Eco-evolutionary feedbacks among pollinators, herbivores, and their plant resources

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Eco-evolutionary feedbacks among multiple species occur when one species affects another species' evolution via its effects on the abundance and traits of a shared partner species. What happens if those two species enact opposing effects on their shared partner's population growth? Furthermore, what if those two kinds of interactions involve separate traits? For example, many plants produce distinct suites of traits that attract pollinators (mutualists) and deter herbivores (antagonists). Here, we develop a model to explore how pollinators and herbivores may influence each other's interactions with a shared plant species via evolutionary effects on the plant's nectar and toxin traits. The model results predict that herbivores indirectly select for the evolution of increased nectar production by suppressing plant population growth. The model also predicts that pollinators indirectly select for the evolution of increased toxin production by plants and increased counterdefenses by herbivores via their positive effects on plant population growth. Unless toxins directly affect pollinator foraging, plants always evolve increases in attraction and defense traits when they interact with both kinds of foragers. This work highlights the value of incorporating ecological dynamics to understand the entangled evolution of mutualisms and antagonisms in natural communities.

KEY WORDS: Eco-evolutionary feedbacks, floral nectar evolution, mutualism, plant-pollinator-herbivore interactions, toxin evolution.

Ecological processes propel evolutionary change. Evolutionary processes in turn mold ecological communities across space and time. Such subtle and complex feedbacks have long been recognized in the context of many species interactions, including predation, parasitism, competition, and to a lesser extent, mutualism (Levins 1968; Pimentel 1968; Antonovics 1976; Roughgarden 1979; Abrams et al. 1993; Jones et al. 2009; McPeek 2017; Afkhami et al. 2021). Ecological feedbacks on evolutionary processes occur because the dynamics of natural selection on interaction-mediating traits are modulated by the abundances of the interacting species (Palkovacs et al. 2011; Talluto and Benkman 2013). Likewise, evolutionary feedbacks on ecological processes occur because the ecological dynamics of interacting species emerge from their evolved trait responses (Yoshida

et al. 2003; Vasseur et al. 2011; Agrawal et al. 2013; Hiltunen and Becks 2014; Cortez 2016). Disentangling feedbacks between population and trait dynamics in a variety of species interactions enhances our mechanistic understanding of community assembly and coevolution (Fussman et al. 2007; Pelletier et al. 2009; McPeek 2017).

In natural communities, most species engage in both negative and positive interactions with a wide variety of other species. For instance, plant species must contend with antagonists such as herbivores, seed predators, competing plant species, and pathogens while simultaneously fostering interactions with mutualists such as pollinators, rhizobial bacteria, mycorrhizal fungi, and seed dispersers. To date, most research on three-species eco-evolutionary feedbacks has focused on communities in which

two or more species fill similar roles in the focal interaction, for example, one predator-two prey communities or communities with many resource competitors (Abrams 1991, 2000; Jones et al. 2009; Evans et al. 2020). Adding a third species can change patterns of selection on traits mediating a two-species interaction via the third species' interaction with one of the other species. For example, Jones et al. (2009) showed that obligate pollinators and seed-consuming exploiters compete directly for plant resources but also act as potentially opposing forces of selection on plant resource traits, indirectly affecting their ability to coexist as the plant evolves in response to both species. Just as ecological indirect effects among three or more species play an important role in structuring communities across space (Vandermeer 1980; Strauss 1991; Abrams et al. 1993; Werner and Peacor 2003), eco-evolutionary indirect effects that cross trophic levels, kingdoms, and interaction types likely play a large role in structuring communities through time (Miller and Travis 1996; terHorst et al. 2018).

Eco-evolutionary feedbacks between multiple types of interactions are an intriguing prospect because they consider feedback among interactions that are governed by separate traits. Pollinators and herbivores enact opposing ecological effects on plants and often interact with different suites of plant traits (Strauss 1997; Irwin et al. 2004; Johnson et al. 2015; Jacobsen and Raguso 2018). Plants reduce herbivore foraging via a suite of defense traits, including morphological features (e.g., leaf toughness, thorns, trichomes) and chemical defenses (e.g., various secondary metabolites). Plants simultaneously attract pollinator foraging, usually with floral reward traits such as nectar volume and composition, as well as floral attractant traits such as flower color, flower shape and size, and floral scent. Nevertheless, a large body of empirical work examines how herbivores can indirectly affect pollinator visitation via physical and chemical changes in the plant's trait expression (Strauss et al. 1996; Krupnick et al. 1999; Kessler et al. 2011; Schiestl et al. 2011; Barber et al. 2012; Ghyselen et al. 2016; Chautá et al. 2017). In some cases, traits involved in herbivore defense, such as toxic secondary metabolites, can also affect pollinator visitation (Adler 2000; Gegear et al. 2007; Adler et al. 2012; Thomson et al. 2015; Jones and Agrawal 2016). Therefore, plant–pollinator–herbivore interactions provide a test case to examine how eco-evolutionary feedbacks between two species shape evolutionary responses of traits that mediate another kind of species interaction, as well as how feedbacks from one trait may affect two kinds of interactions.

In this paper, we explore these multispecies and multi-interaction feedbacks by modeling the evolution of a plant-pollinator-herbivore community module. We model a plant that produces nectar that attracts foraging pollinators. The plant also produces a constitutive toxin that reduces herbivore foraging and increases herbivore mortality. The herbivore, in turn, has a capacity to detoxify the food it consumes. In addition to the benefits the traits confer, each trait imposes production costs on the plant individual's fitness. We also examine scenarios in which the plant's toxin directly affects pollinator foraging, thereby forcing an interaction between attraction and defense. We specifically address the following questions: how do eco-evolutionary feedbacks within an antagonism affect a species' interaction with its mutualist? How does a mutualist perturb the eco-evolutionary feedbacks of antagonism? Last, how do these feedbacks change if a species' trait responses to an antagonist directly affect its interactions with a mutualist? Our model presents a series of natural selection-driven ecological feedbacks that may structure the evolution of plant-pollinator-herbivore communities.

The Model

Our work expands on a previous eco-evolutionary model of a plant's nectar production evolving in response to interactions with a nectar-foraging pollinator (McPeek et al. 2021). That model focused on nectar as the pollinator attractant. Modeling nectar resources for pollinators allows the dynamics of the pollinator population of size N to be linked with the dynamics of the plant population of size R and its nectar pool of size S. Here, we build on this framework by incorporating an antagonistic interaction between that plant and an herbivore. The plant's toxin level evolves in response to the herbivore, and the herbivore's ability to detoxify the plant tissue it eats evolves in response to the plant. Because the present model tracks the traits of two species, we include the species identity in trait names (e.g., plant nectar production rate, $z_{NPR}^{(R)}$). (All model state variables and parameters are listed together in Table 1.)

First, we imagine a plant species of population size R that produces nectar. We use the dynamic variable S to represent the plant's standing nectar volume and the amount of nectar an individual plant holds at any given instant. Each plant produces nectar according to a simple renewal function

$$G(S) = z_{NPR}^{(R)} \left(1 - \frac{S}{z_{RV}^{(R)}}\right) \quad (1)$$

where $z_{NPR}^{(R)}$ is the rate of nectar production when no nectar is present, and $z_{RV}^{(R)}$ is the maximum volume of nectar that a single plant's nectar reservoir can hold. Thus, the rate of nectar filling decreases linearly until $S = z_{RV}^{(R)}$. Here, $z_{NPR}^{(R)}$ and $z_{RV}^{(R)}$ are two quantitative plant traits that evolve via natural selection generated from interacting with the pollinator as well as other ecological sources (McPeek et al. 2021).

Table 1. State variables and parameters used in the model presented in the paper.

State Variables	
R	Plant species abundance
S	Standing nectar volume on a single plant individual
N	Pollinator species abundance
H	Herbivore species abundance
$z_{NPR}^{(R)}$	Maximum nectar production rate for a plant individual
$z_{RV}^{(R)}$	Nectar reservoir volume for a plant individual
$z_{Tox}^{(R)}$	Toxin level for a plant individual
$z_{Detox}^{(H)}$	Detoxification capability for an herbivore individual
Parameters	
c	Maximum number of ovules that can be produced by a single plant
g	Strength of density dependence in regulating the plant population
$\gamma_{NPR}, \gamma_{RV}, \gamma_{Tox}$	Scaling parameters for the fitness costs for ovule production associated with the plant traits $z_{NPR}^{(R)}, z_{RV}^{(R)}, z_{Tox}^{(R)}$, respectively
ψ	Per unit nectar production fitness cost
δ	Fraction of plant ovules that are fertilized with no pollinator assistance
a	Maximum harvest rate of nectar by a pollinator individual
ϑ	Half-saturation constant for the rate of nectar harvesting by a pollinator individual.
τ	Scaling parameter measuring the degree to which a pollinator's foraging rate is affected by $z_{Tox}^{(R)}$ of the plant.
b	Pollinator efficiency of converting harvested nectar into pollinator offspring
f	Intrinsic death rate of the pollinator
m	Maximum foraging rate of the herbivore feeding on the plant
n	Herbivore efficiency of converting consumed plant tissue into herbivore offspring
x	Minimum intrinsic death rate of the herbivore
α	Scaling parameter for the ability of the herbivore to detoxify the toxin in the plant
β	Scaling parameter for the fitness cost of the herbivore eating toxic plant material
ω	Scaling parameter for the maximum fitness cost of the herbivore eating toxic plant material
θ	Scaling parameter for the fitness cost of detoxifying ability of the herbivore
$G_{NPR}^{(R)}, G_{RV}^{(R)}, G_{Tox}^{(R)}$	Additive genetic components of variation for the plant traits $z_{NPR}^{(R)}, z_{RV}^{(R)}, z_{Tox}^{(R)}$, respectively
$G_{Detox}^{(H)}$	Additive genetic component of variation for the herbivore trait $z_{Detox}^{(H)}$

The plant also produces a constitutive level of toxin that deters foraging by an herbivore species. The plant's toxin level is a third quantitative trait of the plant, which we identify as $z_{Tox}^{(R)}$.

We assume that the plant species' population size R changes according to logistic growth:

$$
L\left(R, z_{NPR}^{(R)}, z_{RV}^{(R)}, z_{Tox}^{(R)}\right)
$$
$$
= \left(\left(c - \gamma_{NPR}\left(z_{NPR}^{(R)}\right)^2 - \gamma_{RV}\left(z_{RV}^{(R)}\right)^2 - \gamma_{Tox}\left(z_{Tox}^{(R)}\right)^2\right) - gR\right) \quad (2)
$$

(Verhulst 1838, Pearl and Reed 1920). Equation (2) depicts the per capita component of plant population growth that is independent of the actions of pollinators and herbivores. Plants produce a set number of ovules. The parameter c defines the maximum number of ovules a plant individual can produce based on its local environment. We also assume that each of the plant's three quantitative traits carries a fixed cost of producing and maintaining the necessary biological machinery for the trait: the

parameter γ_X scales how the number of ovules a plant produces decreases given the value of the corresponding plant trait. These per-trait production costs each diminish the plant's ovule production according to a quadratic function. Thus, the plant's ovule production is maximized at c when the values of all three traits are zero. In the last term of the per capita logistic equation, g determines the strength of density dependence experienced by the plant and encapsulates all the extrinsic environmental factors that contribute to regulating the population's abundance in a density-dependent fashion, such as abiotic nutrient availability, space, and resource competition with other plant species in the environment, and interactions with other antagonistic species such as pathogens. We also assume that the plant pays a production cost of ψ for each unit of nectar produced (McPeek et al. 2021).

The plant interacts with a single pollinator species of population size N. The total amount of nectar available for the pollinator population at a given instant in time is RS, the number of plants

in the population times the amount of nectar per plant individual. Each pollinator harvests nectar from a plant according to a modified form of Michaelis–Menten/Monod dynamics

$$F\left(S, z_{Tox}^{(R)}\right) = \frac{aS}{\vartheta + S} e^{\tau z_{Tox}^{(R)}} \tag{3}$$

where a is the maximum harvest rate and ϑ is the nectar volume at which the harvest rate is half of the maximum (Michaelis and Menten 1913; Monod 1949). We also assume that the plant's herbivore-deterring toxin level can also affect pollinator foraging. As the plant's toxin level increases, the pollinator's foraging rate may be affected by toxins (e.g., Adler 2000; Kessler and Halitschke 2009; Stevenson et al. 2017) according to the exponential term in equation (3), where τ scales the degree to which the pollinator's behavior is affected by the toxin for a given value of $z_{Tox}^{(R)}$. When $\tau = 0$, increasing a plant's constitutive toxin level $z_{Tox}^{(R)}$ has no direct effect on pollinator foraging. When $\tau < 0$, increasing a plant's constitutive toxin level $z_{Tox}^{(R)}$ has a negative direct effect on pollinator foraging (e.g., toxin is present in the nectar and acts as a deterrent to nectar feeders, Gegear et al. 2007). When $\tau > 0$, increasing a plant's constitutive toxin level $z_{Tox}^{(R)}$ has a positive direct effect on pollinator foraging (e.g., toxin in nectar attracts pollinators to forage more, Ehlers and Olesen 1997; Kevan et al. 2015; Thomson et al. 2015). The pollinator also has a conversion efficiency for converting harvested nectar into pollinator offspring, denoted as the parameter b, and an intrinsic death rate, denoted as the parameter f.

When pollinators forage on a plant individual's nectar, they provide a fitness benefit by fertilizing some fraction of its ovules. We assume that a fraction δ of a plant's ovules will be fertilized with no pollinator assistance (i.e., it can self-pollinate), so $1 - \delta$ ovules can be fertilized by the pollinators' actions. When $\delta = 0$, the plant is wholly dependent on the pollinator for its reproduction, and this dependency declines as δ increases. Thus, we model the realized fraction of fertilized ovules per plant as the number of ovules produced times the fraction fertilized as

$$B\left(S, N, z_{NPR}^{(R)}, z_{RV}^{(R)}, z_{Tox}^{(R)}\right) = \left(c - \gamma_{NPR}\left(z_{NPR}^{(R)}\right)^2 - \gamma_{RV}\left(z_{RV}^{(R)}\right)^2 \right.$$
$$\left. - \gamma_{Tox}\left(z_{Tox}^{(R)}\right)^2 \right)\left(\frac{\delta + \frac{aS}{\vartheta+S}N}{1 + \frac{aS}{\vartheta+S}N}\right), \tag{4}$$

where the first term is the number of ovules produced (from equation (2)), and the second term is the fraction that is fertilized: this fraction is δ when $N = 0$ and approaches 1 when the pollinator population size N is very large (Figure 1a). This differs from the previous plant-pollinator model in which we assumed that the pollinators conferred an additive fitness benefit to plants (McPeek et al. 2021). Both ways of modeling the pollinator benefit to plants yield qualitatively identical results. We favor this approach because it provides a more biologically explicit descrip-
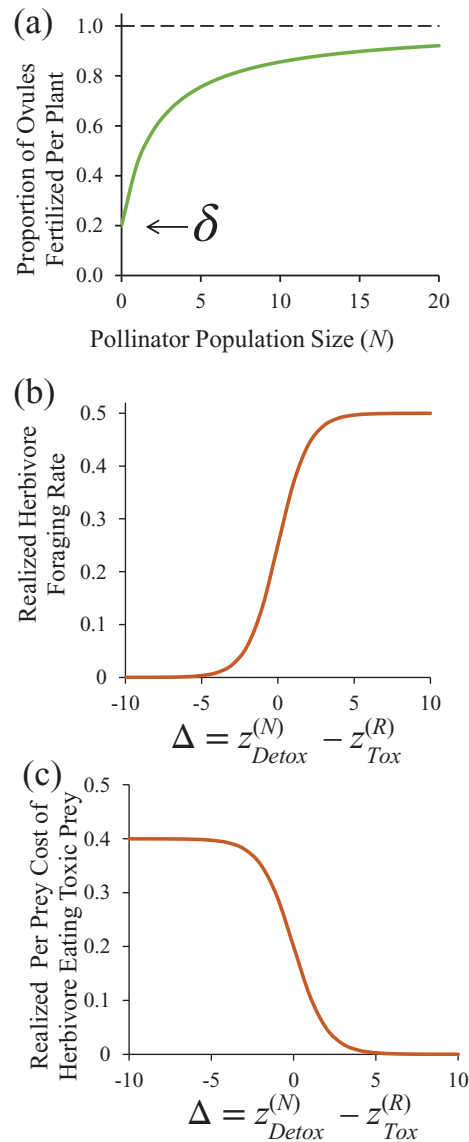
Figure 1. Explication of some model functions. **(a)** Reliance of plants on pollinator foraging, set by a minimum fraction of fertilized ovules δ saturates at high pollinator abundances. **(b)** Herbivores forage on plant tissue according to a logistic function of their relative ability to detoxify plant tissue with a given level of toxin. **(c)** Herbivores pay a per capita fitness cost for each unit of plant tissue they eat, again set by a logistic function of their relative ability to detoxify plant tissue containing a given level of toxin.

tion of how plants accrue benefits from pollinators (McPeek et al. 2022). In the Supporting Information, we provide an analysis of the new approach that is comparable to the evolutionary plant-pollinator analyses presented in McPeek et al. (2021).

The plant species also interacts with one herbivore species of population size H that acts on the plant independent of the pollinator. The herbivore has a physiological ability to detoxify plant tissue that it consumes, which we specify as its quantitative

trait $z_{Detox}^{(H)}$. We assume that the herbivore has a linear functional response for feeding on the plant, with its attack coefficient being a logistic function of the difference between the herbivore's detoxifying capacity and the plant's toxicity, $\Delta = z_{Detox}^{(H)} - z_{Tox}^{(R)}$:

$$D\left(z_{Detox}^{(H)}, z_{Tox}^{(R)}\right) = \frac{m}{1 + e^{-\alpha\Delta}}, \qquad (5)$$

where m is the foraging rate of the herbivore when $z_{Detox}^{(H)} >> z_{Tox}^{(R)}$, and α scales the slope of the relationship between foraging rate and Δ when $\Delta = 0$. Given this attack coefficient, if $z_{Detox}^{(H)} << z_{Tox}^{(R)}$, the herbivore's foraging rate approaches 0 (Figure 1b). The herbivore has a conversion efficiency of n that determines how many offspring it produces per unit of plant tissue consumed (see equation (8) below).

We further assume that producing the detoxification machinery increases the herbivore's intrinsic death rate x according to a quadratic equation

$$X\left(z_{Detox}^{(H)}\right) = x + \theta\left(z_{Detox}^{(H)}\right)^2, \qquad (6)$$

where θ scales the fitness cost for its detoxifying ability.

The herbivore also pays a fitness cost for consuming toxic plant tissue. The magnitude of this cost changes as a function of the herbivore's detoxifying capacity relative to the amount of plant toxin: $\Delta = z_{Detox}^{(H)} - z_{Tox}^{(R)}$. We assume that this cost has a maximum of $\omega z_{Tox}^{(R)}$ when $z_{Detox}^{(H)} << z_{Tox}^{(R)}$ and follows a logistic function

$$D\left(z_{Tox}^{(R)}, z_{Detox}^{(H)}\right) = \frac{\omega z_{Tox}^{(R)} e^{-\beta\Delta}}{1 + e^{-\beta\Delta}}, \qquad (7)$$

where β scales the rate of change in this fitness cost at $\Delta = 0$ (Figure 1c). Equation (7) describes the fitness cost of consuming one plant, so the total fitness cost to a single herbivore is the cost of eating one plant times the number of plants eaten, namely, the product of equations (7), (5), and R.

These assumptions define the set of equations that determine the population dynamics of the abundances of the plant species R, the nectar volume of a single plant S, the pollinator species N, and the herbivore species H:

$$\frac{dR}{Rdt} = \left(c - \gamma_{NPR}\left(z_{NPR}^{(R)}\right)^2 - \gamma_{RV}\left(z_{RV}^{(R)}\right)^2\right.$$
$$\left. - \gamma_{Tox}\left(z_{Tox}^{(R)}\right)^2\right)\left(\frac{\delta + \frac{aS}{\vartheta+S}N}{1 + \frac{aS}{\vartheta+S}N}\right) - gR - \frac{mN}{1+e^{-\alpha\Delta}} - \psi z_{NPR}^{(R)}\left(1 - \frac{S}{z_{RV}^{(R)}}\right).$$
$$\frac{dS}{dt} = z_{NPR}^{(R)}\left(1 - \frac{S}{z_{RV}^{(R)}}\right) - \frac{aS}{\vartheta+S}e^{\tau z_{Tox}^{(R)}}SN \qquad (8)$$
$$\frac{dN}{Ndt} = \frac{baS}{\vartheta+S}e^{\tau z_{Tox}^{(R)}}RS - f$$
$$\frac{dH}{Hdt} = \frac{nmR}{1+e^{-\alpha\Delta}} - \frac{\omega z_{Tox}^{(R)}e^{-\beta\Delta}}{1+e^{-\beta\Delta}}\frac{mR}{1+e^{-\alpha\Delta}} - x - \theta\left(z_{Detox}^{(H)}\right)^2$$

We assume that the plant and herbivore traits both evolve according to the multivariate breeder's equation (Lande 1982, 2007). The per capita population dynamics equation for each species in equation (8) also defines the individual fitnesses of each species based on their trait values. These equations, therefore, also describe the dynamics of natural selection for the evolution of the plant and herbivore traits. Note that only the costs of nectar production appear as functions of the traits $(z_{NPR}^{(R)}, z_{RV}^{(R)})$ of the plant species in the plant equation of (8). To expose the plant's fitness benefit of nectar production, we subsumed the nectar dynamics into the plant equation (McPeek et al. 2021). To do this, we assume that nectar abundance is always at equilibrium with respect to pollinator abundance. We set the nectar equation in (8) to zero, solve for S, and substitute the resulting function into the other equations. The resulting equilibrium nectar abundance is

$$S^* = z_{NPR}^{(R)}\left(\frac{z_{RV}^{(R)} - \vartheta + \sqrt{\left(\vartheta + z_{RV}^{(R)}\right)^2 + 4\left(z_{RV}^{(R)}\right)^2 a\vartheta e^{\tau z_{Tox}^{(R)}}N \Big/ z_{NPR}^{(R)}}}{2\left(z_{RV}^{(R)}ae^{\tau z_{Tox}^{(R)}}N + z_{NPR}^{(R)}\right)}\right) \qquad (9)$$

We can then use the methods outlined by Lande (1982) to define the dynamical equations for the three plant traits and the herbivore trait. These are

$$\frac{dz_{NPR}^{(R)}}{dt} = G_{NPR}^{(R)}\left[\begin{array}{l}\left(c - \gamma_{NPR}\left(z_{NPR}^{(R)}\right)^2 - \gamma_{RV}\left(z_{RV}^{(R)}\right)^2 - \gamma_{Tox}\left(z_{Tox}^{(R)}\right)^2\right)\\ \left(\frac{(1-\delta)a\vartheta e^{\tau z_{Tox}^{(R)}}N\frac{\partial S^*}{\partial z_{NPR}^{(R)}}}{(\vartheta+S^*)^2\left(1 + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N\right)^2}\right) - 2\gamma_{NPR}z_{NPR}^{(R)}\left(\frac{\delta + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N}{1 + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N}\right)\\ -\psi\left(1 - \frac{S^*}{z_{RV}^{(R)}} - \frac{z_{NPR}^{(R)}}{z_{RV}^{(R)}}\frac{\partial S^*}{\partial z_{RV}^{(R)}}\right)\end{array}\right]$$

$$\frac{dz_{RV}^{(R)}}{dt} = G_{RV}^{(R)}\left[\begin{array}{l}\left(c - \gamma_{NPR}\left(z_{NPR}^{(R)}\right)^2 - \gamma_{RV}\left(z_{RV}^{(R)}\right)^2 - \gamma_{Tox}\left(z_{Tox}^{(R)}\right)^2\right)\\ \left(\frac{(1-\delta)a\vartheta e^{\tau z_{Tox}^{(R)}}N\frac{\partial S^*}{\partial z_{RV}^{(R)}}}{(\vartheta+S^*)^2\left(1 + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N\right)^2}\right) - 2\gamma_{RV}^{(R)}z_{RV}^{(R)}\left(\frac{\delta + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N}{1 + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N}\right)\\ -\psi\frac{z_{NPR}^{(R)}}{z_{RV}^{(R)}}\left(\frac{S_1^*}{z_{RV}^{(R)}} - \frac{\partial S^*}{\partial z_{RV}^{(R)}}\right)\end{array}\right]$$

$$\frac{dz_{Tox}^{(R)}}{dt} = G_{Tox}^{(R)}\left[\begin{array}{l}\left(c - \gamma_{NPR}\left(z_{NPR}^{(R)}\right)^2 - \gamma_{RV}\left(z_{RV}^{(R)}\right)^2 - \gamma_{Tox}\left(z_{Tox}^{(R)}\right)^2\right)\\ \left(\frac{(1-\delta)Nae^{\tau z_{Tox}^{(R)}}\left(\vartheta\frac{\partial S^*}{\partial z_{RV}^{(R)}} + \tau S^*(\vartheta+S^*)\right)}{(\vartheta+S^*)^2\left(1 + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N\right)^2}\right)\\ -2\gamma_{Tox}^{(R)}z_{Tox}^{(R)}\left(\frac{\delta + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N}{1 + \frac{aS^*}{\vartheta+S^*}e^{\tau z_{Tox}^{(R)}}N}\right) + \frac{\alpha m e^{-\alpha\Delta}N}{(1+e^{-\alpha\Delta})^2}\end{array}\right]$$

$$\frac{dz_{Detox}^{(H)}}{dt} = G_{Detox}^{(H)}\left[\frac{n\alpha m e^{-\alpha\Delta}R}{(1+e^{-\alpha\Delta})^2}\right.$$
$$- \frac{m\omega z_{Tox}^{(R)}Re^{-\beta\Delta}\left(\alpha e^{-\alpha\Delta}\left(1+e^{-\beta\Delta}\right) - \beta\left(1+e^{-\alpha\Delta}\right)\right)}{\left(1+e^{-\alpha\Delta}\right)^2\left(1+e^{-\beta\Delta}\right)^2}$$
$$\left. - 2\theta z_{Detox}^{(H)}\right]. \qquad (10)$$

In each of these equations, $G_X^{(Y)}$ is the additive genetic variation in trait X for species Y, and the term in square brackets is the partial derivative of the per capita population growth rate of that species with respect to trait X (as in Lande 1982). For simplicity, we assume no genetic covariation among the plant traits.

To analyze a model of this scope, we use computer simulations to explore patterns emerging from interesting and biologically reasonable areas of parameter space. MATLAB code is provided in the Supporting Information.

Results

HERBIVORES INDIRECTLY INCREASE RESOURCES FOR POLLINATORS VIA EVOLUTIONARY EFFECTS ON PLANTS

Incorporating an herbivore into a plant-pollinator interaction causes the plant population to evolve in response to both species. As expected, the plant evolves an increase in its toxin level $z_{Tox}^{(R)}$, allowing it to defend itself more effectively against the herbivore (Figure 2e). In addition, the plant evolves an increase in its nectar reservoir volume $z_{RV}^{(R)}$ (Figure 2b), and in some areas of parameter space, it evolves an increase in its nectar production rate $z_{NPR}^{(R)}$ as well (Figure 2a). An herbivore with a low foraging rate m selects for a higher plant nectar production rate (Figure 2a). However, the plant's nectar production rate peaks at intermediate herbivore foraging rates and declines at higher herbivore foraging rates because the two costs associated with a plant's nectar production rate outweigh the benefits of increasing that rate to attract pollinators. In contrast, the plant's nectar reservoir volume always increases with increasing herbivore foraging rates (Figure 2b). Overall, the plant evolves a higher standing nectar volume when the herbivore is present (Figure 2c).

The evolutionary response of the plant's nectar traits to herbivore foraging can be understood by examining the resulting changes in species abundances when herbivores enter the community (Figure 2d). Herbivores decrease the plant's abundance by consuming plant tissue. Reducing the plant's abundance in turn reduces the pollinator's abundance. When pollinator abundance is low, plants garner higher fitness benefits if they produce more nectar, thus increasing pollinator visitation rates (McPeek et al. 2021; Ratnieks and Balfour 2021). Therefore, the herbivore indirectly imposes natural selection on the plant, favoring an increase in nectar provisioning to the pollinator, thus augmenting the plant's reproductive fitness. Consequently, the equilibrium state for a plant population that interacts with pollinators and herbivores is a smaller plant population in which each plant individual has a higher standing nectar volume (Figure 2c).

POLLINATORS INDIRECTLY INCREASE HERBIVORE DEFENSES VIA EVOLUTIONARY EFFECTS ON PLANTS

In addition to its two nectar traits $z_{NPR}^{(R)}$ and $z_{RV}^{(R)}$, the plant produces a constitutive toxin at a level $z_{Tox}^{(R)}$. The plant evolves higher toxin levels if the herbivore species has a higher foraging rate, but its toxin level approaches an asymptotic maximum value be-

cause of the increased cost to the plant as toxin production is increased (Figure 2e). Thus, the evolutionary increase in nectar provisioning occurs despite an accompanying increase in the plant's toxin level. Introducing a pollinator to a plant-herbivore interaction causes the plant to evolve a higher toxin level and the herbivore to evolve a higher detoxifying ability (Figure 3a). This occurs because pollinators have a positive effect on the plant's abundance (Figure 3b). Pollinators increase the plant's population size via their beneficial foraging activities, thus indirectly shifting natural selection on a plant's toxin production in two ways. First, herbivore abundance increases when plant abundance increases, strengthening selection on plants to increase toxin production (Figure 3). Second, pollinator-aided reproduction lowers an individual plant's toxin production costs, further strengthening selection for higher toxin production. We note that the pollinator's evolutionary indirect effect is driven by its presence in the community, not its traits; pollinator foraging rate a has a relatively low impact on the plant's and the herbivore's evolved trait values and abundances (Figure 3). If the pollinator's foraging rate is too low to impose selection on a plant's nectar production, nectar production ceases, the pollinator goes extinct, and herbivore and plant abundances and trait values converge on the equilibria they occupy when the pollinator is absent (dashed lines, Figure 3).

PLANT RESOURCE LEVELS, PLANT RELIANCE ON ANIMAL-POLLINATION, AND POLLINATOR RESPONSE TO TOXINS AFFECTS THE EVOLUTION OF NECTAR AND TOXINS

Different resource availabilities affect the equilibrium level of the plant's evolved nectar and toxin levels but not the qualitative patterns of how the plant's traits respond to foraging by both pollinators and herbivores (Figure 4). Hypothetically, a plant's reproductive potential, here modeled as the total number of unfertilized ovules (i.e., summed across all flowers), should increase if more resources are available to the plant (Haig and Westoby 1988; Cohen and Dukas 1990). In an environment in which the plant has fewer resources and therefore produces fewer ovules (e.g., $c = 1$), the plant species evolves a lower nectar production rate (Figure 4a) but a slightly higher nectar reservoir volume (Figure 4b), resulting in a higher standing nectar volume (Figure 4c). However, all three species go extinct at high herbivore foraging rates when plants have low c because ecological limitations imposed by resources and herbivores prevent the plant from provisioning enough nectar to maintain the pollinator or from producing enough toxins to fend off the herbivore (Figure 4d,e). In contrast, in an environment in which the plant has more resources and can produce more ovules (e.g., $c = 3$), the plant evolves a higher nectar production rate and a higher toxin level (Figure 4a,e) but little change in its nectar reservoir volume (Figure 4b). These high resource conditions result
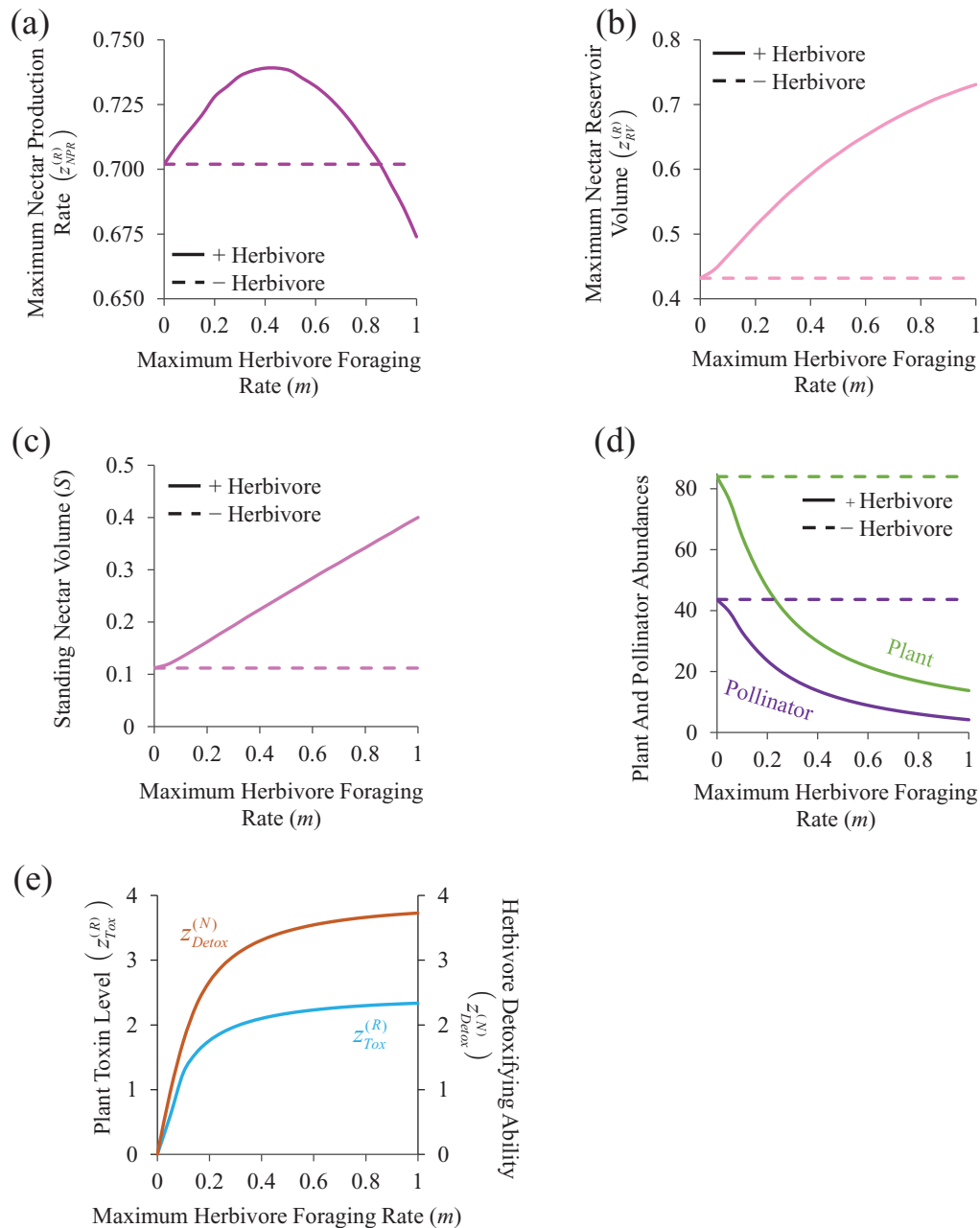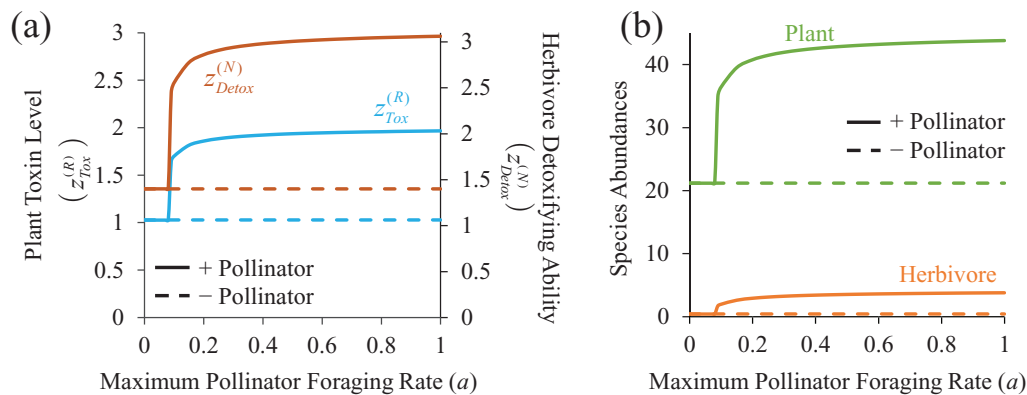
Figure 2. Plants evolve higher nectar provisioning when they interact with both pollinators and herbivores (solid line) than they do when they only interact with pollinators (dashed line). Model parameters, unless otherwise specified, are as follows: $c = 2.0$, $g = 0.02$, $\gamma_{(NPR)}^{(R)} = \gamma_{(RV)}^{(R)} = \psi = \gamma_{TOX}^{(R)} = 0.05$, $\delta = 0.25$, $a = 0.25$ $b = 0.1$, $\vartheta = 0.15$, $f = 0.10$, $n = 0.1$, $x = 0.15$, $y = 0.0$, $\alpha = 1.0$, $\beta = 1.0$, $\omega = 0.05$, $\theta = 0.05$, $G_{NPR}^{(R)} = G_{RV}^{(R)} = G_{TOX}^{(R)} = G_{DETOX}^{(H)} = 0.2$, and $\tau = 0.0$.

in larger plant and pollinator populations but overall smaller standing nectar volumes per plant (Figure 4c,d). Similarly, plants with a lower reliance on pollinator-mediated reproduction (higher δ) evolve a decrease in nectar production but an increase in toxin production (Figure 5a,b). When pollinators contribute less than ten percent of the plant's reproductive output (high δ), the plant evolves to stop producing nectar altogether, and the

plant and herbivore populations persist after pollinators have left the community.

Thus far, we have examined scenarios in which the toxin has no effect on pollinator foraging ($\tau = 0$). When the toxin level has a deterrent effect on pollinator foraging ($\tau < 0$), the plant evolves so that more nectar is available to pollinators (Figure 6c). The plant evolves a higher nectar reservoir volume as τ becomes more

Figure 3. Plants evolve higher toxin concentrations when they interact with both pollinators and herbivores (solid lines) than they do when they only interact with herbivores (dashed lines). Model parameters, unless otherwise specified, are as in Figure 2, $m = 0.25$.

negative (Figure 6b), resulting in an increasingly large standing nectar volume (Figure 6c). The plant evolves a lower nectar production rate when $\tau < 0$ due to the higher cost of the trait (γ_{NPR}, ψ, Figure 6a). These responses occur because a negative τ decreases pollinator foraging (Figure 6d), thereby reducing plant and subsequently pollinator population sizes (Figure 6e). A negative τ also causes the plant to evolve a lower toxin level and the herbivore a lower detoxifying ability because there are fewer herbivores when there are fewer plants to eat (Figure 6f). Thus, the herbivore also has a reduced foraging rate on the plant population when $\tau < 0$ (Figure 6d). At higher negative values of τ, all three species go extinct because the plant's population size drops below a level where it can sustain itself or either of its forager species (Figure 6e).

In contrast, when the toxin induces pollinators to forage more ($\tau > 0$), the plant evolves to provision less nectar to the pollinator via both a lower nectar production rate and a lower nectar reservoir volume, resulting in a lower standing nectar volume (Figure 6a–c). These responses occur because a positive τ increases pollinator foraging on the plant (Figure 6d), slightly increasing the plant's population size (Figure 6e). The pollinator population size decreases slightly with higher positive values of τ because of the lower nectar provisioning rate. Positive values of τ also favor the evolution of a higher toxin level, which leads to selection on the herbivore for a correspondingly higher detoxifying ability in response to the plant (Figure 6f). Thus, the herbivore's foraging rate and population size H are smaller for positive τ.

Discussion

Natural selection imposed by a mutualist on its partner species can feed back to affect the partner species' evolutionary response to an antagonist, and vice versa (Jones et al. 2009; Johnson et al. 2015; Kessler and Chautá 2020). In this paper, we elucidate potential eco-evolutionary feedbacks between two separate kinds of

species interactions. Using an evolutionary consumer-resource model of a plant-pollinator-herbivore interaction, we find that herbivores and pollinators, via their opposing effects on plant abundance, change selection on traits that mediate one another's interactions with the plant species. Herbivores select for higher toxin levels but also for increased nectar production (Figure 2). Herbivory's negative effect on plant abundance reduces pollinator abundance through time, indirectly enhancing selection for nectar resources that maintain pollinator interactions. Pollinators select for increased nectar production, but they also select for plants with higher toxin levels because their positive effect on plant abundance also boosts herbivore abundance (Figure 3). This in turn increases the frequency of herbivore interactions over time. Conditions that could enforce trade-offs in a plant's ability to respond to both consumers, such as lower resources for plants (Figure 4), higher plant dependence on pollinator-mediated reproduction (Figure 5), and direct effects of toxins on pollinator foraging (Figure 6), do not alter the overall patterns of natural selection caused by forager-mediated shifts in species abundances.

Our model predicts that animal-pollinated plants experiencing high herbivory will evolve higher nectar provisioning than those experiencing low herbivory, but their population sizes should be smaller (Figure 2). When herbivores reduce the plant's abundance, the damage they inflict indirectly strengthens selection on plant traits that enhance reproduction, in this case nectar resources for pollinators. The more damaging the herbivore (higher m), the stronger the selection on the plant to enhance reproductive benefits from pollinators via increased nectar provisioning (Figure 2a–c). Although this pathway has not been explored directly, strong empirical evidence supports components of the model's predicted pattern of evolutionary indirect effects. First, herbivores can dramatically reduce plant density, indirectly reducing plant reproductive success and pollinator abundance and altering pollinator species composition (Vázquez and Simberloff 2004; Gómez et al. 2009; Rusman et al. 2018).
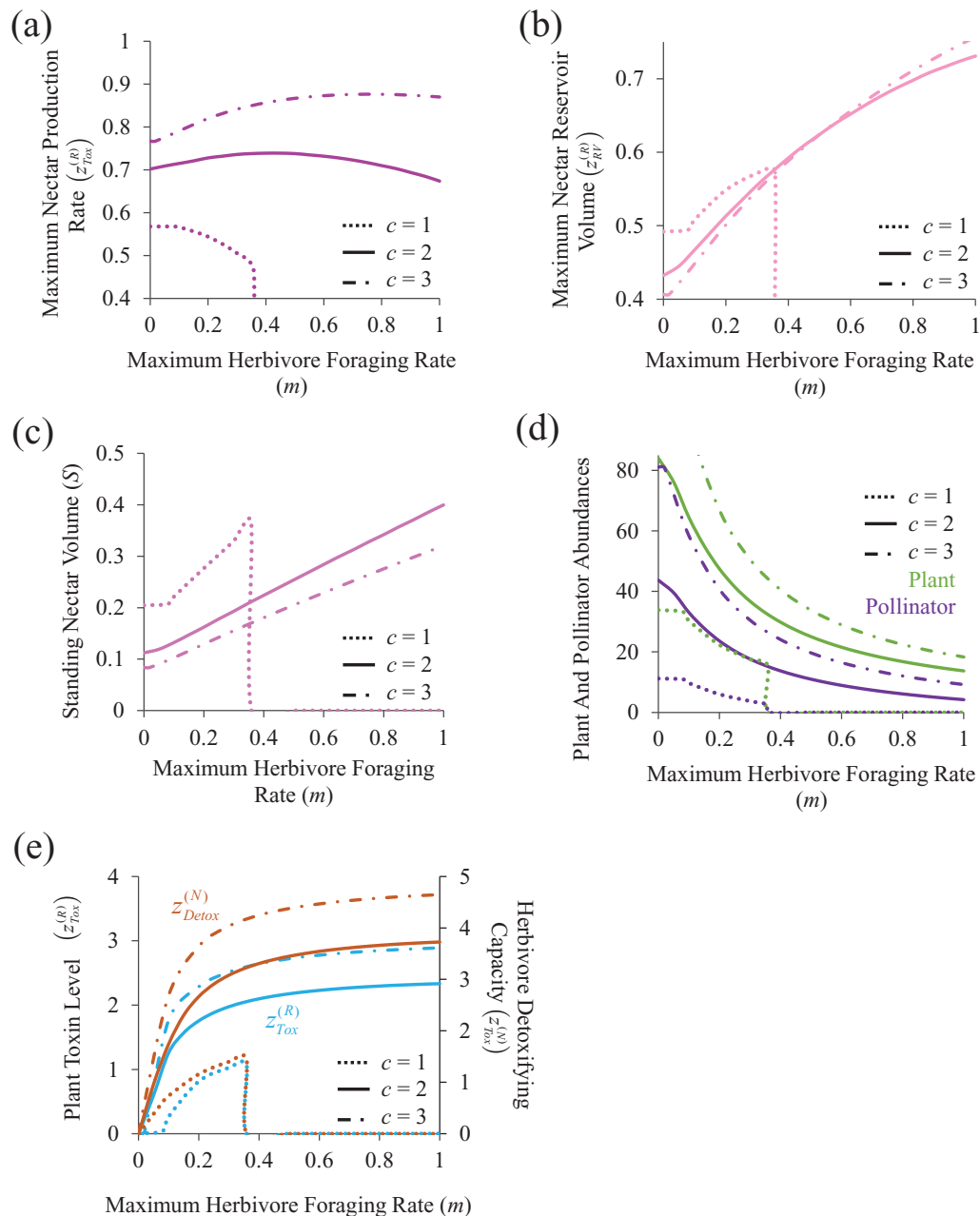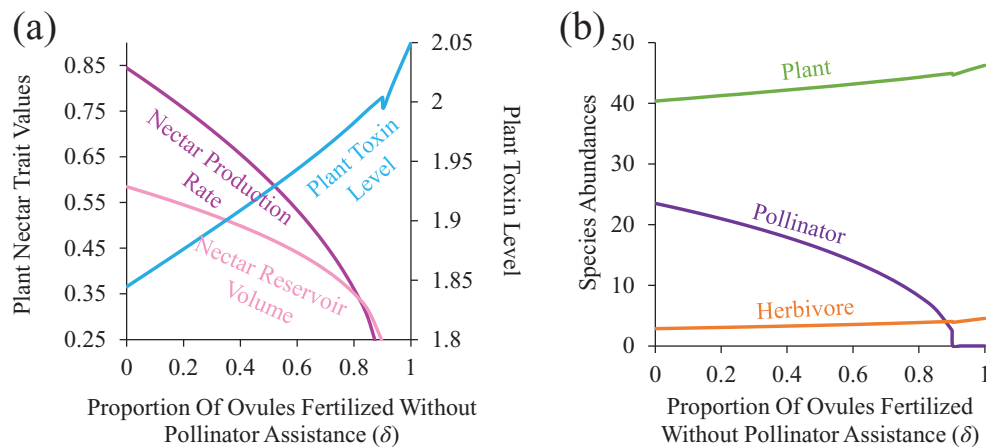
Figure 4. Plants evolve higher toxin and nectar production when they have higher resource levels (e.g., $c = 3$) than they do when they have lower resource levels (e.g., $c = 1$). Model parameters, unless otherwise specified, are as in Figure 2.

Second, herbivores can indirectly select for enhanced reproduction via a variety of plant traits, including flowering phenology, flower number, and floral morphology (García and Ehrlén 2002; Cariveau et al. 2004; Burkhardt et al. 2012; Ågren et al. 2013; Sletvold et al. 2015; Egan et al. 2021). Some plant species have also evolved inducible increases in nectar volume and sugar concentration as plastic responses to herbivory (Bruinsma et al. 2014; Chautá et al. 2017). Such plastic responses indicate the adaptive value of enhancing mutualism when plants are under attack. Klinkhamer and Lugt (2004) also showed that selection

on nectar production rates by bumblebees in *Echium vulgare* was strongest at low plant densities, suggesting that herbivores, by reducing plant abundance, may indirectly select for an increase in floral resource quantity and quality. In combination, these results suggest that herbivore foraging may perpetrate an evolutionary indirect effect on pollinators, although more empirical work is needed to confirm the proposed pathways.

Our model also predicts that plants that interact extensively with both pollinators and herbivores will evolve higher toxin levels than plants that experience pollinator limitation.
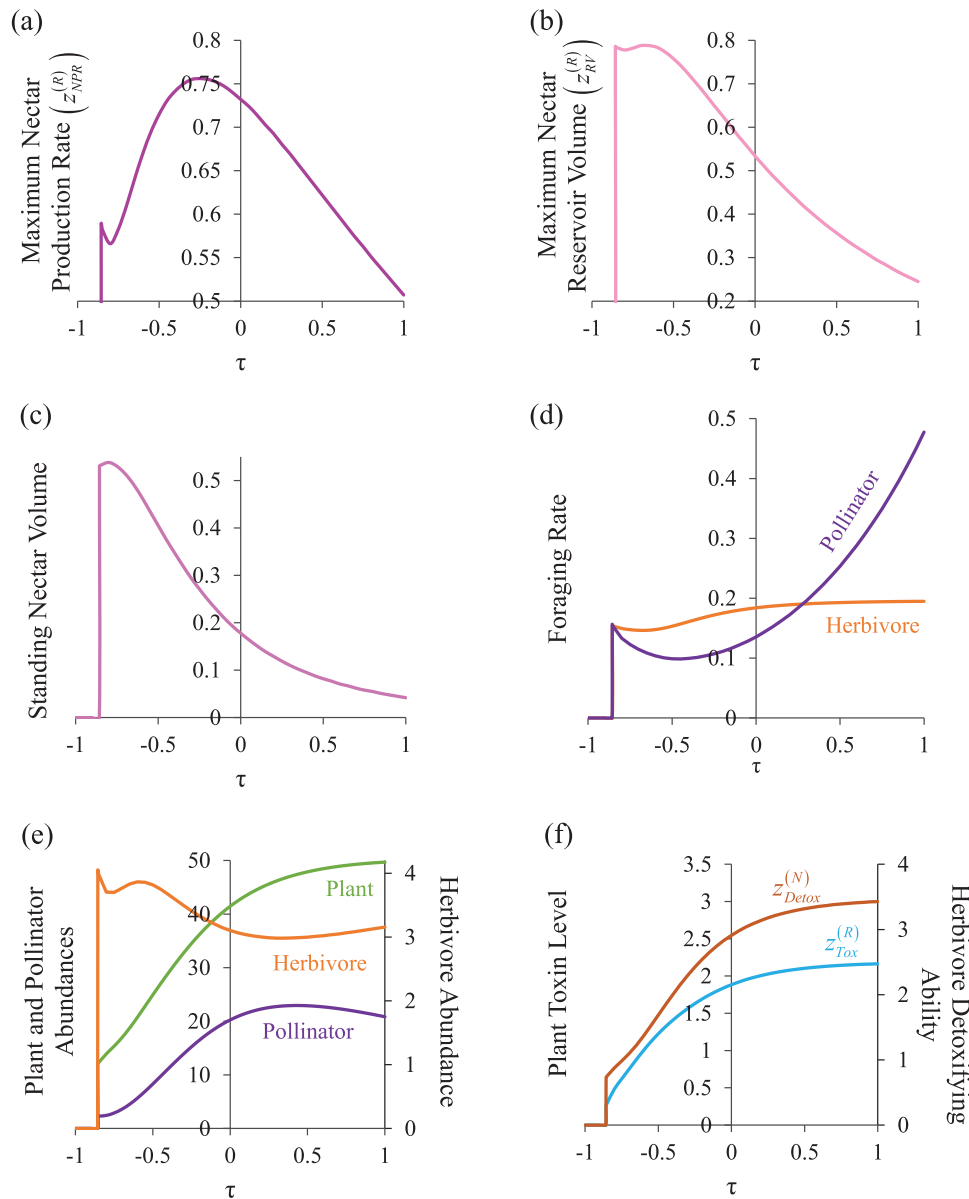
Figure 5. Plants evolve higher toxin levels and lower nectar production when a greater proportion of their ovules are fertilized without pollinator assistance. Model parameters, unless otherwise specified, are as in Figure 2.

By increasing the plant's population size, pollinators indirectly increase the frequency and intensity of herbivore interactions, selecting for increased herbivore defense. Empirical systems and community network models demonstrate increased herbivory via pollinator-mediated shifts in plant abundance (e.g., Herrera 2000; Hale et al. 2020). Our model presents an evolutionary extension to this known ecological effect, showing how pollinators relax the fitness costs associated with responding to the herbivore, which in turn increases selection for enhanced plant defenses and herbivore counterdefences. One way to test this prediction would be to compare toxin production and herbivory levels across plant populations with varying degrees of pollinator limitation. Our model further predicts that herbivores feeding on animal-pollinated plants may evolve correspondingly higher detoxifying abilities in response to the plant's defensive escalation (Figure 3b). To test this, one could manipulate the abundance of a toxic plant population and examine whether increasing the plant's abundance, thereby simulating the ecological effect of pollinators, strengthens selection on herbivore counterdefences over multiple herbivore generations. Of course, the evolution of more effective defenses is more likely for plant species in which these defenses do not affect pollinator foraging (Adler et al. 2001).

When herbivore defenses directly affect pollinator foraging, our model predicts different evolutionary outcomes for the forager-plant community (Figure 6). Specifically, when the pollinator is repelled by toxins in nectar ($\tau < 0$), the plant's and pollinator's abundances decrease, causing the plant to evolve higher nectar provisioning but lower toxin levels. Consistent with this response, Adler et al. (2012) found that *Nicotiana* species that rely on pollinators produced lower levels of alkaloids, known pollinator deterrents, than species with higher selfing rates. Conversely, when the pollinator is attracted by toxins ($\tau > 0$), the plant's abundance increases, causing the plant to evolve lower

nectar provisioning but higher toxin levels. Certain chemical compounds found in nectar, such as caffeine and alcohols, can attract pollinators to forage more frequently and to prefer individuals with these defense compounds in their nectar (Ehlers and Olesen 1997; Couvillon et al. 2015; Kevan et al. 2015; Thomson et al. 2015). Hypothetically, plants could also evolve mechanisms to exclude deterrent toxins from floral resources (Adler et al. 2012; Manson et al. 2012; Cook et al. 2013). While our model does not allow it, the qualitative results are consistent with such a response: pollinator deterrence selects for reduced toxin levels in the relevant tissues. More generally, the present model's results suggest that pollinator physiology and behavior in response to plant defenses are key to understanding correlations between attraction and defense traits. We predict that correlations between nectar volumes and toxin levels should be strongly positive when pollinators are attracted to forage on toxic floral rewards and strongly negative when pollinators avoid toxic individuals. Exploring toxin levels and floral resource volumes in a wider array of toxic plant species will reveal the generality of these relationships among pollinator behavior, plant abundance, and plant traits. We note that our model does not provide a specific mechanism for how toxins affect pollinators, allowing us to model cases when pollinators ingest toxins in nectar (reviewed by Stevenson et al. 2017) and cases when pollinators detect toxins from volatile emissions (e.g., Kessler and Halitschke 2009; Jacobsen and Raguso 2018).

Scenarios in which plants rely less on pollinators for reproduction (higher δ) or when pollinators respond to toxin levels ($\tau \neq 0$) are the only instances in our model where the plant evolves an increase in one kind of trait and a decrease in the other. Otherwise, plants always evolve increased nectar production in correspondence with increased toxin production. Plants that perform best in a population are those that deter herbivore

Figure 6. Plants evolve higher nectar provisioning (panels a–c) and lower toxin concentrations (panel f) but suffer reduced population sizes (panel e) and reduced realized pollinator foraging rates (panel d) when toxins deter pollinator foraging ($\tau < 0$). The converse responses are seen when toxins attract pollinators to forage more ($\tau > 0$). Model parameters, unless otherwise specified, are as in Figure 2. $a = 0.25 = m = 0.25$.

foraging and attract pollinator foraging, selecting for increases in both traits (Herrera et al. 2002; Ohashi et al. 2021). These results run counter to the widely held expectation of a constraining energetic trade-off between attraction traits and defense traits (Lucas-Barbosa et al. 2011). However, our model retains this constraint: plants pay separate reproductive costs when they invest in nectar and toxins. Indeed, plants in the model evolve lower nectar production rates and lower toxin levels when they have access to fewer resources (Figure 4). Another region of the model in which trait costs manifest is in the plant's compensatory response to costs of higher nectar production rates. When the her-

bivore has a higher foraging rate, the plant evolves a higher nectar reservoir volume (Figure 2b) but a lower nectar production rate (Figure 2a, see also McPeek et al. 2021). Plants could also reduce the costs of responding to both foragers by evolving higher selfing rates and reduced reliance on pollinators (Kessler and Halitschke 2009; Johnson et al. 2015; Ramos and Schiestl 2019). In our model, varying the level of non-animal-mediated pollination (changing δ, Figure 5) causes the plant to evolve an increased investment in the interaction with the stronger effects on plant fitness (pollinators at lower δ values, herbivores at higher δ values), but it does not affect the qualitative evolutionary dynamics of

how nectar and toxin traits respond to consumer foraging. Hence, the present model provides ample opportunity for energetic trade-offs to emerge. However, we find that ecologically driven shifts in selection, not constraints, ultimately shape the evolution of plant trait responses.

Our model intentionally condenses complex mechanisms of defense and attraction to capture a diverse range of plant-consumer interactions. For instance, we measure a plant's toxin level not as its concentration in plant tissue but as its effect on herbivore and pollinator foraging rates. By quantifying each plant trait in terms of its effect on consumer behavior and consumer population growth, we provide a direct causal link between plant traits and plant fitness in species interactions. The parameter τ can thus be thought of as the overall effect of plant defenses on pollinator foraging activity. This effect encompasses many situations, including when toxins are present in varying amounts in leaves and nectar (e.g., Adler et al. 2012; Manson et al. 2012), when toxins are more concentrated in pollen than in nectar (e.g., Cook et al. 2013; Palmer-Young et al. 2019), or when toxic volatile compounds rather than ingested toxins are driving the pollinator response (e.g., Kessler et al. 2011). Researchers could further generalize the plant's 'toxin level' to encompass any chemical and morphological defenses plants mount against herbivores; the qualitative patterns resulting from trait-mediated effects on consumers will remain the same. Additionally, trait changes in this model can also be interpreted as adaptive plastic responses by individual plants to pollinator and herbivore interactions (e.g., Abrams and Matsuda 1993), mirroring scenarios of inducible plant defenses (e.g., Adler et al. 2006; Jacobsen and Raguso 2018; Ramos and Schiestl 2020). This change does not alter any of the quantitative or qualitative patterns, only the timing of the plant's response. Regardless of how traits are treated, our model demonstrates that examining their direct and indirect effects on consumer ecology and behavior is critical to understanding the entangled evolution of attraction and defense traits.

Eco-evolutionary feedbacks between mutualistic and antagonistic species interactions may play important roles in community assembly and diversification stretching back across deep time. Flowering plants have codiversified with pollinators and herbivores for millions of years, shaping the interactions we observe today. Herbivory, which evolved prior to animal pollination, may have played a formative role in facilitating the evolution of biotic pollination in angiosperms by strengthening selection on traits that would attract floral visitors (Ehrlich and Raven 1964; Strauss and Whittall 2006; Janz 2011; Johnson et al. 2015; Santangelo et al. 2019). Likewise, pollinators may have played a key role in the evolutionary diversification of plants and herbivores by modulating the strength of selection on plant defenses, including exaptation of pollinator attraction traits for herbivore defense (Armbruster 1997; Armbruster et al. 1997, 2009; Marquis

et al. 2016). While disentangling these feedbacks with historical data alone is impossible, phylogenetic comparative studies can test the predicted outcomes of these eco-evolutionary feedbacks across species. Furthermore, eco-evolutionary feedbacks are active in modern communities. Ample data are available to test the present model's pathways in a variety of plant-pollinator-herbivore interactions as well as other combinations of mutualists and antagonists, such as plant-mycorrhizal fungus-herbivore or plant-pollinator-pathogen interactions. Exploring the evidence for feedbacks in natural communities will also test the robustness of these effects among entire guilds of pollinators, herbivores, and their plant resources.

CONFLICT OF INTEREST
The authors have declared no conflict of interest.

DATA ARCHIVING
There are no data for this work. MATLAB code for the model is available in the Supporting Information.

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