 4.

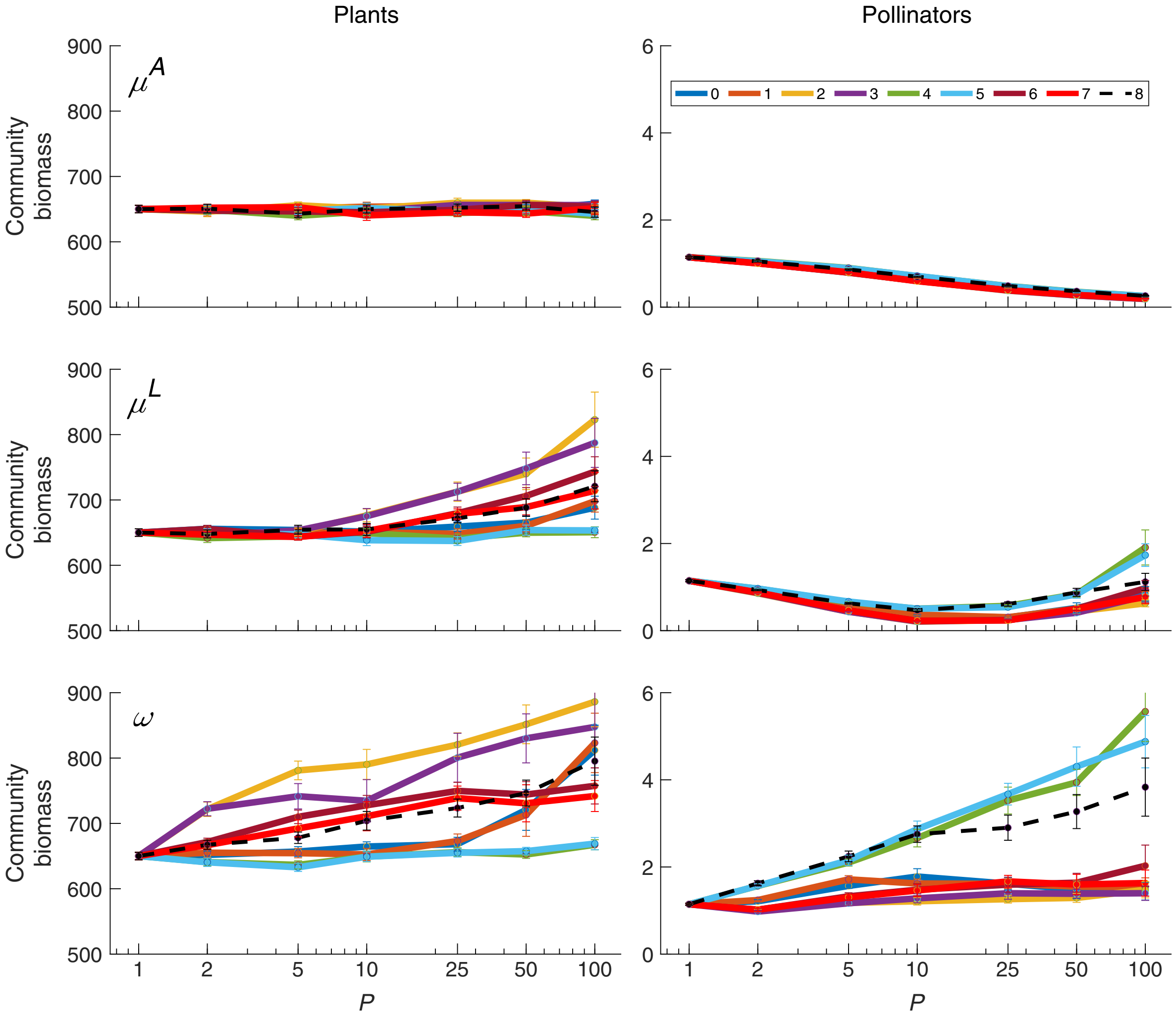

Fig. 3. Asymptotic community biomass of adult plants and pollinators as a function of maximal pressure intensity P on pollinator species. Pollinator parameters experimentally affected were as follows: adult mortality μ^A, larval mortality μ^L, and space competition ω. Line colors show treatments 0–8.

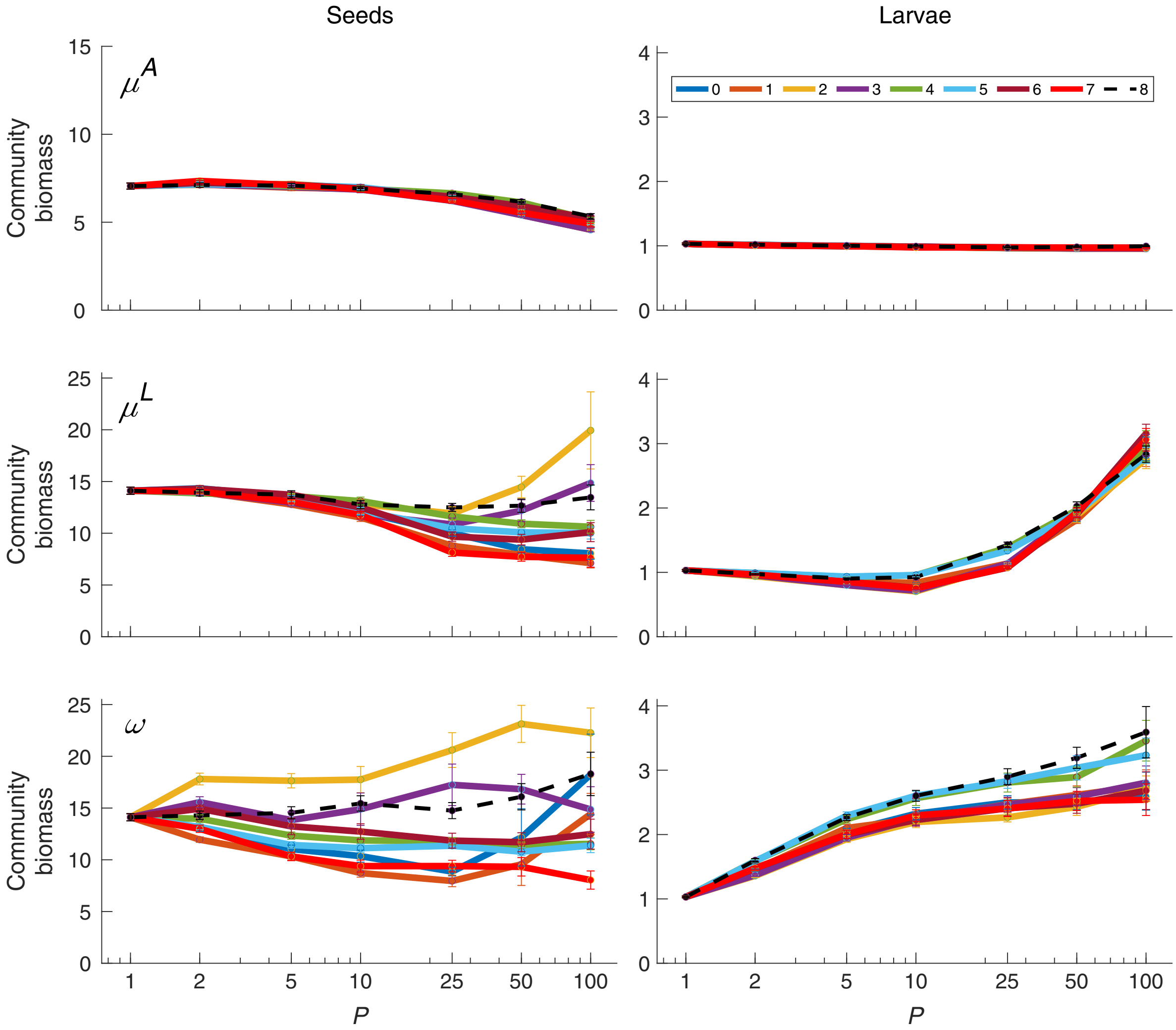

Fig. 4. Asymptotic community biomass of seeds and pollinator larvae as a function of maximal pressure intensity P on pollinator species. Pollinator parameters experimentally affected were as follows: adult mortality μ^A, larval mortality μ^L, and space competition ω. Line colors show treatments 0–8.

DISCUSSION

Our results reveal that among the tested drivers for pollinator decline, increased larval mortality and increased competition for space among larvae had the greatest impacts on the decline of pollinator diversity. In contrast, the largest sustained decreases in pollinator biomass were driven by increased adult mortality in spite of a small increase in pollinator species persistence. Decreased pollinator diversity led in turn to decreased plant diversity. Yet, the type of pollinators under experimental attack greatly influenced plant persistence but did not noticeably affect pollinator persistence: Attacking pollinators with high degree and connected mostly to low-degree plants produced the greatest losses of plant diversity. Conversely, the smallest effects were obtained when attacking pollinators combining low-degree and visiting high-degree plants. Pollinator effectiveness had no noticeable effect on species persistence.

A striking result of our simulation experiment is that persistence of pollinator species did not correlate directly with community biomass. Furthermore, for most of our experiments total biomass increased with decreasing species persistence. This pattern was especially noticeable when attacking pollinators combining low-degree and visiting high-degree plants. A similar, but weaker, trend was observed for plants: When attacking pollinators combining low effectiveness, and high-degree and visiting low-degree plants, plant persistence correlated inversely with biomass. This negative correlation between plant persistence and biomass occurred when using larval mortality and space competition as target attributes. Previous studies have reported both direct and inverse relationships between community biomass and species richness (Bhattarai et al. 2004, Weis et al. 2007, Maynard et al. 2017), and strong interspecific competition seems to be responsible for negative relationships between community biomass and species richness (Maynard et al. 2017). In our model, pollinators compete for space for larval settlement (Eq. 6) and for floral resources through visits (Eq. 9), while plants compete for space (Eq. 3) and for pollinator visitation (Eq. 9). In this competitive context, decreased species richness caused by experimental drivers of pollinator decline led to increased abundance of more tolerant species, which compensated, and sometimes overcompensated, the biomass loss caused by local extinctions.

We favored using a relatively complicated set of ODEs because of the issues we mentioned in the previous paragraph. Since competition seems to have a paramount importance on the community biomass vs. species richness relation, we were keen to describe competition relation in detail. Modeling competition for pollinator visitation and resources motivated us to include flower biomass (F) and floral resources (N) as state variables. Moreover, modeling resource depletion and flower biomass losses because of fertilization added stability to the model. It is well known that simpler models for plant–pollinator systems, say based on Lotka-Volterra equations (see Vázquez et al. 2015, for a review of models), tend to be unduly unstable due to the mostly positive interactions present between pairs of species. Another advantage of the mechanistic approach we took is that many parameters can be estimated from measured biological quantities already published. Our equation constants are derived—within reasonable intervals—from previously observed visitation rates, flower biomasses, nectar per flower, number of flowers per plant, and so on. The drawbacks of using a complicated set of ODEs are having to adjust a larger set of parameters and limiting the possibility for tackling the equations analytically.

Our study offers insights about how the current pollinator crisis may operate to influence community dynamics and persistence. The three drivers of pollinator decline manipulated in our simulation experiments—larval and adult mortality and competition for space—had detectable effects on different community attributes, suggesting that different drivers of global change may affect community dynamics and stability in important, albeit different, ways. For example, our simulation results suggest that habitat destruction, in the extent that it leads to increased competition for space, may have strong detrimental effects on pollinator diversity, while pesticides, pathogens, and other drivers of global change that operate through increased larval and adult mortality may influence both pollinator diversity and biomass, which in turn can influence plant diversity.

Our study highlights that, for biodiversity conservation, lethal effects on larval pollinators and habitat destruction for larvae are most critical, as compared to adult survival. The high importance of larvae over adults for system integrity was also noted in Ramos-Jiliberto et al. (2018). Among pollinator larvae, the most influential ones for system stability are those whose adults visit many plant species that have few connections to other pollinators. This subset of species and developmental stages should be considered with special attention in conservation plans, in order to promote both natural ecosystem maintenance and crop production. The decline in pollinator populations is likely to continue. Therefore, it is of great relevance to disentangling the set of causes, conditions, and mechanisms by which this global pressure is affecting natural and crop ecosystems. Future studies should improve our understanding of this aspect of ecological functioning, vital for human well-being.

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