Title: The equalizing effect of adaptive foraging increases plant coexistence in plant-pollinator networks

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Abstract

Environmental changes have impacted specialist species promoting their replacement by generalists, consequently driving functional homogenization with potential implications for ecosystem function. This problem is particularly relevant for plant-pollinator systems, where numerous rare and specialized species coexist with generalists. Prior research on pollination's role in plant coexistence shows conflicting results: Lotka-Volterra models suggest pollinators negatively impact coexistence by favoring abundant plants, while empirical studies of modular networks show positive effects through niche partitioning. Using a consumer-resource model and modern coexistence theory, we evaluated how nestedness and adaptive foraging affect plant coexistence in plant-pollinator networks through stabilizing mechanisms (increased intraspecific with respect of interspecific competition) and equalizing mechanisms (reduced fitness differences). Nestedness alone reduces coexistence by increasing fitness differences between generalist and specialist species. However, adaptive foraging promotes coexistence by eliminating these differences through equalizing the total visits generalists and specialists receive per plant. This redistribution of pollinator visits caused by adaptive foraging lowers the threshold of visit quality needed for species to persist, enhancing plant coexistence. Our findings show that when a consumer-resource approach is taken, modern coexistence theory supports a positive effect of animal pollination on plant coexistence via an equalizing effect on visits per plant of pollinators' adaptive foraging.

Introduction

Current and past environmental changes have impacted the persistence of specialist species, promoting their replacement by generalist species (Clavel et al. 2011). This replacement drives functional homogenization with potential consequences in ecosystem function and services (Clavel et al. 2011). This problem is particularly relevant for plant-pollinator systems because these systems sustain dozens to several hundreds of specialist species (i.e., with only one or a few realized plant-pollinator interactions, Bascompte and Jordano 2007, Winfree et al. 2018), raising the questions of how they can coexist with generalist species and whether they will continue coexisting given the ongoing pollinator decline (Koh et al. 2016, Zattara and Aizen 2021, Dicks et al. 2021). Moreover, specialist species in these systems tend to be less abundant than generalist species (Vázquez and Aizen 2003, Vázquez et al. 2009, Olito and Fox 2015, Fort et al. 2016), which may increase even further their extinction risk (Davies et al. 2004, Clavel et al. 2011).

Previous studies evaluating the effect of pollination interactions on plant coexistence have led to divergent results. Theoretical work using Lotka-Volterra competition models parameterized with empirical experiments in two-plant-species systems suggests that pollinator interactions are overall negative for plant coexistence by favoring abundant plants (Johnson et al. 2022). This predicted negative effect, however, is limited to species pairs isolated from the rest of the community and pollination interactions considered only implicitly through comparisons of estimated competition coefficients between hand and animal pollinated treatments. Conversely, empirical work measuring pollen deposition and visitation rates in a species-rich, non-nested, highly modular plant-pollinator network suggests that pollination interactions positively affect plant coexistence by advantaging specialist over generalist plant species via pollinator niche partitioning (Wei et al. 2021). The generality of this latter finding, however, is still open to further research because most observed plant-pollinator networks are nested (Bascompte and Jordano 2007), unlike the network studied by Wei et al, which might be an outlier. That is, most networks exhibit a core of hyper-generalist plant and pollinator species that interact with each other and with specialist species, which results in specialist plant species being visited by hyper-generalist pollinator species that also visit generalist plants. This distribution of visits characteristic of nested networks may negatively affect the persistence of the specialist plants via

competition for limited pollinator visits with the more generalist plants, or via receiving lower quality of visits due to increased heterospecific pollen transfer or conspecific pollen dilution.

Here, we bridge previous divergent results on the effect of animal pollination on plant coexistence by developing theoretical understanding of plant coexistence for multispecies systems that considers the consumer-resource nature of plant-pollinator interactions. Our consumer-resource framework advances from previous theoretical work using Lotka-Volterra competition models (Johnson et al. 2022) by modeling explicitly the population dynamics of pollinators that consume floral rewards as well as the dynamics of floral rewards, both affected by the network of species interactions. This explicitly modeled consumer-resource interaction between pollinators and rewards allows us to introduce adaptive foraging of pollinators, which is a widespread behavior in nature (Stephens and Krebs 1987, Brosi and Briggs 2013) and is known to increase persistence in plant-pollinator systems (Valdovinos et al. 2013, 2016, Benadi and Gegear 2018).

We use this consumer-resource framework of mutualistic networks to evaluate the effect of nestedness and pollinators' adaptive foraging on multispecies plant coexistence and the persistence of specialist plant species. Specifically, we used the mutual invasibility criterion developed by Chesson and Kuang (2008) to elucidate which of the mechanisms they proposed (i.e., stabilizing or equalizing, Chesson 2000) better describe the effects of adaptive foraging and nestedness on plant coexistence. In such context, equalizing mechanisms increase species coexistence by reducing average fitness differences between species, while stabilizing mechanisms increase coexistence by increasing the relative effect of intraspecific to interspecific competition (Chesson 2000). We follow Chesson and Kuang (2008) definition of fitness as a species' per-capita growth when its interacting species are absent in the system including itself, but we use the term "demographic potential" instead of fitness to avoid confusion with other more common uses of the term (e.g., in evolutionary biology).

Methods

We use a consumer-resource model for simulating the dynamics of plant-pollinator networks (Valdovinos et al. 2013, 2016, Valdovinos and Marsland 2020), where nodes represent species and links indicate which pollinator species visits which plant species. This model defines

the population dynamics of each plant (Eq. 1) and animal (i.e., pollinator, Eq. 2) species in the network, the dynamics of floral rewards (Eq. 3) made available to pollinators by each plant species, and the foraging effort (Eq. 4) that each pollinator species per-capita assigns to each plant species in its diet (see Table 1 for the definition of parameters, their values, and units; see Table 2 for further explanation of the biological mechanisms encapsulated in the model with their assumptions), as follows:

$$\overbrace{\frac{dp_i}{dt}}^{\text{population growth of plant sp } i} = \overbrace{\gamma_i e_i \sum_{j \in A_i} \sigma_{ij} V_{ij}}^{\text{recruitment from animal pollination reduced by competition}} - \overbrace{\mu_i^P p_i}^{\text{mortality loss}} \tag{1}$$

$$\overbrace{\frac{da_j}{dt}}^{\text{population growth of animal sp } j} = \overbrace{c \sum_{i \in P_j} b V_{ij} \frac{R_i}{p_i}}^{\text{recruitment to adults from rewards consumption}} - \overbrace{\mu^A a_j}^{\text{mortality loss}} \tag{2}$$

$$\overbrace{\frac{dR_i}{dt}}^{\text{floral-rewards dynamics of plant sp } i} = \overbrace{\beta_i p_i - \varphi_i R_i}^{\text{saturated production of rewards}} - \overbrace{\sum_{j \in A_i} b V_{ij} \frac{R_i}{p_i}}^{\text{consumption by pollinators}} \tag{3}$$

$$\overbrace{\frac{d\alpha_{ij}}{dt}}^{\text{adaptive foraging}} = G\alpha_{ij} \left(\overbrace{cb\tau R_i}^{R \text{ consumption from plant } i} - \overbrace{cb\tau \sum_{k \in P_j} \alpha_{kj} R_k}^{\text{average } R \text{ consumption from all } j\text{'s plants}} \right) \tag{4}$$

The consumer-resource aspect of the model is that pollinators deplete floral rewards produced by plants and that pollinators respond to such depletion (and to rewards production) by reassigning their foraging efforts to the plants in their diet with the highest rewards available. Key to our question of plant coexistence is that this model encapsulates processes controlling plant population dynamics (see Table 2) including those driven by animal pollination (i.e., quantity and quality of visits, pollen deposition, seed production) and those driven by competition among plants for other resources (e.g., space, nutrients, water) that determine seed recruitment to adults. Competition for pollinators emerges as a consequence of plant species sharing pollinator species, which affects both the quantity and quality of visits a plant receives. A plant species in the model not only receives fewer visits when its pollinators visit other plant

species, but it also receives lower quality of visits because the pollinators carry heterospecific pollen which dilutes conspecific pollen and, therefore, reduces pollen deposition. Both visit quantities (quantity and quality) are determined by the plant-pollinator network, the foraging efforts that each pollinator species assigns to each plant species, and the abundance of both plant and pollinator species. Competition for all other resources is defined by a classic Lotka-Volterra model, which is independent from the plant-pollinator network (function γ_i in Eq. 1, see Tables 1 and 2), and controls the fraction of seeds that recruit to adult plants.

Table 1. Model state variables, functions, and parameters.

Definition	Symbol	Dimension	Mean value
State Variables			
Density of plant population *i*	p_i	individuals area^{-1}	0.5*
Density of animal population *j*	a_j	individuals area^{-1}	0.5*
Total density of floral rewards of plant population *i*	R_i	mass area^{-1}	0.5*
Foraging effort of *j* on *i*	α_{ij}	None	$\frac{1}{d_j}$ *
Functions			
Visitation rate of *j* to *i* (quantity of visits)	$V_{ij} = \alpha_{ij}\tau a_j p_i$	visits area^{-1} time^{-1}	variable
Quality of visits of *j* (per-capita) to *i* (per-capita)	$\sigma_{ij} = \frac{V_{ij}}{\sum_{k\in P_j} V_{kj}}$	None	variable
Fraction of seeds *i* that recruit to adults	$\gamma_i = g_i\left(1 - \sum_{l\neq i\in P_j} u_l p_l - w_i p_i\right)$	None	variable
Parameters			
Visitation (flying) efficiency	τ	visits area time^{-1} individuals^{-1} individuals^{-1}	1
Expected number of seeds produced by a pollination event	e_i	individuals visits^{-1}	0.8
Per-capita mortality rate of plants	$\mu_i^{(P)}$	time^{-1}	0.02
Conversion efficiency of floral rewards to pollinator births	c	individuals mass^{-1}	0.2

Per-capita mortality rate of pollinators	$\mu^{(A)}$	time^{-1}	0.001
Pollinator extraction efficiency of rewards in each visit	b	individuals visits^{-1}	0.4
Maximum fraction of total seeds that recruit to plants	g_i	None	0.4
Inter-specific competition coefficient of plants	u_l	area individuals^{-1}	0.06
Intra-specific competition coefficient of plants	w_i	area individuals^{-1}	1.2
Production rate of floral rewards	β_i	mass individuals^{-1} time^{-1}	0.2
Self-limitation parameter of rewards production	φ_i	time^{-1}	0.04
Adaptation rate of foraging efforts of pollinators	G	None	2

Values were drawn from a uniform random distribution with the specified mean, and variances of 10% and 0% of means for plant and animal parameters, respectively. That is, all pollinator species had the same parameter values and, therefore, the subscript *j* was dropped for clarity. Parameter were taken from Valdovinos et al. (2013) and (2018). Asterisks indicate initial conditions. P_j and A_i are the subsets of plant species that *j* visits and animal species the visit plant *i*, respectively. d_j is the degree of pollinator *j*, that is, the number of species *j* visits.

Table 2. Model's biological processes (and where they appear), their mathematical expression and assumptions, plus other dynamic quantities shown in results and plant coexistence metrics.

Biological process	In the model	Assumption
Visitation rate (all four equations)	$V_{ij} = \alpha_{ij}\tau_j a_j p_i$	Depends on the pollinator *j*'s foraging effort (α_{ij}) assigned to plant *i*, *j*'s flying efficiency (τ_j), and the plant (p_i) and pollinator (a_j) densities. $\alpha_{ij} = 0$ if pollinator *j* does not visit plant *i*, that is, α_{ij} encapsulates the plant-pollinator network.
Pollen deposition rate by one pollinator species (Eq. 1)	$\sigma_{ij}V_{ij}$	Only a fraction of pollinator visits of *j* to *i* (V_{ij}) deposits pollen, determined by the fraction of conspecific pollen carried by the pollinator (function σ_{ij}, see Table 1).
Total pollen deposition rate (Eq. 1)	$\sum_{j\in A_i}\sigma_{ij}V_{ij}$	Pollen deposition rate summed over all the pollinator species visiting the plant (set A_i).
Total seed production (Eq. 1)	$e_i\sum_{j\in A_i}\sigma_{ij}V_{ij}$	Only a fraction of the total pollen deposited become seeds, determined by the seed production efficiency of the plant species (parameter e_i).
Seed recruitment (Eq. 1)	$\gamma_i e_i\sum_{j\in A_i}\sigma_{ij}V_{ij}$	Only a fraction of seeds produced recruit to adults, determined by the competition among plants (function γ_i).

Consumption of rewards (Eq. 2)	$V_{ij} b_j \frac{R_i}{p_i}$	In each visit, pollinators consume a fraction of the floral rewards offered by the plant individual (R_i/p_i) at a rate b_j.
Recruitment to adult pollinators (Eq. 2)	$c \sum_{i \in P_j} V_{ij} b_j \frac{R_i}{p_i}$	Floral rewards consumed by the pollinator species summed over all the plant species the pollinator species visits (set P_j) are converted into new pollinator adults at a rate c_j.
Production of rewards (Eq. 3)	$\beta_i p_i - \varphi_i R_i$	Floral rewards of a plant population increase with its population density in a saturating manner, with rewards production decelerating as rewards increase up to the maximum of $\beta_i p_i / \varphi_i$ when the rewards production stops.
Adaptive foraging	Equation (4)	A pollinator increases its foraging effort to plants with more rewards, by reassigning its efforts from plant species with less rewards. Foraging efforts are fractions that can take a maximum value of 1 (i.e., the pollinator assigns all its effort to that plant species) and they sum to 1 over all plant species the pollinator visits.
Efforts of a fixed forager (simulations)	$\frac{1}{d_j}$	Pollinators without adaptive foraging are assumed to have fixed foraging efforts across all plant species they visit, equal to one over the number of plant species the pollinator visits or their degree.
Dynamic quantities	**In the model**	**Description**
Total visits per-plant ($\boldsymbol{v_i}$)	$v_i = \sum_{j \in A_i} \alpha_{ij} \tau_j a_j$	Sum of all the visits a plant individual of species *i* receives from all the pollinator species visiting it.
R star ($\boldsymbol{R}^*$)	$\frac{\mu^{(A)}}{c \tau b}$	Rewards at equilibrium needed to support the population of pollinator species *j*. With adaptive foraging the rewards of all persisting plant species reach the same $\boldsymbol{R}^*$, leading to an ideal free distribution.
Recruitment potential after interspecific competition ($\boldsymbol{U_i}$)	$1 - \sum_{l \neq i} \mu_l p_l$	Proportion of recruitment potential reduced by inter-specific competition.
Weighted average quality of visit ($\overline{\boldsymbol{\sigma}}_{\boldsymbol{i}}$)	$\frac{\sum_{j \in A_i} \sigma_{ij} \alpha_{ij} a_j}{\sum_{j \in A_i} \alpha_{ij} a_j}$	Average quality of interactions that plant species *i* receives from its pollinators, adjusted by the visitation efficiency, abundance, and foraging effort of each pollinator species.
Competition-adjusted recruitment potential	$\frac{U_i}{w_i}$	Maximum plant density at equilibrium when total per-plant visits and/or average weighted quality of visits are high.
Critical averaged quality of visits ($\overline{\boldsymbol{\sigma}}_{\boldsymbol{i}}^{\boldsymbol{c}}$)	$\frac{\mu_i^{(P)}}{g_i e_i v_i U_i}$	Minimum value of weighted quality of visits needed for a plant species to persist.
Coexistence metric	**In the model**	**Description**
Niche overlap ($\boldsymbol{\rho_{ik}}$)	Eq. B9	Relative degree of intraspecific vs. interspecific limitation in plants both via competition for seed recruitment and via sharing pollinators.
Demographic potential ($\boldsymbol{k_i}$)	$g_i e_i v_i - \mu_i^{(P)}$	Per-capita production rate of new recruits in the absence of direct competition from other plants minus per-capita mortality rate.

We use this model to simulate the dynamics of 1,200 algorithm-generated networks (Fig. 1A) without and with adaptive foraging, with a total of 2,400 simulations. Simulations without adaptive foraging assume fixed foraging efforts defined as $\alpha_{ij} = 1/d_j$, where d_j is the number of plant species that pollinator species *j* visits (i.e., pollinator *j*'s degree). Simulations with adaptive foraging assume that pollinators prefer plants that have more floral rewards available to them (i.e., their α_{ij} vary following Eq. 4). Foraging efforts take values between 0 and 1, and the sum of foraging efforts of a pollinator species across all the plant species it visits at any given time is 1.

The generated networks (Fig 1A) expand ranges of connectance (*C*) between 0.34 and 0.041 and species richness (*S*) between 15 and 238, with C × S combinations that resemble those observed in empirical networks (Fig. S1) and with an average ratio of pollinator to plant number of species of 2.5. Connectance is calculated as $C = L/(A \times P)$, where L is the realized number of links, and $A \times P$ the potential links between the total number of pollinator species, A, and plant species, P, in the network, while $S = A + P$. These networks cover values from anti-nested to highly nested slightly beyond the ones observed in empirical networks to ensure encompassing the entire empirical range. We generated the networks using the algorithm developed by Thébault and Fontaine (2010). We calculated nestedness and its statistical significance using NODFst (Almeida□Neto et al. 2008), using the R package bipartite (Dormann et al. 2008). However, to compare across networks, we calculated NODFc (Song et al. 2017) using R package maxnodf (Hoeppke and Simmons 2021), which is known to better compare across networks of different sizes. We ran model simulations for 10,000 timesteps using Matlab R2024a (The MathWorks Inc.)

We calculated plant coexistence as the fraction of initial plant species that coexisted (i.e., persisted) until the end of the simulations. To elucidate which proposed coexistence mechanisms (i.e., stabilizing or equalizing, Chesson 2000) better describe the effects of adaptive foraging and nestedness on plant coexistence, we used the mutual invasibility criterion by Chesson and Kuang (2008), as follows:

$$\rho_{ik} < \frac{k_k}{k_i} < \frac{1}{\rho_{ik}} \tag{5}$$

where (ρ_{ik}) is niche overlap between species *i* and *k* (while $1 - \rho_{ik}$ is niche differentiation) and (k_i) is the demographic potential of plant species *i* in absence of other species (also known in the literature as fitness, Chesson 2000). Stabilizing mechanisms increase negative intraspecific interactions relative to negative interspecific interactions via increasing niche differentiation $(1 - \rho_{ik})$, while equalizing mechanisms reduce relative demographic potentials (k_i/k_k). Appendix B shows our derivation of Eq. 5 for our model, with (ρ_{ik}) derived from partial derivatives indicating the effect of each plant species on the per-capita growth rate of the other, and on its own per-capita growth rate.

The mutually invasibility criterion of Eq. 5 was developed for pairwise interactions and indicates whether or not each species can invade a system where the other is present when starting at very low abundances (Chesson and Kuang 2008). This criterion, however, accurately represented the coexistence between every 1,348,134 plant species pairs of our 2,400 simulations, except for 84 pairs involving one species in 6 networks without adaptive foraging. We tested that this was the case by evaluating the criterion at steady state (i.e., at the end of the simulations after 10,000 time-steps) for each plant species pair in each of our simulations and contrasting the outcome of Eq. 5 with whether the pair of species coexisted until the end of the simulations. Note that we are using these calculations as metrics for describing coexistence mechanisms rather than as proof for coexistence given that our simulations can tell us for certain whether plant species coexisted or not.

Results

We found that nestedness decreases and adaptive foraging increases plant coexistence, respectively (Fig. 1A). However, niche overlap (ρ_{ik}) — which includes intra-specific and inter-specific effects between plant species via both competition for seed recruitment and shared pollinators — is equivalent between simulations without and with adaptive foraging (Fig. 1B). Niche overlap is also equivalent between non-nested and nested networks, which we do not show as it looks identical to Fig. 1B (i.e., similar to just replacing the legend “Without AF” and “With AF” for non-nested and nested networks).

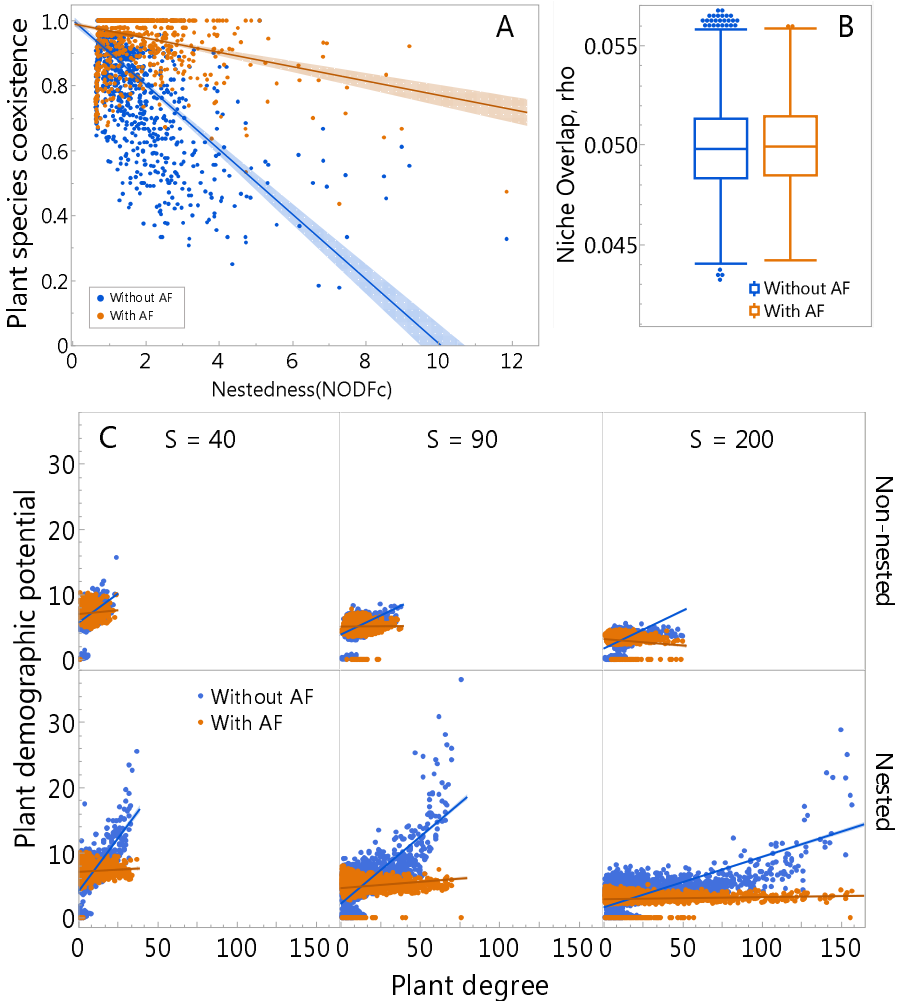

Fig. 1. Nestedness decreases and adaptive foraging (AF) increases plant coexistence via equalizing mechanisms. A) AF weakens the strong negative relationship between plant coexistence and nestedness, measured as NODFc. Each dot represents plant coexistence (i.e., the fraction of plant species that persisted until the end of the simulations) for one of the 1200 networks with and without AF (2400 total). Blue dots and lines represent simulations without AF, while orange dots and lines represent simulations with AF. **B)** AF has no effect on niche overlap (ρ_{ik}), as indicated by the similarity between the orange and blue box plots. Box plots display the median (middle line), the interquartile range (box), and the 95% confidence intervals (error bars) of the mean niche overlap across all plant species in all simulations. **C)** Nestedness exacerbates and AF eliminates differences in demographic potential between generalist and specialist plants. Dots represent plant demographic potential (see definition in Table 2) for each plant species in each simulation against its degree (i.e., number of pollinator species visiting it), separated by network richness (S) and whether the network is non-nested or nested. Blue and orange dots correspond to simulations without and with AF, respectively. Lines correspond to linear regressions used as reference to show tendencies. Regressions without AF have slopes between 0.1 and 0.6 and R^2 between 0.15 and 0.6, while all regressions with AF have near zero slopes and R^2. See Table A1 for all statistics.

Nestedness and adaptive foraging, however, strongly affected plant demographic potential (Fig. 1C). In networks without adaptive foraging, generalist plants (higher degree) exhibit much higher demographic potential than specialist plants (lower degree), particularly in nested networks (Fig. 1C). Adding adaptive foraging to the networks' dynamics equalizes the demographic potential across plant species. That is, nestedness increases differences in demographic potential between generalist and specialist plants while adaptive foraging decreases those differences. In fact, adaptive foraging eliminates all positive relationships between demographic potential and degree (see that all positive slopes and R^2 of regressions without AF become near zero with AF in Table A1).

To better understand how the equalizing mechanism works in this model, we looked closer at the expression of demographic potential we derived in Appendix B (Eqs. B10-B13), defined as per-capita production rate of new recruits in the absence of direct competition from other plants minus per-capita mortality rate:

$$k_i = g_i \sum_{j \in A_i} e_i \alpha_{ij} \tau_j a_j - \mu_i^{(P)} = g_i e_i v_i - \mu_i^{(P)} \tag{6}$$

A key component of such demographic potential is the total per-capita visits a plant species receives ($v_i = \sum_{j \in A_i} \alpha_{ij} \tau_j a_j$), which is determined by the foraging effort pollinator *j* assigns to *i* (α_{ij}), the foraging efficiency of pollinator *j* (τ_j), and the pollinator *j*'s density (a_j).

Eq. 6 shows a linear, direct, and positive relation between demographic potential and total per-plant visits, which is demonstrated by our simulations in Fig 2A-B. Moreover, Fig. A3 in Appendix A shows the same equalizing effects of adaptive foraging and unequalizing effect of nestedness shown in Fig. 1C but for total per-plant visits in the y-axis instead of demographic potential. That is, generalist species receive many more visits per-plant than specialists, difference that is amplified in nested compared to non-nested networks, while adaptive foraging equalizes the visits that specialists and generalists receive. In fact, adaptive foraging eliminates the positive relationship between total visits per-plant and plant degree (see all statistics in Table A2 of Appendix A). That is, the effect of nestedness and adaptive foraging on demographic potential is driven by their respective effects on total visits per-plant.

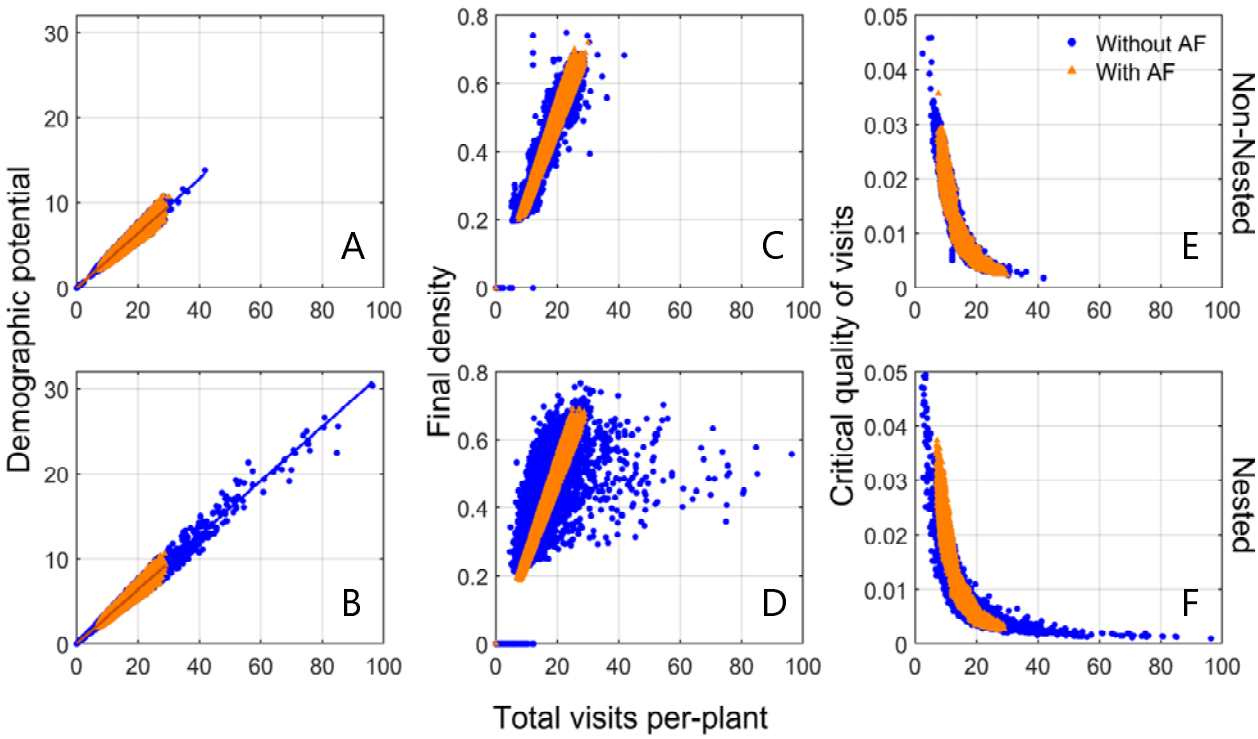

Fig. 2. Total visits per-plant determines plant demographic potential (A,B) plant density (C,D) and the critical quality of visits (E,F). Each dot represent data for each plant species in non-nested (A, C, E) and nested (B, D, F) without (blue) and with (orange) adaptive foraging (AF). Lines in panels A-C represent linear regressions, with statistics: A) without AF: demographic potential = -0.01 + 0.32*total visits per-plant R^2=0.96; with AF: demographic potential = 0.00 + 0.32*total visits per-plant R^2=0.96, B) without AF: demographic potential = -0.01 + 0.32*total visits per-plant R^2=0.98; with AF: demographic potential = -0.01 + 0.32*total visits per-plant R^2=0.97, C) without AF: plant density = 0.013 + 0.024*total visits per-plant R^2=0.95; with AF: plant density = 0.007 + 0.025*total visits per-plant R^2=0.98, D) without AF: plant density = 0.040 + 0.021*total visits per-plant R^2=0.82; with AF: plant density = 0.006 + 0.025*total visits per-plant R^2=0.98.

Total visits per-plant also positively affected plant abundance at the end of the simulations (Fig 3A-B). To better understand this relationship, we derived plant density at equilibrium in Appendix C, with expression:

$$p_i^* = \frac{U_i}{w_i} - \frac{\mu_i^{(P)}}{g_i w_i e_i \bar{\sigma}_i v_i} \tag{7}$$

The positive relation between plant density at equilibrium (p_i^*) and total per-plant visits (v_i) is saturating, with a maximum value of U_i/w_i. This maximum value can be interpreted as the competition-adjusted plant recruitment potential. That is, sufficiently high pollinator visits

decrease the negative effect of plant mortality on abundance to zero, allowing plants to reach their maximum abundance, which is determined by seed recruitment.

Eq. 7's derivation provides a key variable for understanding plant coexistence: the per-capita weighted average quality of visits received by plant species *i* ($\bar{\sigma}_{\boldsymbol{i}}$, see Table 2). The higher ($\bar{\sigma}_{\boldsymbol{i}}$) the stronger the positive relation between plant density at equilibrium (p_i^*) and total per-plant visits (v_i). Fig. A4 shows that nested networks with adaptive foraging exhibit the highest quality of visits, which explains the tight and direct relationship between plant abundance and total per-plant visits in Fig 2A-B. Defining quality-weighted visits as ($Q_i = \bar{\sigma}_{\boldsymbol{i}} v_i$) and solving for it in Eq. 6 after imposing p_i^*>0 (see Appendix C), gives us the critical values a plant species needs to persist:

$$Q_i^c = \frac{\mu_i^{(P)}}{g_i e_i U_i} \quad or \quad \bar{\sigma}_i^c = \frac{\mu_i^{(P)}}{g_i e_i v_i U_i} \tag{8}$$

When $Q_i > Q_i^c$ or $\bar{\sigma}_{\boldsymbol{i}} > \bar{\sigma}_i^c$, plant species *i* persists and reaches its equilibrium (Eq. 6). When $Q_i \leq Q_i^c$ or $\bar{\sigma}_{\boldsymbol{i}} \leq \bar{\sigma}_i^c$, plant species *i* goes extinct, reaching the other equilibrium (i.e., $p_i^* = 0$). Simulation results presented in Fig. 3E-F confirm the inverse relationship described in Eq. 7 between the total visits per-plant (v_i) and the critical value of the weighted average quality of visits ($\bar{\sigma}_i^c$) received by a plant species. That is, the higher the total per-plant visits a species receives, the lower the quality of those visits can be for the species to persist, and vice versa, as fewer visits are needed when their quality is high.

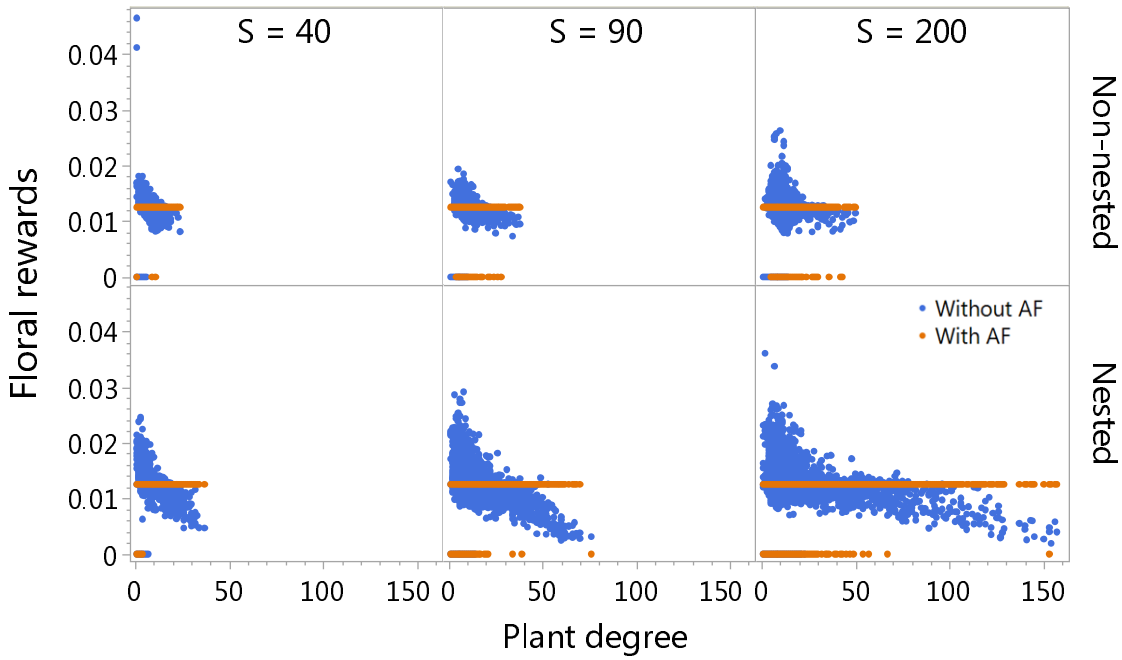

Fig. 3. Final floral rewards with respect of plant degree. Each dot represent data for each plant species in non-nested (top) and nested (bottom) panels at richness levels (S) of 40, 90, and 200 species; without (blue) and with (orange) adaptive foraging (AF). Without AF, generalist plant species contain much lower floral rewards compared to specialist species. With AF, the floral rewards of all persisting plant species converge to the same value of 0.0125.

To understand what drives adaptive foraging to produce its equalizing effect, we analyzed the distribution of floral rewards with and without adaptive foraging (Fig. 3). In the absence of adaptive foraging, generalist plant species contain much lower floral rewards compared to specialist species (blue dots in Fig. 3; also illustrated in Fig. 4A), particularly in nested networks. However, when adaptive foraging is introduced, the floral rewards of all persisting plant species converge to the same value of 0.0125 (orange dots in Fig. 3; also illustrated in Fig. 4C), regardless of network nestedness, species richness, or plant degree. Appendix D shows that this value comes from the equilibrium being $R^* = \frac{\mu^{(A)}}{c\tau b}$. That is, the striking differences in reward distributions among plants are driving foraging efforts to be reassigned in a way that favors the demographic potential of specialist plants, as explained in the next paragraph using Fig. 4.

Recall from Tables 1 and 2 that the initial foraging efforts without and with adaptive foraging are both $\alpha_{ij} = \frac{1}{d_j}$, where d_j is j's degree or number of plant species j visits (illustrated in

Fig. 4A). These efforts then stay at the same value throughout the entire simulation without adaptive foraging (Fig. 4B) or adjust dynamically according to Eq. 4 in the case of with adaptive foraging (Fig. 4C and D). With adaptive foraging, the initially higher floral rewards of specialist plants drive the reallocation of pollinators' foraging efforts from generalist to specialist plants (Fig. 4D; illustrated in Fig. 4C). This reallocation process can be intuitively understood from the difference between the blue and orange dots in Fig. 3, which reflects the floral reward gains adaptive pollinators achieve by shifting foraging efforts from generalist to specialist plants, thereby causing the equalizing effect by decreasing the total per-plant visits received by generalists while increasing those received by specialists.

The effort reallocation shown in Fig. 4D results in an overall increase in total per-plant seed production, particularly for specialist plants (see Fig. A5 in Appendix A). We found, however, an inverse relationship between seed recruitment (γ_i) and total per-plant seed production (Figs. 4E and 4F), which dilutes the effect of increased seed production on plant abundance. That is, an increase in seed production is counterbalanced by a steep decrease in seed recruitment driven by intra-specific competition for resources other than pollination (see definition of γ_i in Table 1). This relationship explains why niche overlap measured as (ρ_{ik}) is the same without and with AF (Fig. 1B). That is, any effect of adaptive foraging on niche overlap via affecting seed production gets counterbalanced by seed recruitment, which keeps the negative intraspecific effects among plants relative to their negative interspecific effects (i.e., ρ_{ik}) the same.

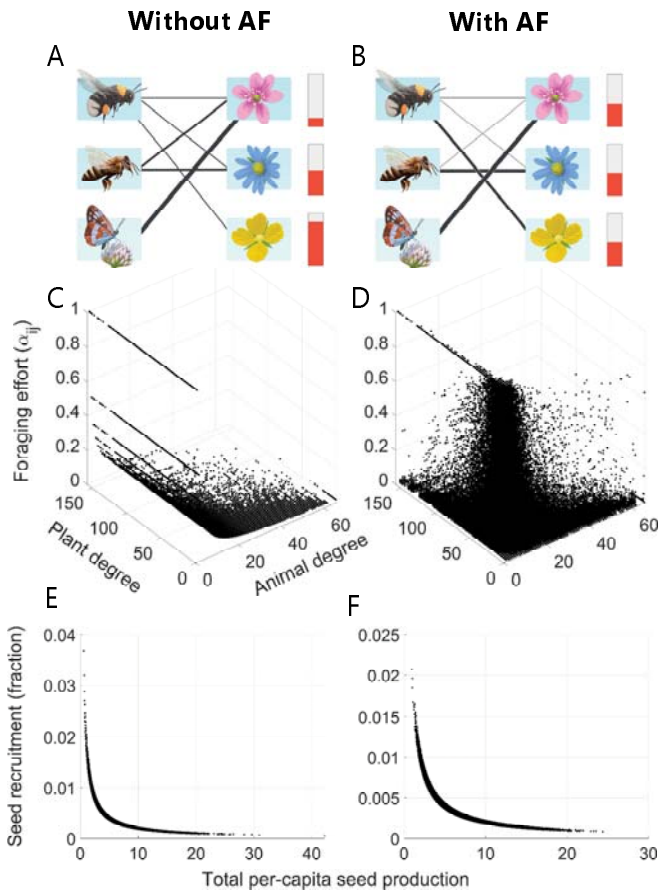

Fig. 4. Adaptive foraging (AF) enables generalist pollinators to reallocate their foraging efforts from specialist to generalist plant species within their diet. Illustration of model behavior (A, B), final foraging efforts of all 1200 networks plotted against plant and pollinator degrees connected by those foraging efforts (C, D), and seed recruitment vs total per-capita seed production for every plant species that persisted (E, F) without (A, C, E) and with (B, D, F) adaptive foraging. Panel A also illustrates initial efforts with AF before generalist pollinators reassign their foraging efforts. Without AF, pollinators assign a fixed foraging effort to each plant species they visit (i.e., $\alpha_{ij} = \frac{1}{d_j}$, where d_j is j's degree; A, C). This effort distribution results in generalist plants receiving more and higher quality visits and reduced floral rewards (red bars in A) compared to specialist plants. With AF, pollinators reallocate more foraging effort to plant species in their diet that initially have higher floral rewards available (specialist plant species, see A). This reallocation causes specialist plants to receive more and higher-quality visits compared to without AF. (A) and (B) depict nested networks, and the line thickness connecting each pollinator species to the plant species in its diet is scaled to illustrate each foraging effort value (i.e., each dot in (C) and (D)). Note that the line thickness in panel (D) is limited by the small network illustrated, where the most generalist pollinator species visits only 3 plant species. If a pollinator visiting 15 plant species were illustrated, the differences in link thickness would have been more pronounced, like those of high-degree pollinators in panel (D). Foraging efforts take values between 0 and 1, and their sum across all plant species of one pollinator species is 1. Pollinators with degree 1 always act as fixed foragers with

effort 1 as they lack other plant species in their diet to reassign efforts to, which explains the line of effort values at 1 in (D).

Discussion

Increasing concerns of generalist species replacing specialists across various ecosystems worldwide (Clavel et al. 2011) make the question of how generalist and specialist species coexist in plant-pollinator networks more relevant than ever in the Anthropocene. However, previous studies on the effects of pollination interactions on plant coexistence have yielded mixed results, with a Lotka-Volterra model suggesting negative effects by pollinators favoring abundant plants (Johnson et al. 2022), while an empirical study in a modular network indicating positive effects through niche partitioning favoring specialist plants (Wei et al. 2021). Here, we argue that this question is better answered by using a consumer-resource (Valdovinos et al. 2013, Valdovinos 2019, Valdovinos and Marsland 2020) instead of a Lotka-Volterra framework and by studying nested instead of modular networks. Specifically, we used a consumer-resource model to evaluate the effects of nestedness and adaptive foraging on plant coexistence, and used elements of modern coexistence theory (Chesson 2000) to organize and communicate our results.

We found that nestedness reduces plant species coexistence by increasing the differences in demographic potential between generalist and specialist species, while adaptive foraging promotes plant coexistence by eliminating these differences. This equalizing effect arises because adaptive foraging increases the demographic potential of specialist plant species while decreasing that of generalists. Conversely, we found no effect of nestedness or adaptive foraging on niche overlap, measured by the (ρ) metric used in modern coexistence theory (Chesson 2000, Chesson and Kuang 2008). Previous theoretical work using our consumer-resource model (Valdovinos et al. 2013, 2016, Valdovinos and Marsland 2020) and empirical work (Wei et al. 2021), however, have shown that pollinators partition their foraging niches in a way that also partitions plant niches (follow thick lines in Fig. 4C). The contrasting results between our findings and previous studies using the same consumer-resource model can be attributed to the definition of the niche overlap metric (ρ). This metric is defined as the ratio of direct intraspecific effects to direct interspecific effects, where niche partitioning results in an increase of intraspecific effects relative to interspecific effects (Chesson 2000, Chesson and Kuang 2008). In our case, the niche partitioning of pollination services consisting of generalists receiving mostly visits by specialist pollinators and specialists receiving mostly visits of generalist

pollinators (follow line thickness in Fig. 4B) that results in increased seed production, gets diluted by the compensatory effects of competition for seed recruitment. That is, the niche overlap metric (ρ) applied to our model is driven by seed recruitment not by pollination services.

The equalizing effect of adaptive foraging occurs through a redistribution of total visits. That is, adaptive foraging increases the number of visits specialists receive per individual (hereafter, per plant) while reducing the visits generalists receive per plant. This differential benefit of adaptive foraging on the demographic potential of specialist over generalist plant species occurs through the niche partitioning of pollination services found by previous studies (Valdovinos et al. 2016, Wei et al. 2021) mentioned above, and shown by our simulations in Fig 4C. That is, generalist pollinators with adaptive foraging prefer specialist over generalist plant species in their diet, which increases the quantity (Fig. A3) and quality (Fig. A4) of visits that specialist plants receive and keep them above the critical value of quality of visits needed for the plants to have viable populations. Moreover, here we found a mathematical relationship proving that an increase in total visits per-plant lowers the minimum quality of visits required for a plant species to persist, which explains why adaptive foraging enhances the persistence of specialist species and facilitates coexistence between generalist and specialist plant species.

This equalizing effect of adaptive foraging is driven by the differential in rewards to be obtained by pollinators when reallocating their foraging efforts from specialist to generalist plants. In the absence of adaptive foraging, generalist plant species contain much lower floral rewards compared to specialist species, particularly in nested networks. When adaptive foraging is introduced, the floral rewards of all persisting plant species quickly converge to the same R^* value at equilibrium obtained by an ideal-free distribution mechanism. That is, pollinators keep reallocating their foraging efforts until all floral rewards are the same across plant species and there is no more benefit to be gained by further reallocation. In fact, floral rewards available to pollinators determine whether a plant population attracts fast enough foraging efforts during the transient dynamics to meet its minimum quality of visits to persist (Valdovinos and Marsland 2020, Valdovinos et al. 2023). If a plant species' rewards drop below R^*, its population starts a non-reversible process to extinction. This non-reversible process, for example, can occur to a plant species that receives too few visits (and therefore decreases in abundance due to low reproduction, which keeps decreasing its offered rewards further below R^*) or too many low-

quality visits that deplete the rewards below R^* but do not meet the quality of visits needed for the plant to persist.

Environmental changes are driving the replacement of specialist species by generalists, resulting in functional homogenization that threatens ecosystem functioning (Clavel et al. 2011). Plant-pollinator systems, which support numerous specialist plant species with few floral visitors (Bascompte and Jordano 2007, Winfree et al. 2018), are particularly vulnerable to this homogenization. While previous research using Lotka-Volterra competition models and modern coexistence theory suggested that pollinator interactions reduced plant coexistence by favoring abundant plants (Johnson et al. 2022), these findings relied on phenomenological competition between plant pairs without explicit pollination mechanisms. Our research advances this understanding by separately modeling animal pollination and plant competition for recruitment. Through a consumer-resource approach that distinguishes between competition for pollinators and for seed recruitment, we show that animal pollination promotes plant coexistence through the equalizing effects of pollinators' adaptive foraging.

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Data and Code Accessibility Statement

The code used to produce all results of this work is publicly available at GitHub repository https://github.com/Valdovinos-Lab/Plant_Coexistence.

Author Contribution Statement

F.S.V. conceptualized, designed, and acquired funding for this study, run simulations, conducted analyses, created figures, and wrote the manuscript. T.K. conducted mathematical analyses in close collaboration with F.S.V and R.M.III. All authors reviewed the manuscript.

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