

# Appendix A from F. S. Valdovinos and R. Marsland III, “Niche Theory for Mutualism: A Graphical Approach to Plant-Pollinator Network Dynamics” (Am. Nat., vol. 197, no. 4, p. 393)

## Analysis of Adaptive Foraging Equation

In this appendix, we show that the adaptive foraging dynamics given in equation (4) cause the zero net growth isocline (ZNGI) of a pollinator species  $j$  to rotate about a point in rewards space, whose coordinates are given by the minimum reward abundance  $R_{ij}^*$  required for the pollinator to survive under a pure specialist strategy focused on plant species  $i$ .

First of all, setting  $da_j/dt = 0$  in equation (2), with  $\alpha_{ij} = 1$  and  $\alpha_{kj} = 0$  for all  $k \neq i$ , we obtain the equilibrium condition under the pure specialist strategy:

$$0 = c_{ij}\tau_{ij}b_{ij}a_jR_i - \mu_j^A a_j. \quad (\text{A1})$$

Solving for the reward abundance, we obtain

$$R_{ij}^* = \frac{\mu_j^A}{c_{ij}\tau_{ij}b_{ij}}. \quad (\text{A2})$$

This is the same as equation (7), but we have added an index  $j$  to indicate that this point can in general be different for each pollinator species, depending on the choice of parameters.

Next, we confirm that the adaptive foraging dynamics of equation (4) preserve the constraint  $\sum_{i \in P_j} \alpha_{ij} = 1$  imposed in the initial conditions, by computing

$$\frac{d}{dt} \sum_{i \in P_j} \alpha_{ij} = G_j \sum_{i \in P_j} \alpha_{ij} \left( c_{ij}\tau_{ij}b_{ij}R_i - \sum_{k \in P_j} \alpha_{kj}c_{kj}\tau_{kj}b_{kj}R_k \right) \quad (\text{A3})$$

$$= G_j \left( 1 - \sum_{i \in P_j} \alpha_{ij} \right) \sum_{k \in P_j} \alpha_{kj}c_{kj}\tau_{kj}b_{kj}R_k. \quad (\text{A4})$$

Thus, if  $\sum_{i \in P_j} \alpha_{ij} = 1$  at any point in time, the derivative vanishes, and it remains equal to this value for all times.

Finally, we show that this constraint on the sum of  $\alpha_{ij}$  guarantees that the point  $R_{ij}^*$  defined above always lies on the ZNGI, that is, that  $da_j/dt$  always vanishes there:

$$\frac{da_j}{dt} = \sum_{i \in P_j} c_{ij}\alpha_{ij}\tau_{ij}b_{ij}a_jR_{ij}^* - \mu_j^A a_j \quad (\text{A5})$$

$$= \sum_{i \in P_j} \alpha_{ij}\mu_j^A a_j - \mu_j^A a_j = 0. \quad (\text{A6})$$

# Appendix B from F. S. Valdovinos and R. Marsland III, “Niche Theory for Mutualism: A Graphical Approach to Plant-Pollinator Network Dynamics” (Am. Nat., vol. 197, no. 4, p. 393)

## Conditions for Coexistence among Plant Species

Unlike the population growth rate of pollinators that entirely depends on rewards abundances, the population growth rate of plants in the Valdovinos et al. model considers other factors (e.g., space or nutrient limitation) that are captured by a generic Lotka-Volterra-type function of plant competition composed of intraspecific (or self-limitation) and interspecific competition coefficients ( $w_i$  and  $u_i$ , respectively) that affect plant recruitment rate ( $\gamma_i$  in eq. [D3]) and are independent of the mutualistic interaction with pollinators. The standard conditions for stable coexistence in Lotka-Volterra models therefore represent a necessary condition for plant coexistence. Whether a plant species actually persists at equilibrium also depends on whether it receives sufficient pollination services, which will be discussed in appendix C below.

To simplify our analysis, in the main text we focus on the case of low interspecific competition (i.e.,  $u_i \ll w_i$ ), which is also the regime where all the relevant numerical simulations were performed (Valdovinos et al. 2013, 2016, 2018), so we can safely approximate  $p_i^* \approx 1/w_i$  under conditions of adequate pollination.

To go beyond this regime and obtain necessary coexistence conditions with nonnegligible interspecific competition, we must examine the stability of the fixed points of the plant dynamics given by equation (1). To keep the problem tractable, we will treat  $\alpha_{ij}$  as fixed parameters and assume that  $a_j$  quickly relax to the equilibrium value  $a_j^*(p_k)$  corresponding to the current plant abundances. Under these assumptions, the stability of the plant equilibrium depends on the eigenvalues of the Jacobian matrix

$$J_{ik} = \frac{\partial}{\partial p_k} \frac{dp_i}{dt} = \frac{\partial \gamma_i}{\partial p_k} \sum_{j \in A_i} e_{ij} \sigma_{ij} V_{ij} + \gamma_i \frac{\partial}{\partial p_k} \sum_{j \in A_i} e_{ij} \sigma_{ij} V_{ij} - \mu_i^p \delta_{ik}, \quad (\text{B1})$$

evaluated at the equilibrium point  $p_i^*$ . If all eigenvalues have negative real parts, then the equilibrium is stable.

To further streamline the calculation, we will assume that  $w_i = w$  for all  $i$  and  $u_i = u$  for all  $i$ . This allows us to state the results in terms of the relative strength of interspecific ( $u$ ) versus intraspecific ( $w$ ) competition. Evaluating the derivatives, we then find

$$J_{ik} = - \left( g_i \sum_{j \in A_i} e_{ij} \sigma_{ij} V_{ij} \right) [(w - u) \delta_{ik} + u] + \gamma_i \sum_{j \in A_i} e_{ij} \sigma_{ij} \alpha_{ij} \tau_{ij} p_i^* \frac{\partial a_j^*}{\partial p_k} + \left( \gamma_i \sum_{j \in A_i} e_{ij} \sigma_{ij} \alpha_{ij} \tau_{ij} a_j^* - \mu_i^p \right) \delta_{ik}. \quad (\text{B2})$$

The final term in parentheses is equal to  $d \log p_i / dt$  for  $p_i > 0$ , so it must vanish whenever all of the plants coexist. To determine the sign of the eigenvalues for the remaining portion, it is convenient to define the diagonal matrix  $\mathbf{D}$  with components

$$D_{ik} = \delta_{ik} g_i \sum_{j \in A_i} e_{ij} \sigma_{ij} V_{ij} \quad (\text{B3})$$

and a matrix  $\mathbf{A}$  with components

$$A_{ik} = \frac{\gamma_i \sum_{j \in A_i} e_{ij} \sigma_{ij} \alpha_{ij} \tau_{ij} p_i^* (\partial a_j^* / \partial p_k)}{g_i \sum_{j \in A_i} e_{ij} \sigma_{ij} V_{ij}}. \quad (\text{B4})$$

We can now write the Jacobian  $\mathbf{J}$  in matrix notation as

$$\mathbf{J} = -\mathbf{D}[(w - u)\mathbf{I} + \mathbf{U} - \mathbf{A}], \quad (\text{B5})$$

where  $\mathbf{I}$  is the identity matrix and  $\mathbf{U}$  is a matrix with elements  $U_{ij} = u$ .

In the low mortality limit  $\mu_i^P \rightarrow 0$ , the steady state occurs at  $\gamma_i \rightarrow 0$ , so  $\mathbf{A} \rightarrow 0$ . In this case, the eigenvalues of  $[(w - u)\mathbf{I} + \mathbf{U}]$  can be evaluated exactly, with one eigenvalue equal to

$$\lambda^+ = w + (P - 1)u \quad (\text{B6})$$

and the rest equal to

$$\lambda^- = w - u. \quad (\text{B7})$$

For any symmetric matrix  $\mathbf{M}$  with all negative eigenvalues (a so-called stable matrix), the product  $\mathbf{DM}$  with any diagonal matrix  $\mathbf{D}$  with all positive entries also has all negative eigenvalues. This property of maintaining stability under multiplication by a positive diagonal matrix  $\mathbf{D}$  is known as D-stability, and it has been proven that all sign-symmetric stable matrices are also D-stable (Hershkowitz and Keller 2003). Applying this to the case at hand, we see that the eigenvalues of  $\mathbf{J}$  are all negative if and only if  $\lambda^- > 0$ . Thus, we recover for arbitrary numbers of species the classic result of modern coexistence theory for two species: stable coexistence requires that intraspecific competition ( $w$ ) is stronger than interspecific competition ( $u$ ; Chesson 2000).

To determine the impact of nonzero  $\mathbf{A}$ , we focus on the case where all pollinators are pure specialists, with identical parameters. Then  $\mathbf{A}$  is proportional to the identity matrix:

$$\mathbf{A} = \frac{1 - [(P - 1)u + w]p^*}{a^*} \frac{\partial a^*}{\partial p} \mathbf{I}, \quad (\text{B8})$$

where  $p_i^* = p^*$  and  $a_j^* = a^*$  for all  $i$  and  $j$ , since all of the parameters are the same. Since the pollinators feed on the rewards produced by the plants,  $\partial a^* / \partial p$  is always positive. The smallest eigenvalue of  $[(w - u)\mathbf{I} + \mathbf{U} - \mathbf{A}]$  becomes

$$\lambda^- = \tilde{w} - u, \quad (\text{B9})$$

where the effective intraspecific competition coefficient  $\tilde{w}$  is

$$\tilde{w} = w - \frac{1 - [(P - 1)u + w]p^*}{a^*} \frac{\partial a^*}{\partial p}, \quad (\text{B10})$$

which is always less than  $w$ . This means that the low-mortality criterion  $w > u$  remains a necessary condition for coexistence. We conjecture that this remains true for arbitrary pollinator parameters and connectivity because there is no obvious reason why competition between different species of pollinators should selectively provide additional intraspecific feedback for the plants.

## Appendix C from F. S. Valdovinos and R. Marsland III, “Niche Theory for Mutualism: A Graphical Approach to Plant-Pollinator Network Dynamics” (Am. Nat., vol. 197, no. 4, p. 393)

### Minimum Visit Quality for Specialist Plants

We consider the equilibrium condition for a specialist plant of species  $i$ , which is visited by just one pollinator species  $j$ , obtained from equation (1) by substituting in for  $\gamma_i$  and  $V_{ij}$  using the linear model described in the first section of “Methods.” We set  $u_i = 0$ , as discussed in the main text and in appendix B, in order to obtain the minimal visit quality required for survival, under ideal conditions with no direct competition from other plant species. We find

$$0 = \frac{dp_i}{dt} = g_i(1 - w_i p_i) e_{ij} \sigma_{ij} \tau_{ij} \alpha_{ij} a_j - \mu_i^p. \quad (C1)$$

The pollinator population density  $a_j$  can be found by solving the equilibrium condition for the rewards, obtained from equation (3):

$$0 = \frac{dR_i}{dt} = \beta_i p_i - \phi_i R_i - b_{ij} \tau_{ij} \alpha_{ij} a_j R_i. \quad (C2)$$

To solve this, we recall that in the equilibrium state of interest, where the adaptive foraging is also at equilibrium, the reward abundances are equal to  $R_i^*$ , as defined in equation (7). Thus, we arrive at

$$a_j = \frac{\beta_i p_i - \phi_i R_i^*}{b_{ij} \tau_{ij} \alpha_{ij} R_i^*}. \quad (C3)$$

Substituting into equation (C1), we have

$$0 = g_i(1 - w_i p_i) e_{ij} \sigma_{ij} \frac{\beta_i p_i - \phi_i R_i^*}{b_{ij} R_i^*} - \mu_i^p. \quad (C4)$$

This is a quadratic equation in  $p_i$ , which can be solved to obtain

$$p_i = \frac{1}{w_i} \left[ 1 - \frac{1}{2}(1 - d_i) \left( 1 - \sqrt{1 - \frac{4}{s_{ij} \sigma_{ij} (1 - d_i)}} \right) \right], \quad (C5)$$

where

$$d_i = \frac{\phi_i R_i^* w_i}{\beta_i} \quad (C6)$$

is the fraction of floral rewards that are lost to dilution when the plant population is at its carrying capacity  $1/w_i$  and

$$s_{ij} = \frac{g_i e_{ij} \beta_i (1 - d_i)}{w_i \mu_i^p b_{ij} R_i^*} \quad (C7)$$

is the number of seedlings produced per plant lifetime under optimal conditions, where there are no other plant species nearby to contaminate the pollen and the field is kept clear of all competing plants. Specifically,  $g_{ij}$  is the number of individual seedlings produced per pollinator visit,  $(1 - d_i)\beta_i/(\mu_i^P w_i)$  is the harvested rewards mass per unit area over the plant's lifetime (i.e., over the average lifetime of an individual plant in the corresponding stochastic version of this model), and  $b_{ij}R_i^*$  is the rewards mass density harvested per visit.

# Appendix D from F. S. Valdovinos and R. Marsland III, “Niche Theory for Mutualism: A Graphical Approach to Plant-Pollinator Network Dynamics” (Am. Nat., vol. 197, no. 4, p. 393)

## Saturating Functional Responses

In the version of the model presented in the main text, which was employed in all of the previous simulations, the pollinator growth rates are linear functions of rewards abundances. In reality, both the quantity of rewards extracted per visit  $f_{ij}$  and the visit frequency  $V_{ij}$  are likely to saturate at high rewards levels. All of the qualitative results obtained in the main text apply to these more realistic models as well. In this appendix, we provide mathematical expressions for these two types of saturation, along with the expressions corresponding to equation (7) that specify the point  $R_i^*$  in rewards space, where adaptive foraging reaches a nontrivial steady state.

The original publication presenting the model (Valdovinos et al. 2013) contained a discussion of saturating rewards extraction, with each pollinator capable of obtaining a finite quantity  $b_{ij}^{\max}$  of rewards per visit, following Holling’s type II growth kinetics (Holling 1959):

$$f_{ij} = b_{ij}^{\max} \frac{R_i}{\kappa_{ij}P_i + R_i}. \quad (\text{D1})$$

Setting  $da_j/dt = 0$  and  $\alpha_{kj} = \delta_{ik}$  in equation (2) and substituting in with this formula for  $f_{ij}$ , we find that the equilibrium rewards level  $R_{ij}^*$  for the specialist strategy satisfies:

$$c_{ij}\tau_{ij}b_{ij}^{\max} = \mu_j^A \frac{\kappa_{ij}P_i + R_{ij}^*}{P_i R_{ij}^*}. \quad (\text{D2})$$

This equation reveals a set of two sufficient conditions to give all pollinator species  $j$  the same  $R_{ij}^*$  (as required for adaptive foraging to admit of a steady state with all these species sharing rewards from species  $i$ ): (i) the mass-specific rewards uptake rates  $c_{ij}\tau_{ij}b_{ij}^{\max}$  for different  $j$  must scale linearly with the mortality rates  $\mu_j^A$  and (ii)  $\kappa_{ij}$  must be the same for all  $j$ .

In addition to the finite capacity of a pollinator to extract rewards on each visit, it is reasonable to assume that there is a maximum number of visits that an animal can make per unit time. Using the same type II kinetics, we obtain the following expression for the total visitation rate of pollinator species  $j$  on plant species  $i$ :

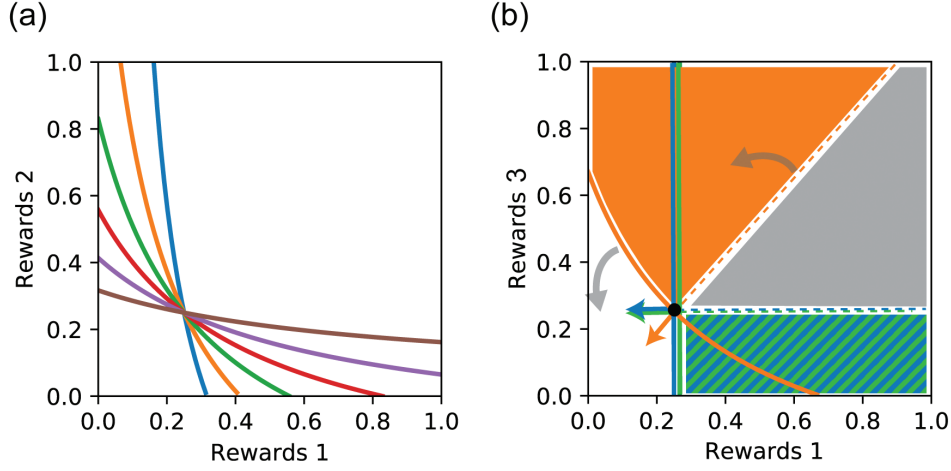
$$V_{ij} = a_j \frac{\tau_{ij}\alpha_{ij}P_i}{1 + \sum_k \tau_{kj}\alpha_{kj}h_{kj}P_k + \sum_k \omega_{jk}a_k}. \quad (\text{D3})$$

Here,  $h_{kj}$  is the handling time for pollinator species  $j$  foraging on plant species  $k$ , and  $\omega_{jk}$  quantifies the magnitude of direct interference between pollinators. Direct interference significantly complicates the geometric interpretation, so we will set  $\omega_{jk} = 0$  here. If the saturation of visit frequency is the only relevant nonlinearity and the rewards uptake per visit is still linear in  $R_i$ , then the zero net growth isoclines (ZNGIs) remain linear. When both kinds of saturation are present, the specialist equilibrium point  $R_{ij}^*$  is defined by

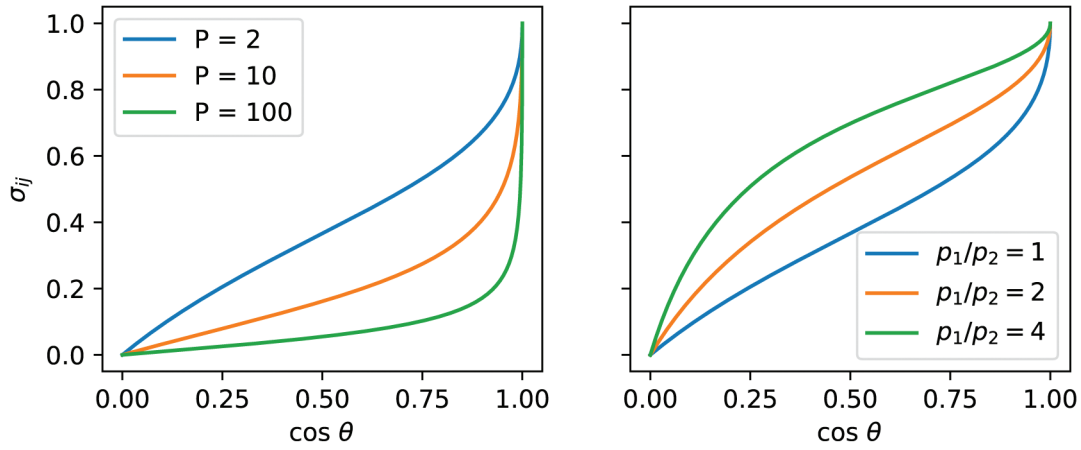
$$c_{ij}\tau_{ij}b_{ij}^{\max} = \mu_j^A \frac{(\kappa_{ij}P_i + R_{ij}^*)(1 + \sum_k \tau_{kj}\alpha_{kj}h_{kj}P_k)}{P_i R_{ij}^*}. \quad (\text{D4})$$

Giving all species the same set of  $R_{ij}^*$  requires two more assumptions beyond what was required for saturating rewards extraction alone: (i) the handling time  $h_{kj}$  must be inversely proportional to the visitation efficiency  $\tau_{kj}$  for all pollinator species  $j$  visiting a given plant species  $k$  and (ii) all of the plant population densities (for nonextinct plants) must be the same. Both of these are trivially satisfied under conditions similar to the simulations discussed in the main text, where the only differences between species come from the topology of the interaction network and all other parameters are species independent.

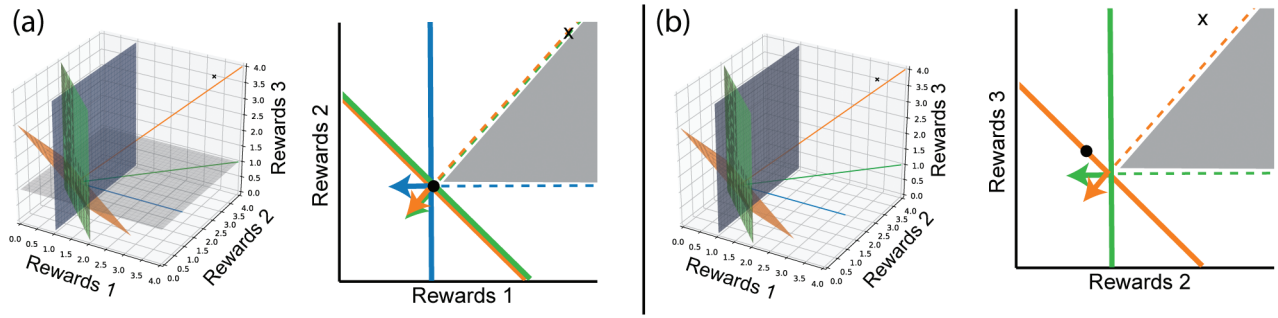
Figure D1 shows that the ZNGIs are no longer linear under saturating rewards extraction but that the graphical arguments from the main text still hold. The key point is that when all parameters are species independent (except for interaction network topology), the initial impact vectors are required by symmetry to be perpendicular to the ZNGIs and adaptive foraging tends to rotate them away from the rewards axes corresponding to generalist plants, just as in the linear model. Since these are the two essential features necessary for recovering the simulation results, we expect that the same phenomena will be observed even in the presence of saturation.



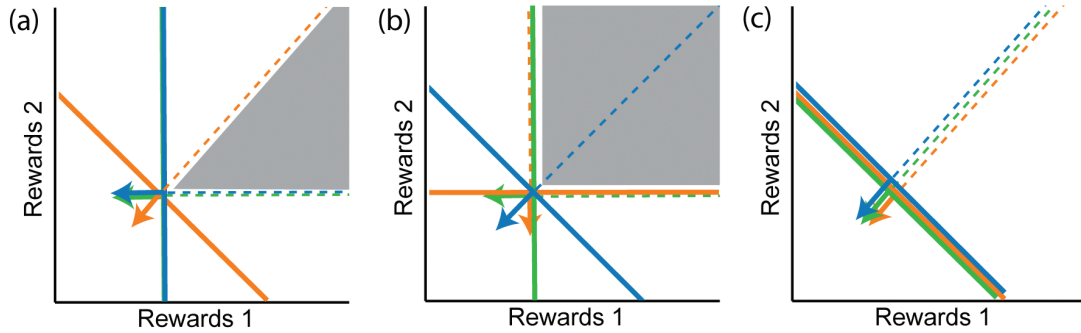
**Figure D1:** Saturating growth laws. *a*, Scaling the maximum mass-specific rewards uptake rate  $c_{ij}\tau_{ij}b_{ij}^{\max}$  with the pollinator mortality rate  $\mu_j^A$  ensures that all species have the same minimum viable rewards level  $R_{ij}^*$  under a specialist strategy on each plant species  $i$ . As in the linear model, this implies that all zero net growth isoclines (ZNGIs) cross at this point and rotate about it during adaptive foraging. *b*, ZNGIs, impact vectors, supply vector, and coexistence cone for the nested network of figure 2, with saturating rewards uptake following equation (D1). Gray arrows indicate the direction of rotation of the ZNGI and coexistence cone boundary under adaptive foraging.



**Figure D2:** Relation between angle and quality. *Left*, visit quality  $\sigma_{ij} = \alpha_{ij}\tau_{ij}p_i / \sum_{k \in P_j} \alpha_{kj}\tau_{kj}p_k$  versus cosine of the angle  $\theta$  between the impact vector of pollinator species  $j$  and (negative) rewards axis  $i$  ( $\cos \theta = \alpha_{ij}\tau_{ij}b_{ij} / \sum_{k \in P_j} (\alpha_{kj}\tau_{kj}b_{kj})^2$ ). All plants are assumed to have identical abundances  $p_i$ , all foraging efficiencies  $\tau_{ij}$  and per-visit rewards extraction  $b_{ij}$  are equal, and the foraging effort not expended on plant  $i$  is equally distributed over all other plant species. Each line represents a different value of the total number of plant species  $P$ . *Right*, same as previous panel but for  $P = 2$  and different values of the ratio  $p_1/p_2$  of the two plant abundances. Note that  $\sigma_{ij} = 0$  always corresponds to  $\cos \theta = 0$ , that  $\sigma_{ij} = 1$  always corresponds to  $\cos \theta = 1$ , and that between these two extremes the relationship is always monotonic.



**Figure D3:** Additional projections. Shown are projections of the three-plant, three-pollinator system of fig. 2 onto the other two planes: *a*, rewards 1/rewards 2; *b*, rewards 2/rewards 3. Note that the blue species is not visible in the second projection because the zero net growth isocline is parallel to the projection plane and the impact vector is perpendicular to the plane.



**Figure D4:** Complete set of possible projections without adaptive foraging. There are only three distinct two-dimensional projections of the coexistence cone that are possible in the absence of adaptive foraging. The shape of the projected cone depends only on the existence of pollinators that service one of the two plants in the projection but not the other. *a*, One plant has a specialist pollinator. *b*, Both plants have specialist pollinators. *c*, Neither plant has a specialist pollinator.