

Analytical thresholds reveal mechanisms of cross-scale dynamics in adaptive mutualistic networks

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CENTRAL QUESTION

Can mechanistic cross-scale network models be analytically decomposed to identify critical conditions governing community dynamics, species persistence, ecosystem services, and species invasions?

ANSWER

Yes. An analytical decomposition of a consumer-resource plant–pollinator model with adaptive foraging identifies threshold conditions linking foraging, rewards, pollination quality, recruitment, and network structure to community outcomes.

FIELD MAP COORDINATES

Persistence and fragility; Scaling; Inference and prediction.

Abstract

Cross-scale integration remains a persistent challenge in ecology. Mechanistic network models can advance this integration by linking individual- and population-level processes with emergent community structure and dynamics, but their complexity often leaves their implications understood primarily through computer simulations. Here, I analyze a consumer-resource model of plant–pollinator interactions with adaptive foraging to show how simulation-discovered patterns can be translated into analytical threshold relationships. The model connects individual-level foraging, floral rewards, visitation, and pollination quality to population dynamics, competition for shared resources and services, and emergent community and network structure. Analytical decomposition identifies threshold conditions for population persistence, finite-density establishment, sustained pollination services, and community-level effects of network structure mediated by adaptive foraging. These relationships clarify how rewards, visitation, pollination quality, recruitment, and network architecture jointly constrain community outcomes. By connecting simulation-motivated patterns to analytical threshold conditions, this work shows how mechanistically detailed models can produce general insight into the biological processes and constraints that shape ecological communities.

Introduction

Cross-scale integration remains one of ecology’s most persistent challenges [1, 2]. This difficulty is increasingly consequential as ecological prediction requires extrapolation beyond historical conditions. Predicting responses to novel environmental conditions requires models that connect individual behavior, physiology, and resource use with population, community, and ecosystem dynamics [3, 4]. Traditional single-scale or phenomenological models have greatly contributed to ecological theory and prediction, but they can be limited when responses to environmental change depend on shifts in the underlying processes that generate system dynamics [5, 6]. Mechanistic cross-scale models offer a complementary approach by explicitly representing how lower-level processes, such as individual behavior, physiology, and resource use, interact with higher-level outcomes, such as population growth, community persistence, network structure, and ecosystem function. By tracing how environmental perturbations alter these processes and their feedbacks, such models can help predict emergent community dynamics under conditions without close historical precedent. Yet this mechanistic realism often comes at the cost of apparent analytical intractability: by coupling processes across biological scales, these models are typically explored through simulation, leaving unclear whether they can also reveal general mathematical princi-

ples. This tension raises the central question of this paper: Can mechanistic cross-scale network models be analytically decomposed to identify critical conditions governing community dynamics, species persistence, ecosystem services, and species invasions?

This tension reflects a broader debate in theoretical ecology over the relationship between model simplicity, mechanistic realism, and generality [7, 8]. Simple models have been indispensable for deriving foundational ecological principles [9, 10, 11, 12]. Yet the assumption that mechanistic complexity necessarily prevents general insight can be misleading. In ecology, mechanisms are not merely additional parameters or equations; they are biological hypotheses about how organisms behave, interact, and affect one another across scales. Cross-scale mechanistic models of adaptive behavior and bioenergetic constraints have shown that individual-level mechanisms can scale up to affect population stability, coexistence, network structure, and responses to environmental change [13, 14, 15, 16, 17]. Including such mechanisms explicitly allows models to ask not only whether system-level patterns emerge, but also why they emerge: which processes drive them, how those processes interact, and what ecological consequences follow. Initial complexity, therefore, need not imply permanent intractability. The same cross-scale couplings that make a model difficult to analyze may also impose constraints that, once derived, make its dynamics decomposable.

Computer simulations can play a central role in this process. Rather than serving only as substitutes for analysis, they can be the first step in a longer theoretical workflow by exposing recurrent patterns, unexpected outcomes, and candidate organizing variables that guide later mathematical analysis. I illustrate this approach with an adaptive consumer-resource model of plant–pollinator interactions that links individual-level foraging, floral rewards, visitation, and pollination quality with population dynamics, interspecific competition for shared resources and services, and emergent community and network structure [18, 19, 20]. Previous simulations of this model showed that adaptive foraging can stabilize communities, reorganize interaction networks, buffer some species against decline, and generate nonlinear responses to species introductions and network connectance [18, 19, 21, 22, 23]. These simulation-derived patterns motivate the analytical decomposition developed here.

Here, I analytically decompose the model by following its cross-scale architecture from plant demography and pollinator energetics to reward dynamics, visitation balance, pollination service, and network-mediated outcomes. This sequential

analysis identifies threshold relationships for population persistence, finite-density establishment, and sustained pollination service. Plant persistence requires pollination service above a critical value set by demographic losses and the available recruitment niche, whereas pollinator persistence requires floral rewards sufficient to offset mortality. Reward dynamics close the equilibrium by determining sustainable visitation, and visitation quality determines whether plants remain above their persistence thresholds. Extending these results beyond equilibrium shows how declines can become self-reinforcing through coupled reward–visitation–recruitment feedbacks and how adaptive foraging translates network structure, including connectance, into community-level outcomes. Together, the results show how simulation-derived patterns can be converted into explicit biological constraints governing community dynamics. The model structure, cross-scale feedbacks, prior simulation results, and new mathematical findings are summarized conceptually in Box 1, Figure 1, Box 2, and Box 3.

Model Framework and Analytical Results

I analyze the model under two foraging scenarios that bracket the behavioral range of the system (Box 1, Eq. B4). In the fixed foraging baseline, each pollinator j allocates effort uniformly across its diet, such that $\alpha_{ij} = 1/d_j$ for all $i \in \mathcal{P}_j$, where $d_j = |\mathcal{P}_j|$ is the pollinator's binary degree and $\mathcal{P}_j$ is the set of plant species connected to pollinator j in the binary network. Thus, in this baseline, the quantitative distribution of foraging efforts is determined solely by the binary network structure: which pollinator species visits which plant species. In the adaptive foraging scenario, foraging efforts change according to Eq. B4: pollinators redirect effort toward plants offering above-average rewards, and this reallocation continues until rewards equalize at a common level R^* across the active diet (plants receiving positive effort). For this scenario, I define the active equilibrium diet as $\mathcal{P}_j^+ = \{i \in \mathcal{P}_j : \alpha_{ij}^* > 0\}$ and the active degree as $d_j^+ = |\mathcal{P}_j^+|$. Thus, $d_j^+ \leq d_j$, with equality only when all binary links receive positive equilibrium effort. Fixed foraging serves as a structural null model, but the core of the analysis focuses on the adaptive scenario to reveal how cross-scale feedbacks determine community persistence. Table 2 provides a side-by-side comparison of the emergent outcomes under both behavioral regimes. Throughout the analysis below, the common visitation-efficiency parameter τ (defined in Box 1) is retained where it enters the effective conversion rate $c' = cb\tau$; elsewhere, its numerical value is fixed at $\tau = 1$ and the factor is suppressed from expanded expressions. Appendix Table A1 reports the corresponding dimensionally explicit forms.

BOX 1

A consumer-resource model of plant–pollinator networks

This work analyzes the consumer-resource model of Valdovinos et al. [18], in which plant and pollinator species are connected by links indicating which pollinator j visits which plant i . The model tracks four coupled quantities: plant abundance p_i , pollinator abundance a_j , floral rewards R_i , and the per-capita foraging effort α_{ij} that pollinator j allocates to plant i :

$$\frac{dp_i}{dt} = \gamma_i e_i \sum_{j \in \mathcal{A}_i} \sigma_{ij} V_{ij} - \mu_i^P p_i, \quad (\text{B1})$$

$$\frac{da_j}{dt} = c \sum_{i \in \mathcal{P}_j} b V_{ij} \frac{R_i}{p_i} - \mu^A a_j, \quad (\text{B2})$$

$$\frac{dR_i}{dt} = \beta_i p_i - \phi_i R_i - \sum_{j \in \mathcal{A}_i} b V_{ij} \frac{R_i}{p_i}, \quad (\text{B3})$$

$$\frac{d\alpha_{ij}}{dt} = G c' \alpha_{ij} \left(R_i - \sum_{k \in \mathcal{P}_j} \alpha_{kj} R_k \right), \quad (\text{B4})$$

with $\sum_{i \in \mathcal{P}_j} \alpha_{ij} = 1$ for each pollinator j , and visitation rate $V_{ij} = \alpha_{ij} \tau a_j p_i$. The analysis retains τ in the effective conversion rate $c' = c b \tau$ but otherwise fixes its numerical value at 1 and suppresses it from expanded expressions; Appendix Table A1 reports the corresponding dimensionally explicit forms. Here, $\mathcal{P}_j$ is the set of plants visited by pollinator j , and $\mathcal{A}_i$ is the set of pollinators visiting plant i . See Appendix Table A1 for model notation, parameter definitions, and dimensions.

Plant dynamics (Eq. B1). Recruitment passes through three filters: pollination quality $\sigma_{ij} = V_{ij} / \sum_{k \in \mathcal{P}_j} V_{kj}$, seed-set fraction e_i , and the germination–competition fraction $\gamma_i = g_i (1 - \sum_{l \neq i} u_l p_l - w_i p_i)$, where u_l and w_i are inter- and intraspecific competition coefficients for non-pollinator resources. Mortality occurs at per-capita rate μ_i^P .

Pollinator dynamics (Eq. B2). Pollinator recruitment is proportional to rewards extracted during visits, $b V_{ij} R_i / p_i$, converted to new adults at rate c , with mortality at rate μ^A . Because pollinator species share the same demographic and reward-conversion parameters in this formulation, differences in pollinator abundance arise from their interaction partners and the resulting reward intake.

Reward dynamics (Eq. B3). Rewards accumulate through plant production, $\beta_i p_i$, are lost through reward decay or self-limitation, $\phi_i R_i$, and are depleted by pollinator consumption, $b V_{ij} R_i / p_i$.

Foraging effort dynamics (Eq. B4). Effort shifts toward plants offering above-average rewards and away from those offering below-average rewards, at rate $G c'$ ($c' = c \cdot b \cdot \tau$). If pollinator j maintains effort on all of its available links, rewards equalize across the plants it visits; if effort on some links declines to zero, reward equalization occurs only among the plants that remain in use.

Plant equilibrium density, persistence threshold, and the roles of pollination and competition

Dividing Eq. B1 by p_i and substituting $V_{ij} = \alpha_{ij} \tau a_j p_i$, plant per-capita growth takes the compact form

$$\frac{1}{p_i} \frac{dp_i}{dt} = g_i (U_i - w_i p_i) e_i Q_i - \mu_i^P, \quad (1)$$

where $Q_i \equiv \sum_{j \in \mathcal{A}_i} \sigma_{ij} \alpha_{ij} a_j$ is quality-weighted pollination service, and $U_i \equiv 1 - \sum_{l \neq i} u_l p_l$ is the fraction of the recruitment niche remaining after interspecific competition. Eq. (1) has two equilibria: the trivial equilibrium, $p_i^* = 0$, representing local extinction, and a non-trivial equilibrium, $p_i^* > 0$, satisfying $g_i (U_i^* - w_i p_i^*) e_i Q_i^* = \mu_i^P$. Solving for the non-trivial equilibrium gives

$$p_i^* = \frac{U_i^*}{w_i} - \frac{\mu_i^P}{g_i w_i e_i Q_i^*}. \quad (2)$$

The germination–competition factor $g_i (U_i - w_i p_i)$ is not truncated at zero, consistent with the formulation implemented in the simulations of this model. The analysis is

therefore restricted to biologically admissible states satisfying $U_i - w_i p_i \geq 0$, for which this factor is nonnegative. This restriction is satisfied automatically at any positive plant equilibrium. Specifically, the equilibrium identity gives

$$U_i^* - w_i p_i^* = \frac{\mu_i^P}{g_i e_i Q_i^*} > 0, \quad (3)$$

provided $\mu_i^P > 0$ and $Q_i^* > 0$. Thus, the germination–competition factor is strictly positive at any positive plant equilibrium, and p_i^* remains strictly below the competitive ceiling U_i^* / w_i . For transient states, I treat the biologically admissible domain $U_i - w_i p_i \geq 0$ as a maintained assumption, consistent with the biological interpretation that recruitment cannot be negative.

The non-trivial equilibrium (Eq. (2)) separates into two terms: the first, U_i^* / w_i , is the competitive ceiling set by the interspecific and intraspecific recruitment environment; the second is a mortality discount that shrinks as pollination service Q_i^* increases (Table 1). Equilibrium abundance therefore increases with Q_i^* but saturates toward U_i^* / w_i as

$Q_i^* \rightarrow \infty$. This separation clarifies the complementary roles of pollination and competition. Pollination service and the available recruitment niche, which incorporates interspecific competition, jointly determine whether a plant can maintain positive abundance. Intraspecific self-limitation contributes to setting the ceiling on equilibrium abundance that no amount of additional pollination can exceed.

Imposing $p_i^* > 0$ on Eq. (2) yields the minimum pollination threshold below which plant i cannot maintain a positive equilibrium:

$$Q_i^c \equiv \frac{\mu_i^P}{g_i e_i U_i^*}, \quad (4)$$

such that plant i has a positive equilibrium if and only if $Q_i^* > Q_i^c$; at equality, the non-trivial equilibrium collapses to zero. The threshold Q_i^c quantifies how much pollination service plant i needs to persist: it rises with increased mortality and interspecific competition pressure, represented by low U_i^* , and falls with greater germination and recruitment efficiency (Table 1). Notably, intraspecific competition w_i is absent from Q_i^c : self-crowding vanishes at the zero-abundance boundary and therefore does not enter the boundary threshold for positive equilibrium abundance. Interspecific competition nevertheless contributes directly to this threshold through U_i^* .

Table 1: Cross-scale quantities and persistence conditions. Five derived quantities link pollinator biology, plant demography, reward dynamics, foraging behavior, and network structure. Together, they characterize key equilibrium relationships and persistence conditions. Full state variables, functions, parameters, and dimensions are listed in Appendix Table A1.

Quantity	Formula	Biological levels	Cross-scale interpretation
Equilibrium reward R^*	$R^* = R^c = \frac{\mu^A}{c b \tau}$	Pollinator biology (μ^A, c, b, τ); governs R_i and α_{ij}	Common reward level across plants receiving positive equilibrium effort under adaptive foraging. It equals the zero-growth threshold R^c : positive pollinator growth requires $\bar{R}_j > R^c$, whereas a persisting pollinator at equilibrium satisfies $\bar{R}_j^* = R^c$.
Equilibrium visitation pressure v_i^*	$v_i^* = \frac{\beta_i p_i^* - \phi_i R^*}{b R^*}$	Plant reward budget (β_i, p_i^*, ϕ_i); pollinator biology (R^*); behavior and abundance ($\sum_j \alpha_{ij}^* a_j^*$)	Total effort-weighted visitation that plant i sustains at equilibrium; links plant abundance and reward dynamics to behavioral-level visitation.
Pollination threshold Q_i^c	$Q_i^c = \frac{\mu_i^P}{g_i e_i U_i^*}$	Plant vital rates (μ_i^P, g_i, e_i); available recruitment niche (U_i^*)	Pollination threshold for plant i when rare. Below Q_i^c , the plant declines; above it, the plant can persist at positive abundance.
Plant equilibrium abundance p_i^*	$p_i^* = \frac{U_i^*}{w_i} - \frac{\mu_i^P}{g_i w_i e_i Q_i^*}$	Recruitment competition (U_i^*, w_i); plant vital rates (μ_i^P, g_i, e_i); pollination service (Q_i^*)	Plant equilibrium separates into a competitive ceiling U_i^*/w_i and a pollination-dependent mortality discount; pollination and interspecific competition determine persistence; self-limitation caps abundance.
Pollinator effort-weighted mean reward $\bar{R}_j$	$\bar{R}_j = \sum_{i \in \mathcal{P}_j} \alpha_{ij} R_i$	Foraging effort (α_{ij}); reward dynamics (R_i); binary plant partners of pollinator j ($\mathcal{P}_j$)	Effort-weighted mean reward experienced by pollinator j across its binary diet; links receiving zero effort make no contribution. Positive growth requires $\bar{R}_j > R^c$; equality gives zero growth.

Note. The binary diet of pollinator j is $\mathcal{P}_j$, with degree $d_j = |\mathcal{P}_j|$, whereas its active equilibrium diet is $\mathcal{P}_j^+ = \{i \in \mathcal{P}_j : \alpha_{ij}^* > 0\}$, with active degree $d_j^+ = |\mathcal{P}_j^+|$. Under uniform fixed foraging, the equilibrium unweighted reward budget across the binary diet is $\mathcal{R}_j^* = \sum_{i \in \mathcal{P}_j} R_i^* = R^c d_j$. Under adaptive foraging, reward equalization across the active equilibrium diet gives $\mathcal{R}_j^* = \sum_{i \in \mathcal{P}_j^+} R_i^* = R^* d_j^+ = R^c d_j^+$. When all binary links are active, $d_j^+ = d_j$. These degree-scaled expressions are reward-budget identities, not independent physiological thresholds. Pollinator growth is governed by the effort-weighted mean reward $\bar{R}_j$: positive growth requires $\bar{R}_j > R^c$, whereas a persisting pollinator at equilibrium satisfies $\bar{R}_j^* = R^c$. Positive plant equilibrium abundance requires $Q_i^* > Q_i^c$.

Key results from simulation studies

Previous simulations of the model in [Box 1](#) identified the following outcomes, which the present analysis accounts for and explains mechanistically. Parentheses map each result to the corresponding findings in [Box 3](#).

R1. Adaptive foraging drives niche partitioning across scales. Adaptive foraging shifts effort toward high-reward plants, benefiting specialists that retain more unconsumed rewards than heavily visited generalists. This redistributes reward consumption among pollinators and pollination services among plants, enabling vulnerable specialists to persist [18, 19, 20]. (*Findings 2, 3, 5*)

R2. Adaptive foraging reverses the effects of binary network structure. Under fixed foraging, nestedness reduces persistence of communities and connectance increases persistence of communities; under adaptive foraging, these effects reverse. Thus, the same binary network structure can produce opposite outcomes depending on foraging behavior [19]. (*Finding 5*)

R3. Introduced-species traits better predict invasion success, whereas binary network structure better predicts impacts on native species. High foraging efficiency best predicts pollinator invasion success; high reward production, specialization, and high pollen attachability promote plant invasion success. Binary network structure mediates impacts on natives: diet overlap and the fraction of plants visited shape pollinator-invasion impacts, whereas plant richness buffers plant-invasion impacts [21, 22]. (*Findings 2 and 4*)

R4. Pollination governs plant transient persistence, whereas competition determines final abundance. Among persisting plants, final abundance is determined by recruitment competition, making pollination appear inconsequential at equilibrium. Yet pollination acts as a transient gatekeeper: plants must secure sufficient high-quality visits before rewards fall below levels that sustain pollinator effort. Otherwise, foraging effort can decline to zero on those plants, leading to extinction [20, 22]. (*Findings 1, 2, and 4*)

R5. Nestedness, moderate connectance, and adaptive foraging jointly maximize pollination services. Empirical, nested, moderately connected networks produced the highest pollen deposition rates when paired with adaptive foraging. Higher-than-empirical connectance reduced pollination services, whereas adaptive foraging enhanced them across network structures [23]. (*Finding 5*)

Pollinator zero-growth threshold and equilibrium density

Dividing Eq. B2 by a_j , the pollinator per-capita growth takes the compact form

$$\frac{1}{a_j} \frac{da_j}{dt} = c' \bar{R}_j - \mu^A, \quad \bar{R}_j \equiv \sum_{i \in \mathcal{P}_j} \alpha_{ij} R_i, \quad (5)$$

where $c' \equiv cb\tau$ is the effective conversion rate from floral rewards to pollinator growth and $\bar{R}_j$ is the foraging-effort-weighted mean standing reward available to pollinator j . Setting Eq. (5) equal to zero yields the effort-weighted reward threshold at which pollinator j has zero per-capita growth:

$$R^c \equiv \frac{\mu^A}{c'}. \quad (6)$$

Thus, pollinator j has positive per-capita growth when $\bar{R}_j > R^c$, zero per-capita growth when $\bar{R}_j = R^c$, and negative per-capita growth when $\bar{R}_j < R^c$. At any positive equilibrium with $a_j^* > 0$, this condition must hold with equality, so that $\bar{R}_j^* = R^c$. The threshold R^c quantifies how much effort-weighted floral reward is needed to balance pollinator mortality: it rises with increased mortality and falls with more efficient reward-to-animal conversion (Table 1). Notably, R^c is the same for every pollinator species because all share the same parameters μ^A and c' . Given these shared parameters, differences in growth, feasibility, and abundance therefore arise from differences in $\bar{R}_j$, which is determined by the binary network structure, that is, the plant species in j 's diet, $\mathcal{P}_j$, and by how foraging effort, α_{ij} , is distributed across those plants (see next subsection). Because $\bar{R}_j$ is effort-weighted, links assigned zero foraging effort do not contribute to the

reward experienced by pollinator j , even if they are present in the binary network structure.

The reward dynamics (Eq. B3) determine pollinator equilibrium abundance, which cannot be obtained from the pollinator per-capita equation (Eq. 5) alone because it contains no self-limiting term. Setting $dR_i/dt = 0$ and rearranging terms gives

$$a_j^* = \frac{1}{\alpha_{ij}^*} \left[\frac{\beta_i p_i^* - \phi_i R_i^*}{b R_i^*} - \sum_{\substack{k \neq j \\ k \in \mathcal{A}_i}} \alpha_{ik}^* a_k^* \right], \quad \alpha_{ij}^* > 0. \quad (7)$$

where the fraction inside brackets is the total effort-weighted visitation pressure that plant i can sustain at its equilibrium reward level, and the summation subtracts the visitation pressure already supplied by other pollinators. The bracketed quantity is therefore the contribution that pollinator j must provide to plant i ; dividing by α_{ij}^* gives the abundance of pollinator j required to generate that contribution on this link. This expression should be interpreted as a local reward-balance condition, not as a closed-form solution for pollinator abundance: a_j^* depends on the abundances of all other pollinators sharing plant i , and on the reward level R_i^* that is itself shaped by total visitation. Closure requires the coupled reward, foraging, and population dynamics, developed in the next subsection.

Rewards and foraging: R^* as pollinator zero-growth threshold, community budget, and the cross-scale mediator of specialist pollinator fate

Under the replicator dynamics (Eq. B4), effort shifts continuously toward plants offering above-average rewards and

away from those offering below-average rewards. This redistribution continues until plants receiving positive equilibrium effort provide the same standing reward. Thus, adaptive foraging equalizes rewards across used links, and this equality can propagate across pollinators and plants connected through positive-equilibrium foraging effort. It need not apply to links that are present in the binary network structure but receive zero effort at equilibrium. Because pollinator effort is normalized such that $\sum_{i \in \mathcal{P}_j} \alpha_{ij} = 1$, the term $\sum_{i \in \mathcal{P}_j} \alpha_{ij} R_i$ is the foraging-effort-weighted mean reward available to pollinator j . When the plants receiving positive equilibrium effort from pollinator j share a common value R^* , this weighted mean collapses to R^* regardless of diet breadth or effort distribution:

$$\sum_{i \in \mathcal{P}_j} \alpha_{ij}^* R_i^* = R^* \sum_{i \in \mathcal{P}_j} \alpha_{ij}^* = R^*. \quad (8)$$

Terms with $\alpha_{ij}^* = 0$ do not contribute to this weighted mean, even if the corresponding links are present in the binary network structure.

As shown above, pollinator j has positive per-capita growth when $\bar{R}_j > R^c$, zero per-capita growth when $\bar{R}_j = R^c$, and negative per-capita growth when $\bar{R}_j < R^c$ (Eq. 6). Any persisting pollinator at a positive equilibrium must have zero net growth, so this condition holds with equality. Substituting the equalized reward level R^* into the zero-growth condition therefore gives

$$R^* = R^c = \frac{\mu^A}{c'} = \frac{\mu^A}{cb\tau}, \quad (9)$$

which holds simultaneously for every persisting pollinator within a connected set of positive-equilibrium foraging links, given the shared pollinator parameters μ^A and c' . Eq. (9) defines both a population-level zero-growth condition and a community-level reward constraint. At the population scale, each persisting pollinator must experience the effort-weighted mean reward $\bar{R}_j^* = R^c$ at equilibrium. Under adaptive foraging, the plants receiving positive equilibrium effort from pollinator j share the common reward level $R^* = R^c$. Summing this common reward over the active equilibrium diet gives the corresponding unweighted equilibrium reward budget:

$$\mathcal{R}_j^* = \sum_{i \in \mathcal{P}_j^+} R_i^* = R^* d_j^+ = R^c d_j^+. \quad (10)$$

This reward-budget identity scales linearly with pollinator j 's active degree, d_j^+ (Table 1). Links present in the binary network structure but receiving zero equilibrium effort do not enter the adaptive-foraging identity. Thus, Eq. (10)

is a reward-budget identity, not an additional physiological requirement: pollinator growth is governed by the effort-weighted mean reward $\bar{R}_j$ in Eq. 5. This active-degree-scaled budget is a cross-scale emergent property: pollinator biology sets the common zero-growth reward level, while active degree specifies the number of plants over which the equalized standing-reward budget is evaluated. It is also an instance of the ideal free distribution [24], in which consumers redistribute across patches until all used patches yield equal returns, here the standing reward level R^* .

Degree scaling arises under both foraging scenarios, but the relevant degree and underlying mechanism differ (Appendix). Under uniform fixed foraging, effort is positive and equal across all d_j links in the binary diet, so the zero-growth condition constrains the arithmetic mean reward and implies the binary-diet reward-budget identity $\mathcal{R}_j^* = \sum_{i \in \mathcal{P}_j} R_i^* = R^c d_j$. Under adaptive foraging, reward equalization applies only across the active equilibrium diet and implies the active-set reward-budget identity $\mathcal{R}_j^* = \sum_{i \in \mathcal{P}_j^+} R_i^* = R^* d_j^+ = R^c d_j^+$. If all binary links remain active, then $d_j^+ = d_j$, and the two identities have the same numerical form. In both cases, pollinator growth is governed by the effort-weighted mean reward $\bar{R}_j$, not by an independent total-reward requirement. What adaptive foraging changes is not the physiological zero-growth threshold R^c , but rather how the reward landscape is reorganized and whether pollinators attain the required effort-weighted mean reward.

Without adaptive foraging, effort is fixed by the imposed foraging pattern. This can leave rewards unequal across plants and visitation misallocated relative to the reward levels required for pollinator zero growth, a dynamic that previous simulations showed can drive specialist pollinators to extinction in nested networks. Because specialists tend to visit only the most generalist plants, they face intense competition from the broader pollinator community, which can deplete local rewards below the zero-growth threshold. With adaptive foraging, generalist pollinators redirect their effort toward plants offering above-average rewards. This behavioral shift can release the visitation pressure on heavily visited generalist plants, allowing their rewards to recover toward R^* . Under those conditions, the specialist pollinator's zero-growth condition can be met. This survival occurs not because the specialist redistributes its own effort, since a species with $d_j = 1$ has nowhere else to go, but because generalists have reduced their pressure on the shared plant. Specialist persistence is therefore an indirect, cross-scale consequence of adaptive foraging, where the individual decisions of generalists determine the reward environment and ultimate persistence of specialists.

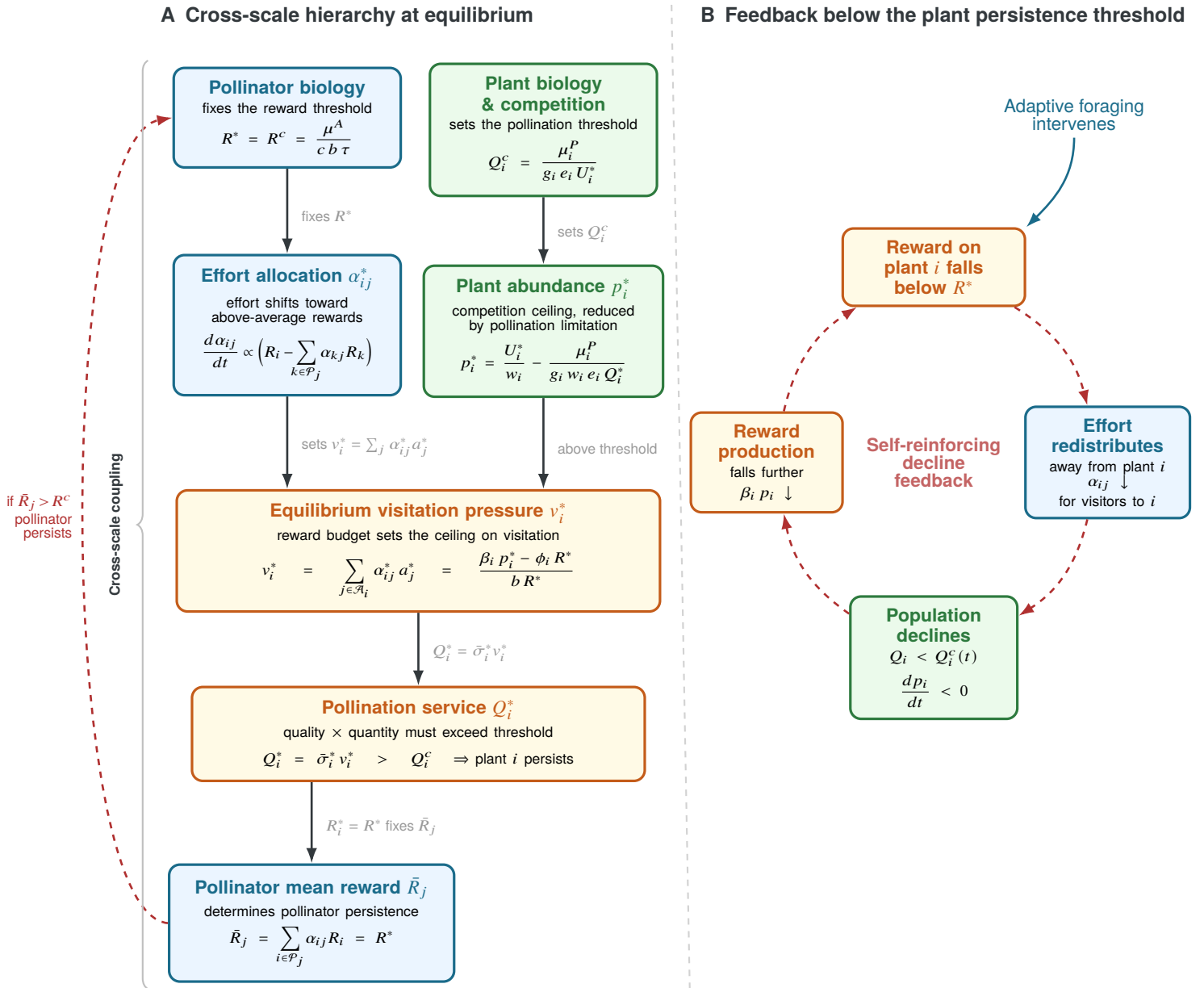


Figure 1: Cross-scale feedbacks determine persistence. (A) At equilibrium, foraging allocation, reward dynamics, pollination service, and population abundance couple processes across biological scales. Pollinator persistence requires the effort-weighted mean reward to reach the biologically determined threshold R^c ; adaptive foraging equalizes rewards at $R^* = R^c$ across links receiving positive equilibrium effort. Plant persistence requires $Q_i^* = \bar{\sigma}_i^* v_i^* > Q_i^c$, where the boundary threshold Q_i^c depends on plant demography and interspecific competition. (B) Pollination service below the instantaneous low-density threshold $Q_i^c(t)$ can initiate a self-reinforcing decline. Declining plant abundance reduces reward production, potentially lowering reward below R^* and redirecting foraging effort away from the plant. The resulting loss of visitation can keep $Q_i < Q_i^c(t)$ and maintain negative per-capita growth. At positive abundance, the exact growth condition also includes intraspecific competition (Eq. 1). Colors indicate biological domains: blue, pollinator traits and behavior; green, plant demography and competition; and orange, rewards and pollination service. See Table 1 for definitions of key quantities.

Visitation, Q_i^c , and the cross-scale determinants of plant persistence

The plant analysis above derived the boundary pollination threshold in Eq. 4. Equality at this threshold corresponds to zero per-capita growth at the zero-abundance boundary, whereas a positive plant equilibrium requires the strict inequality $Q_i^* > Q_i^c$. At positive abundance, the zero-growth

balance instead follows from Eq. 1 and includes abundance-dependent intraspecific competition. However, the actual pollination service Q_i^* remains unresolved because it depends on pollinator abundance, foraging behavior, and visit quality. The pollinator and reward analyses established that adaptive foraging links pollinator persistence to a common reward level, $R^* = R^c$, across plants connected through positive-

equilibrium foraging effort. The present analysis closes the loop by deriving the local reward-balance condition that constrains the equilibrium visitation pressure v_i^* received by plant i under this reward landscape. Together with visit quality, this condition determines whether pollination service exceeds the boundary threshold required for positive plant abundance.

Setting $dR_i/dt = 0$ and substituting $R_i^* = R^*$ yields the equilibrium constraint on visitation pressure (Table 1):

$$v_i^* \equiv \sum_{j \in \mathcal{A}_i} \alpha_{ij}^* a_j^* = \frac{\beta_i p_i^* - \phi_i R^*}{b R^*}, \quad (11)$$

for plants maintained at the common reward level R^* . The left-hand side is the abundance-weighted foraging effort directed at plant i , which I refer to as visitation pressure. This quantity depends jointly on pollinator abundances, foraging allocations, and the binary network structure. The right-hand side gives the visitation pressure that plant i 's reward production can sustain at standing reward R^* and plant abundance p_i^* . At equilibrium, reward production and reward removal must balance: the net reward production rate, $\beta_i p_i^* - \phi_i R^*$, equals the reward removed per unit time, $b R^* v_i^*$. This is the mutualistic analogue of Tilman's supply-consumption balance [20], expressed here as a reward zero-net-growth isocline condition. Thus, Eq. (11) is a local balance condition for visitation pressure, not a closed-form solution for v_i^* independent of p_i^* or the rest of the community. It also implies that positive visitation pressure at R^* requires $\beta_i p_i^* > \phi_i R^*$.

This reward balance closes the quantity left open in the plant analysis and motivates a decomposition of pollination service into two distinct constraints. Substituting v_i^* into the expression for Q_i^* yields:

$$Q_i^* = \bar{\sigma}_i^* v_i^*, \quad (12)$$

where

$$\bar{\sigma}_i^* = \frac{\sum_{j \in \mathcal{A}_i} \sigma_{ij}^* \alpha_{ij}^* a_j^*}{v_i^*}, \quad (13)$$

is the abundance- and effort-weighted mean visit quality received by plant i at equilibrium, defined when $v_i^* > 0$. The quantity v_i^* acts as a reward-budget constraint: it specifies the visitation pressure that plant i can sustain at abundance p_i^* and reward level R^* . The quantity $\bar{\sigma}_i^*$ acts as an efficiency constraint: it determines how much of that visitation pressure is converted into successful pollination. This conversion depends on the identity of visiting pollinators, the distribution of their foraging effort, and the resulting visit-quality terms σ_{ij}^* . Together, Eqs. (9)–(12) provide an equilibrium decomposition of plant persistence. Pollinator biology fixes the zero-growth reward level R^* . The reward balance constrains the visitation pressure v_i^* that each plant can sustain at that reward level. Finally, the product $Q_i^* = \bar{\sigma}_i^* v_i^*$ determines whether pollination service exceeds the boundary threshold required for positive plant abundance, $Q_i^* > Q_i^c$. At a positive plant equilibrium, the exact zero-growth balance follows from Eq. 1 and includes the intraspecific competition term $w_i p_i^*$. Plant persistence therefore requires both constraints to be satisfied simultaneously: the reward budget must sustain sufficient visitation pressure, and the network must convert

that visitation pressure into sufficiently effective pollination to exceed the boundary threshold.

The consequences of this decomposition are sharpest in nested networks. Without adaptive foraging, effort is fixed by the imposed foraging pattern and tends to be concentrated on generalist plants. Specialist plants consequently receive fewer visits, and the pollinators that do visit them are often generalists whose effort is spread across many species, reducing visit quality. Both v_i^* and $\bar{\sigma}_i^*$ can therefore be depressed. Specialist plants may fall below Q_i^c despite adequate pollinator abundance in the network, and can go extinct while generalists persist. With adaptive foraging, effort continuously redistributes toward plants retaining above-average rewards. Specialist plants, which are less heavily visited and therefore can carry more unconsumed rewards than generalists, attract increasing foraging effort as rewards equilibrate across the network. This redistribution can increase visitation pressure and alter the composition of visits, raising v_i^* , $\bar{\sigma}_i^*$, or both. Under those conditions, the plant persistence condition can be met through the redistribution of foraging effort.

Transient dynamics, cascades, invasibility, and the role of connectance

The preceding analyses characterize the network equilibrium structure by defining the plant and pollinator zero-growth thresholds, Q_i^c and R^c , and by establishing the common reward level R^* for pollinators at positive equilibrium under adaptive foraging (Eqs. 4, 6, 9). They also decompose pollination service into distinct reward-budget and efficiency constraints (Eqs. 11, 12). The focus now shifts from equilibrium decomposition to the dynamics between equilibria: how perturbations propagate through the network, why some state transitions can become self-reinforcing, and what the same zero-growth thresholds imply for the finite-density establishment of new species.

During transient dynamics, the available recruitment niche may change as competitor abundances change. I therefore define the instantaneous low-density pollination threshold as $Q_i^c(t) \equiv \mu_i^P / [g_i e_i U_i(t)]$, which reduces to Eq. 4 when the competitive environment is evaluated at equilibrium. Near low plant abundance, a perturbation that reduces Q_i below $Q_i^c(t)$ produces negative per-capita growth and can initiate a self-reinforcing decline (Figure 1B). More generally, at positive abundance, the exact instantaneous zero-growth condition follows from Eq. 1 and includes the intraspecific term $w_i p_i$. Declining plant abundance p_i reduces reward production, $\beta_i p_i$. This reduction can depress the standing reward R_i , which in turn can reduce visitation pressure and pollination service further. Recovery from low abundance requires Q_i to increase strictly above $Q_i^c(t)$; equality gives zero per-capita growth at the low-density boundary. However, because reward production scales with plant abundance, a plant at low abundance may be unable to generate sufficient reward to attract pollinators and restore positive growth. This feedback can operate in specialist plants receiving diluted visitation from effort-spread generalist pollinators, in generalist plants losing foraging effort to higher-reward alternatives under high connectance, and in introduced plants that begin at abundances too low to generate the reward necessary for establishment.

In nested networks with moderate connectance, generalist plants are often the most buffered nodes against pollination failure. They receive many visits in the network and are frequently visited by specialist pollinators that have few or no alternative plant links. This reliance can provide a stable base of high-quality visits that keeps Q_i above the relevant instantaneous growth threshold. High connectance can erode this protection. When specialist pollinators acquire links to additional plant species, they may redirect effort toward higher-reward alternatives. If rewards on generalist plants fall below those alternatives, this behavioral shift can reduce visitation pressure to the formerly buffered hub. If Q_i falls below the relevant instantaneous growth threshold, the self-reinforcing decline described above can be triggered, converting a buffered generalist plant into a vulnerable node.

The plant per-capita growth equation and boundary pollination threshold (Eqs. 1 and 4) also constrain establishment. Consider an introduced plant i that shares pollinators with resident plants of positive abundance. If, for each pollinator shared with resident plants, those residents continue to contribute positively to the denominator of the visit-quality term σ_{ij} (Box 1) as $p_i \rightarrow 0$, and pollinator abundances and foraging efforts remain bounded, then

$$\begin{aligned} V_{ij} &= O(p_i), & \sigma_{ij} &= O(p_i), & Q_i &= O(p_i), \\ \frac{1}{p_i} \frac{dp_i}{dt} &= -\mu_i^P + O(p_i). \end{aligned} \quad (14)$$

Here, $O(p_i)$ denotes a quantity whose magnitude is bounded by a constant multiple of p_i as $p_i \rightarrow 0$. Consequently, $\lim_{p_i \rightarrow 0} p_i^{-1} dp_i/dt = -\mu_i^P < 0$, so under these resident-community conditions the introduced plant cannot invade from infinitesimal rarity. It instead faces a finite-density establishment barrier: at low abundance, limited reward production can restrict visitation and pollination service, keeping per-capita growth negative. A high reward production rate β_i can

help overcome this barrier at a low but finite abundance, but establishment also depends on resident-community composition, foraging allocation, visit quality, recruitment ability, and network position. This limit does not cover other boundary configurations, including cases in which a pollinator visits only the introduced plant or no positive resident contribution remains in the denominator of the visit-quality term; in such cases, σ_{ij} need not be $O(p_i)$ and a separate boundary analysis is required.

The same logic extends to pollinators. An introduced pollinator species can invade when the effort-weighted mean reward it experiences in the resident network exceeds its own zero-growth threshold, R^c (Eq. 6). This excess reward is the requirement for positive per-capita growth at low pollinator density (Eq. 5). If the resident community already operates at $R^* = R^c$ for resident pollinators with the same demographic and conversion parameters, then an invader sampling the same reward landscape finds rewards at the zero-growth threshold rather than above it. Without a reward surplus, such an invader cannot increase. Successful invasion therefore requires conditions that decouple the invader's growth threshold from the resident equilibrium reward level. First, the resident community may not have fully depleted rewards to R^* , leaving available rewards above the invader's R^c . Second, the invader may possess a higher reward-to-animal conversion efficiency c' , or lower mortality μ^A , which lowers its own R^c below the standing reward level. This route introduces parameter asymmetry relative to resident pollinators and therefore falls under the equal-parameter limitation discussed below. Third, the invader may use a subset of plants whose rewards remain above the community-wide zero-growth level. Under these scenarios, invasibility remains tightly linked to the same reward threshold that structures resident persistence. Thus, R^* functions as a population-level zero-growth condition, a community-level reward constraint, and a benchmark for cross-guild invasibility.

BOX 3

Novel findings from the mathematical analysis

F1. Pollination and interspecific competition determine plant persistence; intraspecific competition limits abundance. Positive equilibrium abundance requires pollination service to exceed Q_i^c , a boundary threshold that incorporates plant demography and interspecific competition through U_i^* . Intraspecific competition w_i does not affect this persistence threshold because self-crowding vanishes at the zero-abundance boundary. Instead, it limits positive equilibrium abundance, which decomposes into a competitive ceiling (U_i^*/w_i) and a pollination-dependent mortality discount (Eq. 2).

F2. The common equilibrium reward links three biological scales. Under equal pollinator parameters, adaptive foraging equalizes rewards across positive-equilibrium links at $R^* = R^c$ (Eq. 9), linking: (i) *population persistence*, because a persisting pollinator satisfies $\bar{R}_j^* = R^c$, whereas positive growth requires $\bar{R}_j > R^c$; (ii) *the community reward budget*, because the active equilibrium diet satisfies $\mathcal{R}_j^* = \sum_{i \in \mathcal{P}_j^+} R_i^* = R^* d_j^+ = R^c d_j^+$ (Eq. 10); and (iii) *invasibility*, because an introduced pollinator can establish only when its effort-weighted mean reward exceeds its own zero-growth threshold.

F3. Pollination service decomposes into quantity and quality constraints that must both be satisfied. At equilibrium, $Q_i^* = \bar{\sigma}_i^* v_i^*$ (Eqs. 11–12). Positive plant abundance requires $Q_i^* > Q_i^c$: the reward budget must sustain sufficient visitation quantity, and the network must convert those visits into sufficiently effective pollination. These constraints act jointly with the interspecific competitive recruitment environment contained in Q_i^c .

F4. Low-density feedbacks create persistence and establishment barriers. At the zero-abundance boundary, intraspecific competition vanishes, and positive growth requires $Q_i > Q_i^c(t) = \mu_i^P / [g_i e_i U_i(t)]$; at equilibrium, $Q_i^c(t)$ reduces to Q_i^c . For a declining resident, low abundance can reduce rewards and visitation, keeping pollination service below this threshold and reinforcing decline (Figure 1B). For an introduced plant, the conditions of Eq. 14 prevent this threshold from being exceeded at infinitesimal rarity, creating a finite-density establishment barrier.

F5. Nestedness can create the network conditions that make adaptive foraging effective; high connectance can erode them. Nestedness can generate an asymmetry in unconsumed rewards between generalist and specialist plants, giving pollinators a reward gradient to follow, while specialist pollinators visiting generalist plants can help keep those plants above Q_i^c . High connectance can erode both conditions: as connectance increases, specialist pollinators acquire additional links, weakening the association that protected generalist plants, while specialist plants become accessible to a broader pollinator set, reducing the reward asymmetry that directed effort toward them.

First principles connect structure, behavior, persistence, and invasions

The analytical framework derived above provides a mechanistic explanation for the dynamics observed in previous simulations (Box 2). By mapping these numerical results onto the mathematical findings organized in Box 3, this analysis shows how the model's complex outcomes can be understood as consequences of a common set of first principles. Rather than serving as a complete closed-form solution for all equilibrium abundances, the framework decomposes community persistence into coupled constraints linking reward production, adaptive foraging, pollinator growth, pollination service, and plant recruitment. This decomposition explains how cross-scale feedbacks shape community-level persistence and establishment.

First, Eq. 2 decomposes p_i^* into a competitive ceiling and a pollination-dependent mortality discount. This decomposition clarifies a result from previous simulations: pollination determines whether plant species cross the threshold for persistence, but in the parameter regimes explored in previous simulations, it had little influence on the final equilibrium abundance of surviving plants (Result 4 in Box 2). This occurs because the pollination-dependent discount, $\mu_i^P / (g_i w_i e_i Q_i^*)$, declines as pollination service increases, causing surviving plants to approach the competitive ceiling U_i^*/w_i . The strength of this separation depends on parameter regime: when plant mortality is low or pollination service is sufficiently high, the discount becomes small and abundance is

dominated by recruitment competition; when mortality is high or pollination service remains close to the threshold, abundance remains more sensitive to variation in pollination. The pattern that pollination governed persistence while competition largely determined final abundance is therefore a simulation result for the regimes explored. More generally, the analysis shows that pollination service and the available recruitment niche, which incorporates interspecific competition, jointly determine whether a positive plant equilibrium is feasible, whereas intraspecific self-limitation caps positive abundance.

Second, the derivations specify how network structure and foraging behavior interact to determine persistence (Results 1, 2, and 5). The analysis identifies two linked pathways that operate in nested networks. Nestedness concentrates specialist pollinator species on generalist plant species, where they may experience strong competition for rewards. Adaptive generalist pollinators can redistribute effort toward plants retaining higher standing rewards, reducing visitation pressure on heavily shared plants and allowing local rewards to recover toward the pollinator zero-growth level $R^* = R^c$. This indirect behavioral shift can allow specialist pollinators to meet their zero-growth condition even though they cannot redistribute their own effort when $d_j = 1$ (part (i) of Finding 2). A complementary pathway operates for plants through pollination quality: generalist plants can receive reliable, high-quality visits from specialist pollinators, helping keep pollination service above Q_i^c . High connectance can erode

both mechanisms. By adding links to pollinators that would otherwise be restricted to generalist plants, high connectance weakens their dependence on those generalist plants and can shift foraging effort away from generalist plants toward alternative plants with higher standing rewards. If this shift reduces effective pollination below Q_i^c , the self-reinforcing decline described in Figure 1B can be triggered.

Finally, this framework links native persistence and biological invasions through the same growth thresholds (Results 3 and 4). For pollinators, invasion requires the effort-weighted mean reward experienced by the invader to exceed its own zero-growth threshold. Thus, an alien pollinator can establish if resident standing rewards exceed its required R^c , or if higher conversion efficiency, lower mortality, or access to a high-reward subset of plants lowers its threshold below the reward level it experiences; the parameter-asymmetry route is subject to the equal-parameter limitation discussed below. For plants, finite-density establishment is constrained by the same pollination threshold that governs persistence: the invader must generate enough reward, receive enough visitation pressure, and convert that visitation into sufficient effective pollination to exceed Q_i^c . High reward production can lower the finite initial abundance needed to overcome the low-abundance feedback by attracting visits sooner, but it does not remove the establishment barrier; establishment also depends on visit quality and the network's redistribution of foraging effort. Thus, the same first principles that explain native persistence also provide a mechanistic basis for understanding invasion outcomes.

Discussion

The central question of this paper was whether a complex mechanistic cross-scale ecological model can be analytically decomposed into coupled thresholds, and whether that decomposition can convert mechanistic detail into general principles of persistence, collapse, and invasion that were not apparent from simulations alone. The answer is yes. Complex mechanistic models are often viewed as too parameter-rich to yield general theoretical insight, but this criticism can overlook what mechanistic detail makes possible. In ecological models, mechanisms are not merely additional parameters or equations; they are biological hypotheses about how organisms behave, interact, and affect one another across scales. Here, analytical decomposition reduces the model's cross-scale feedbacks to a set of coupled thresholds linking individual foraging behavior, floral reward dynamics, plant recruitment, pollinator demography, and binary network structure. These constraints show that persistence, extinction, and invasion depend not on binary network structure, demography, behavior, or rewards alone, but on how thresholds couple these processes across scales. Community persistence therefore emerges, in the model, from this cross-scale coupling.

The analytical decomposition developed here rests on quantities that sequentially constrain others (Figure 1A). Under

equal pollinator demographic parameters, pollinator biology fixes a common pollinator zero-growth reward requirement, realized at equilibrium as R^* , which constrains the reward landscape and shapes foraging allocation across the active network. The foraging dynamics that produce this equilibrium are governed by the replicator equation [13, 18], in which effort is continuously redistributed toward higher-reward plants until all plants in the active set—those receiving positive equilibrium effort—yield equal returns. Here, that individual-level process scales up: R^* becomes a community-level constraint on the actively used portion of the network, shaping the visitation each plant can sustain and, through it, whether that visitation meets the plant threshold Q_i^c (Figure 1A). Because each threshold or derived quantity (R^* , Q_i^c , v_i^* , $\bar{\sigma}_i^*$, and, for invaders, R^c ; Table 1) encodes cross-scale interactions into an analytically separable expression, the causal chain remains both biologically interpretable and mathematically modular.

The mathematical modularity of these quantities supports explicit, parameter-grounded predictions under novel conditions [5, 6]. A physiological stressor increasing pollinator mortality (μ^A) increases the pollinator zero-growth reward level (R^*), shifting the persistence landscape in a direction and by a magnitude that follow directly from the analytical threshold expression. An environmental stressor reducing plant recruitment potential (U_i^*) elevates the plant zero-growth threshold (Q_i^c), with consequences for plant persistence that are similarly traceable through the analytical threshold expressions. Such mechanism-based interpretation can be difficult to obtain from phenomenological models [5, 8] and illustrates what cross-scale analytical frameworks can contribute. The threshold expressions identify where a perturbation enters and how it shifts the relevant biological constraints, while realized community dynamics remain determined by the coupled state of the system.

The derived thresholds also inform transient dynamics, exposing feedback processes that can dominate ecologically relevant timescales [25, 26]. During a transient, changes in competitor abundances alter the available recruitment niche $U_i(t)$ and therefore the pollination service required for positive plant growth. Near the zero-abundance boundary, this requirement is represented by the instantaneous threshold $Q_i^c(t) = \mu_i^P / [g_i e_i U_i(t)]$; at positive abundance, the exact instantaneous growth condition also includes intraspecific competition, as specified by Eq. 1. When a perturbation reduces pollination service below the relevant instantaneous threshold, it can initiate a self-reinforcing feedback: declining plant abundance reduces aggregate reward production, which can depress standing rewards and further reduce visitation. Recovery requires pollination service to rise strictly above the instantaneous low-density threshold and, at positive abundance, to satisfy the exact growth condition that includes intraspecific competition. Such recovery may be unattainable within the closed dynamics without external rescue or parameter change.

Table 2: Equilibrium outcomes with and without adaptive foraging. Without adaptive foraging, effort is uniform across the binary diet; with adaptive foraging, effort follows Eq. B4. Here, R^c is the pollinator zero-growth threshold, R^* is the common reward across plants receiving positive equilibrium effort, Q_i^c is the plant persistence threshold, and $\mathcal{R}_j^*$ is the equilibrium unweighted reward budget.

Feature	Without adaptive foraging	With adaptive foraging
<i>Core mechanisms</i>		
Reward distribution	Rewards can remain unequal because they are shaped by network structure and fixed effort.	Rewards equalize at $R^* = R^c$ across plants receiving positive equilibrium effort from persisting pollinators.
Foraging effort allocation	Effort is uniform across the binary diet, with $\alpha_{ij} = 1/d_j$ for $i \in \mathcal{P}_j$.	Effort shifts toward above-average rewards until rewards equalize across the active equilibrium diet.
<i>Species persistence</i>		
Specialist plants	Can fall below Q_i^c when fixed effort provides insufficient visitation.	Can persist when redirected effort raises pollination service above Q_i^c .
Generalist plants	Often receive enough visitation from multiple pollinators to maintain $Q_i^* > Q_i^c$.	May lose generalist effort but retain visitation from specialists lacking alternative links.
Specialist pollinators	Can experience $\bar{R}_j < R^c$ when high visitation depletes rewards on shared plants.	Can persist when generalists reduce effort on shared plants, allowing rewards to recover toward $R^{c\dagger}$.
Generalist pollinators	Access multiple reward sources, but persistence still requires $\bar{R}_j \geq R^c$.	Redistribute effort across their diets, with persisting pollinators satisfying $\bar{R}_j^* = R^c$.
<i>Network-level effects</i>		
Degree-scaled reward budget	For a persisting pollinator at equilibrium, uniform fixed foraging gives $\mathcal{R}_j^* = \sum_{i \in \mathcal{P}_j} R_i^* = R^c d_j$.	For a persisting pollinator at equilibrium, reward equalization gives $\mathcal{R}_j^* = \sum_{i \in \mathcal{P}_j^+} R_i^* = R^* d_j^+ = R^c d_j^+$.
Nestedness effect	Can disadvantage specialists when fixed effort concentrates visitation on generalist plants.	Can create reward asymmetries that make adaptive redistribution effective.
Connectance effect	Can increase persistence by broadening visitation and reward access.	Can weaken reward gradients by giving pollinators additional links.
Threshold mechanism	Persistence requires sufficient reward intake for pollinators and pollination service for plants.	Redistribution changes whether species attain $\bar{R}_j \geq R^c$ and $Q_i > Q_i^c$ (Box 3; Fig. 1B).

[†]Simulation-based result [18, 19, 23].

These same mathematical boundaries also inform community assembly and invasion. Whether species are being lost following a perturbation or gained during assembly, the rewards produced by the resident community constrain whether species-specific growth requirements can be met. For pollinators, invasion requires the effort-weighted mean reward in the resident community to exceed the invader's zero-growth reward level, R^c . For plants, Eq. 14 shows that, when shared pollinators continue to receive positive resident contributions to visit quality, an introduced plant cannot invade from infinitesimal rarity. Establishment instead requires a finite initial density at which reward production, visitation pressure, and visit quality generate sufficient pollination service for positive growth before demographic decline eliminates the invader. Thus, the resident reward landscape simultaneously determines whether resident pollinators meet their

population-level persistence condition, imposes a community-level reward budget, and acts as an environmental filter for cross-guild invasibility. This shared analytical framework shows how individual-level adaptive foraging dynamics can scale up to shape community-level patterns of biodiversity and persistence. This shared threshold structure was not visible in the simulation studies that first characterized invasion dynamics in this model [21, 22], and only becomes apparent when the model's threshold structure is resolved analytically.

This mechanistic decomposition also clarifies how adaptive foraging interacts with nested binary network structure to promote species persistence. The analytical framework presented here shows that this persistence-promoting effect [18, 19] arises from the combination of a structural anchoring mechanism and a behavioral redistribution mechanism. First, nestedness places specialist pollinators on generalist plants,

and because these pollinators are constrained to a single plant partner with $\alpha_{ij} = 1$, they provide reliable high-quality visitation that cannot be reallocated elsewhere, helping keep generalist plants above Q_i^c . Second, generalist pollinators adaptively redistribute effort among the plants they visit, releasing heavily shared plants so rewards can recover toward R^* for specialist pollinators while directing effort toward less-visited specialist plants with higher standing rewards that would otherwise receive insufficient pollination service. Together, these mechanisms explain why nestedness can promote community persistence when coupled with adaptive foraging: constrained specialists anchor visitation to generalist plants, while flexible generalists redistribute effort in ways that support both specialist pollinators and specialist plants. High connectance can undermine persistence by eroding these same rescue mechanisms, especially when additional links weaken formerly exclusive associations with generalist plants and allow foraging effort to shift away from generalist plants toward alternatives with higher standing rewards. Because these mechanisms emerge from the coupling between binary network structure, adaptive foraging effort, and consumer-resource dynamics, they may operate in other mutualistic systems sharing this architecture, including multiplex networks where mutualistic and antagonistic interactions co-occur [27].

Two limitations define important directions for extending this framework. First, the analysis requires parameter equality among pollinator species: conversion efficiency c , per-visit reward extraction b , and mortality rate μ^A are shared, producing one common R^* for all pollinators. This assumption is necessary here for isolating the role of network structure. Under Tilman's R^* rule, allowing these parameters to vary would introduce fitness differences that drive competitive exclusion within shared-resource subsets [28, 29]. Without counteracting stabilizing mechanisms, the pollinator with the lowest zero-growth reward requirement would exclude its competitors, making survival depend on parameter asymmetry rather than network architecture [18, 19, 20]. Yet real pollinators differ substantially in body size, metabolic rate, and mortality [30, 31, 32, 33]. Future work should therefore identify how adaptive foraging interacts with stabilizing mechanisms such as predation, environmental variability, or storage effects to allow natural networks to persist despite the zero-growth hierarchies imposed by trait variation. Second, the model assumes a fixed potential network topology. Pollinators can redistribute effort among established partners, but entirely novel interactions cannot form. In natural systems, species may sometimes avoid extinction by foraging outside their historical network or by shifting phenology [e.g., 34, 35, 36, 37]. Computational extensions of this [38] and other modeling frameworks [39, 40] show that such topological and temporal flexibility can buffer communities against co-extinction. Incorporating these dynamic rescue mechanisms into the analytical boundaries derived here is an important next step toward predicting network resilience under severe perturbation.

The implications of this analysis extend beyond this specific model of plant–pollinator mutualism. In ecological networks where consumers dynamically reallocate effort among re-

sources, behavioral equilibrium can impose a mathematical constraint on population dynamics. Here, that constraint allowed the demographic equations to be decomposed into zero-growth thresholds, revealing how species-level persistence depends on community-level rewards, interaction structure, and adaptive foraging. This result suggests a broader strategy for ecological theory: using mechanistic models and simulations to identify recurrent patterns and candidate organizing variables, then using analytical decomposition to determine the biological conditions under which those patterns arise. Simulations are therefore not an endpoint, but a starting point for theory. The analysis presented here shows how mechanistic detail can be converted into general insight by identifying the thresholds, feedbacks, and cross-scale constraints that determine when ecological networks persist, assemble, invade, or collapse.

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Data and code availability

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Competing interests

The author declares no competing interests.

AI use statement

AI-assisted tools were used to improve prose. The author reviewed and edited all AI-assisted text and remains fully responsible for the content of the manuscript.

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