VOL. 198, NO. 4 THE AMERICAN NATURALIST OCTOBER 2021

The Evolution of Resource Provisioning in Pollination Mutualisms

Sarah J. McPeek,^{1,*} **Judith L. Bronstein,**^{2} **and Mark A. McPeek**^{3}

1. Department of Biology, University of Virginia, Charlottesville, Virginia 22904; 2. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721; 3. Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755

Submitted January 2, 2021; Accepted May 15, 2021; Electronically published August 18, 2021

Dryad data: https://doi.org/10.5061/dryad.7m0cfxptq.

ABSTRACT: Resource dynamics influence the contemporary ecology of consumer-resource mutualisms. Suites of resource traits, such as floral nectar components, also evolve in response to different selective pressures, changing the ecological dynamics of the interacting species at the evolutionary equilibrium. Here we explore the evolution of resource-provisioning traits in a biotically pollinated plant that produces nectar as a resource for beneficial consumers. We develop a mathematical model describing natural selection on two quantitative nectar traits: maximum nectar production rate and maximum nectar reservoir volume. We use this model to examine how nectar production dynamics evolve under different ecological conditions that impose varying cost-benefit regimes on resource provisioning. The model results predict that natural selection favors higher nectar production when ecological factors limit the plant or pollinator's abundance (e.g., a lower productivity environment or a higher pollinator conversion efficiency). We also find that nectar traits evolve as a suite in which higher costs of producing one trait select for a compensatory increase in investment in the other trait. This empirically explicit approach to studying the evolution of consumer-resource mutualisms illustrates how natural selection acting via direct and indirect pathways of species interactions generates patterns of resource provisioning seen in natural systems.

Keywords: consumer-resource interactions, pollination mutualisms, floral nectar evolution, indirect effects.

Introduction

Many species relationships involve exchanges of energy or material resources that alter the population dynamics of the interacting species. Herbivores consume plants, thus increasing their own abundance and in many cases reducing the size of the plant population (Crawley 1989). Plant species compete with one another for nutrients, depressing each other's abundances by consuming those limiting resources (Tilman 1982; Goldberg 1990). Consumer-resource dynamics have long been a unifying theme in theoretical considerations of antagonistic species relationships, such as predation, parasitism, and resource competition (Murdoch et al. 2003). Crucially, consumer-resource dynamics are influenced by species traits. For instance, plants with higher concentrations of inducible toxic alkaloids may experience reduced herbivory (e.g., Karban et al. 1997), and plants with a stronger ability to take up nitrogen will be better competitors for that limiting resource (e.g., Gutschick 1981). As these traits experience natural selection and evolve, the ecological dynamics of the consumer-resource interaction will evolve as well (e.g., Roughgarden 1972; Slatkin 1980; Taper and Case 1985; Abrams and Chen 2002; Vasseur and Fox 2011; McPeek 2017*a*, 2017*b*, 2019). By studying how natural selection acts on traits that affect consumer-resource dynamics, we gain insights into the ecological conditions that shape the evolution of energy flow in communities.

Many mutualisms can also be classified as consumer-resource interactions because they too are trait-mediated interactions that involve an exchange of energy or materials (Herre et al. 1999; Holland et al. 2005; Holland and DeAngelis 2009, 2010; Jones et al. 2012; Bronstein 2015). In consumer-resource mutualisms, the resource is not the individual itself but rather a product that the individual produces in exchange for some form of benefit from its consumer. For example, larvae of some lycaenid butterflies provide nutritive secretions to ants, which directs the ants' predatory behaviors toward lycaenids' natural enemies rather than toward the lycaenids themselves (Pierce et al. 2002). Many plants produce sugar-rich fruits that are fed upon by animals that then disperse the seeds, increasing the likelihood that some will germinate (Simmons et al. 2018). To date, consumer-resource mutualisms have received little attention as a major component of consumer-resource theory (but see Holland et al. 2005). This is a

---

* Corresponding author; email: sjm8dj@virginia.edu.

ORCIDs: S. J. McPeek, https://orcid/org/0000-0001-7175-8976; M. A. McPeek, https://orcid/org/0000-0001-7794-9466.

American Naturalist, volume 198, number 4, October 2021. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/715746

severe oversight, as consumer-resource mutualisms can have profound impacts on the structure of diverse ecological communities (e.g., Stachowicz 2001; Johnson 2015). Furthermore, the benefit of product consumption for the resource provider is often an indirect result of how its own resource provisioning affects the consumer's behavior, providing a unique opportunity to study how trait-mediated indirect effects influence ecological and evolutionary dynamics in consumer-resource interactions (Abrams 1995; Werner and Peacor 2003).

In consumer-resource mutualisms, the dynamics of the resource can be treated separately from the population dynamics of the interacting species. This differs notably from consumer-resource antagonisms wherein species deplete each other's abundances, not each other's resource products. Explicitly modeling mutualistic resources has provided critical mechanistic insights into how resource dynamics may shape mutualism ecology (Soberon and Martinez del Rio 1981; Valdovinos et al. 2013; Revilla 2015; Bachelot and Lee 2018; Valdovinos 2019). For example, a provider has a finite ability to produce resources. Its maximum rate of resource provisioning will constrain the consumer and resource-provider's population growth rates and thus the fitness benefits that can be accrued by each from the interaction (Soberon and Martinez del Rio 1981; Revilla 2015). The consumer species' foraging behavior further affects the resource dynamics of the interaction by determining the rate of resource depletion (Valdovinos et al. 2013; Revilla 2015). Overall, consumer-resource theories of mutualism suggest that a provider species' optimal rate of resource provisioning balances the costs and benefits of provisioning for a partner (Pyke 1981; Soberon and Martinez del Rio 1981; Bachelot and Lee 2018). If we further conceptualize resource dynamics as trait dynamics, we can add an evolutionary perspective to this cost-benefit framework: species should evolve resource trait combinations that maximize their fitness via their provisioning for a mutualistic consumer.

Incorporating natural selection on resource traits into theories of consumer-resource mutualism can generate empirical predictions about how resource-provisioning traits, as well as the species relationships they mediate, may evolve under varying cost-benefit regimes. For instance, an evolutionary perspective on consumer-resource mutualism holds potential for explaining the astonishing diversity of plant traits associated with pollination mutualisms. Many pollination interactions are consumer-resource mutualisms in which plants produce floral nectar and pollen that feed animals, which then move pollen between flowers as they seek more food from the plants (Willmer 2011). Crucially, traits that influence a plant's nectar supply dynamics, such as a plant's rate of nutrient uptake from the environment, the quantity and chemical composition of the nectar a plant produces, and the rate at which a plant can replenish its nectar as the consumer depletes its standing crop, all play a key role in mediating a plant's interaction with pollinators (Nicolson et al. 2007). While empirical studies have examined diverse aspects of nectar quality and quantity in natural plant populations, we have little understanding of the causes and strengths of natural selection on the traits that underlie its production dynamics in different ecological settings (Parachnowitsch et al. 2019). An empirically explicit theory of mutualism evolution will provide directions for future inquiry into the past, present, and future ecological forces that drive the evolution of resource provisioning in consumer-resource mutualisms, including pollination.

To this end, we develop a consumer-resource model of a mutualist plant's evolving nectar-provisioning dynamics in a pairwise plant-pollinator interaction. The model describes the fitness landscapes of two plant traits that influence nectar quantity, nectar production rate and nectar reservoir volume, under a range of ecological conditions and various pollinator foraging capabilities. Nectar production rate captures a plant's physiological capacity to produce and secrete nectar and determines how fast depleted nectar can be replenished; nectar reservoir volume captures a plant's total nectar-holding capacity, reflecting traits such as floral corolla depth and the number and size of flowers on a plant individual. Together, these traits define the total resource pool available to consumers, which directly affects the local abundance of pollinators and the frequency of plant-pollinator interactions and indirectly affects the abundance of plants via interactions with pollinators. Our resource trait–centered model generates testable predictions about how consumer-resource mutualisms evolve in natural communities.

Model of Nectar Evolution in a Plant-Pollinator Interaction

We begin by defining the dynamics of a plant population with a population size R_1. To attract pollinators, individuals produce nectar. Plants have two quantitative traits that determine their nectar production dynamics. We assume that the average values of these traits are constant over an individual's lifetime, and we treat a population's mean trait values as averages across all flowers on all plants. We also assume that these two traits are genetically uncorrelated and can evolve independently of one another. The first quantitative trait is the maximum rate at which an individual can produce and secrete nectar into flowers: we represent this trait as z_{NPR}. The second trait is the maximum volume of nectar that an individual plant can hold, summed across all flowers on the plant (hereafter, "reservoir volume"): we represent this trait as z_{RV}. The model analyzed here does not consider whether reservoir volume is distributed across many small or a few large flowers (e.g., Cohen and Shmida 1993; Venable 1996). For simplicity, we assume that plants always replenish nectar to its maximum holding capacity within an individual flower. We also assume that all other properties of nectar remain constant (e.g., sugar and amino acid content and concentration). Additionally, we do not consider selection on flowering phenology, floral longevity, or seasonal variation in nectar production, and we also do not consider pollen as an additional resource for consumers. We are primarily concerned with the population's average trait expression across the entire flowering period, since these measures describe the average total resource pool available to consumers at a given time.

Plants in this model replenish nectar dynamically as pollinators deplete their supply. We define the standing volume of nectar currently available to pollinators on a single plant (hereafter, "standing nectar volume") as S_1. At any moment, the total volume of nectar on all plants in the population is thus $R_1 S_1$. Individual plants produce nectar to fill their reservoirs according to a simple logistic resource renewal function:

$$z_{\mathrm{NPR}}\left(1-\frac{S_1}{z_{\mathrm{RV}}}\right). \tag{1}$$

The production rate when $S_1 = 0$ in all flowers on a plant is equal to the maximum nectar production rate z_{NPR}, and this rate decreases linearly until a plant's reservoir is full (fig. 1*A*). For a given constant nonzero rate of nectar depletion, an increase in either z_{NPR} or z_{RV} will increase the equilibrium volume of nectar S_1 on a plant. (Descriptions of all state variables and model parameters used in this model are provided in table 1.)

We assume that the plant population displays logistic growth in the absence of pollinators, such that its per capita growth rate is

$$c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}}) - d_1 R_1 \tag{2}$$

(Verhulst 1838; Pearl and Reed 1920). Here, $c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}})$ is the plant population's intrinsic rate of increase, which is a function of the values of the two traits (see below), and d_1 is the strength of density dependence from limiting factors that regulate its population size but are not explicitly modeled (Pianka 1972; Schoener 1973; Schaffer and Leigh 1976; Schaffer 1981). In the absence of pollinators, the plant population will increase to an equilibrium population size of $R_1^* = c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}})/d_1$ if the plant exists in favorable environmental conditions and does not need the pollinator's fitness benefit to maintain a population, that is, $c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}}) > 0$. In this scenario, the plant is a facultative mutualist. However, if the plant is an obligate

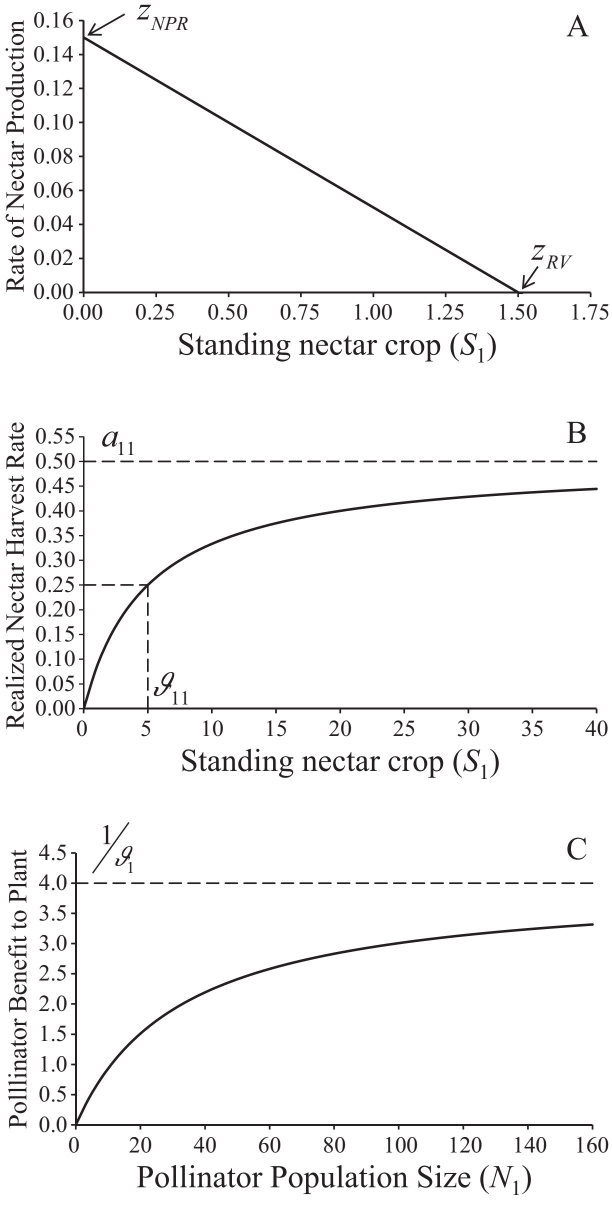

Figure 1: Illustrations of the functional relationships for various components of the plant and pollinator dynamics. *A*, The rate at which nectar is produced to fill the nectar reservoir of the plant decreases linearly as nectar volume increases in the reservoir (eq. [1]). The maximum rate (z_{NPR}) of filling occurs when the reservoir is empty and stops when the volume reaches z_{RV}. In this panel, $z_{\mathrm{NPR}} = 0.15$ and $z_{\mathrm{RV}} = 1.5$. *B*, The realized nectar consumption rate (i.e., the attack coefficient) increases with the plant trait according to a Michaelis-Menten function (eq. [5]; $a_{11}(S_1) = a_{11}S_1/[\vartheta_{11} + S_1]$), in which a_{11} is the asymptotic maximum and ϑ_{11} is the half-saturation constant (i.e., the trait value at which the nectar consumption rate is at half the asymptote). In this panel, $a_{11} = 0.5$ and $\vartheta_{11} = 5.0$. *C*, The fitness benefit received by the plant from benefits with pollinators follow Holling's saturating functional response that saturates at $1/\phi_1$ (eq. [6]). In this panel, $\phi_1 = 0.25$.

Table 1: State variables and parameters used in the model

	Description
State variables:	
R_1	Population abundance of plant
N_1	Population abundance of pollinator
S_1	Mean standing volume of nectar on a plant individual
z_{NPR}	Mean trait value for nectar production rate
z_{RV}	Mean trait value for reservoir volume
Parameters:	
c_1	Maximum intrinsic rate of increase for plant
d_1	Strength of intraspecific density dependence for plant
a_{11}	Maximum consumption rate for pollinator feeding on nectar
b_{11}	Conversion efficiency in fitness for pollinator feeding on nectar
f_1	Intrinsic death rate for pollinator
γ_{NPR}	Scaling parameter for decline in plant intrinsic rate of increase with increasing values of z_{NPR}
γ_{RV}	Scaling parameter for decline in plant intrinsic rate of increase with increasing values of z_{RV}
ϕ_1	Scaling parameter determining the maximum fitness benefit that an individual plant can receive from interacting with the pollinator population
ϑ_{11}	Michaelis-Menten half-saturation constant for pollinator feeding on nectar
ψ_1	Scaling parameter for fitness cost of producing one unit of nectar

mutualist (i.e., it cannot reproduce without pollinators) or is in poor environmental conditions where it cannot maintain a population without the pollinator's fitness benefit—that is, $c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}}) < 0$—the population will decline to extinction when pollinators are absent.

We assume that individual plants may pay three different costs of producing nectar depending on the values of the two traits. First, producing the machinery necessary to make nectar may be costly (e.g., nectaries; Nicolson et al. 2007). This cost is expressed as a decrease in the plant population's intrinsic rate of increase (in eq. [2]) according to a quadratic function of z_{NPR}. Second, producing the structures to hold nectar (e.g., increasing the number or depths of flowers) may be costly as well, also decreasing the plant population's intrinsic rate of increase according to a quadratic function of z_{RV} (e.g., Nobel 1977; Ashman 1994). Based on these assumptions, the population's intrinsic rate of increase is then

$$c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}}) = c_1 - \gamma_{\mathrm{NPR}} z_{\mathrm{NPR}}^2 - \gamma_{\mathrm{RV}} z_{\mathrm{RV}}^2, \tag{3}$$

where c_1 is the maximum intrinsic rate of increase when $z_{\mathrm{NPR}} = z_{\mathrm{RV}} = 0$ and γ_{NPR} and γ_{RV} scale the decline in the plant's intrinsic rate of increase as z_{NPR} and z_{RV} increase. From an evolutionary perspective, these two scaling parameters also modulate the steepness of the selection gradient that acts on a plant's nectar production traits via individual fitness effects on the population's intrinsic rate of increase. Finally, individuals may pay an incremental cost for every unit of nectar produced:

$$\psi_1 z_{\mathrm{NPR}}\left(1 - \frac{S_1}{z_{\mathrm{RV}}}\right), \tag{4}$$

which is simply the realized nectar production rate (eq. [1]) times a constant ψ_1 that scales the fitness cost for each unit of nectar a plant produces.

The plant population interacts with a pollinator that has a population size N_1. Just like any consumer, a pollinator uses a resource, in this case the nectar produced by the plant, to gain energy and produce offspring. Pollinators consume nectar at a rate that scales with the amount of available nectar on each plant according to the Michalis-Menten/Monod relationship

$$a_{11}(S_1) = \frac{a_{11} S_1}{\vartheta_{11} + S_1}, \tag{5}$$

where a_{11} is the asymptotic maximum consumption rate and ϑ_{11} is the half-saturation constant (fig. 1*B*; Michaelis and Menten 1913; Monod 1949). We also assume that the pollinator population has an intrinsic density-independent death rate given by f_1. These assumptions entail that the nectar provided by the plant is the main factor limiting local pollinator abundance.

While foraging for nectar, pollinators incidentally provide a fitness benefit to plants by transferring pollen between flowers. This benefit is also a function of the nectar consumption rate $a_{11}(S_1)$. Consistent with Holland and DeAngelis (2009, 2010), we assume that this fitness benefit saturates with increasing pollinator population size according to

$$B(S_1, N_1) = \left(\frac{a_{11}(S_1)N_1}{1 + a_{11}(S_1)\phi_1 N_1}\right) = \frac{\dfrac{a_{11}S_1}{\vartheta_{11} + S_1}N_1}{1 + \dfrac{a_{11}S_1}{\vartheta_{11} + S_1}\phi_1 N_1}, \tag{6}$$

where ϕ_1 defines the maximum fitness benefit that an individual plant can receive from pollinator foraging. This maximum fitness benefit when pollinator abundance is very large is thus $1/\phi_1$ (fig. 1*C*). This fitness benefit can be measured as the increase in female plant fitness due to a greater number of ovules being fertilized by the actions of the pollinators as they forage for nectar. Specifically, $c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}})$ is a fitness component of the plant that defines the plant population's rate of increase independent of the pollinator's actions (i.e., how many plant ovules are fertilized by vectors other than pollinators), $B(S_1, N_1)$ defines the supplement of this fitness component given local pollinator population size, and $1/\phi_1$ is the maximum value of $B(S_1, N_1)$ if pollen is deposited in excess of the amount needed to fertilize all ovules. Note that we do not consider male fitness in this model. As stated above, if $c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}}) > 0$, the plant can maintain a population in the absence of pollinators under the local conditions it experiences. However, if $c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}}) < 0$, the plant must receive a sufficient fitness increase from the actions of pollinators (i.e., pollinators must fertilize enough additional ovules to generate a sustaining per capita fitness) in order for $c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}}) + B(S_1, N_1) > 0$: otherwise, the plant population will become extinct when no pollinators are present.

Given these assumptions, the dynamics of the plant population R_1, its total nectar pool R_1S_1, and the pollinator population N_1 are given by the following set of differential equations (note that the plant and pollinator equations are expressed in their per capita forms but the nectar equation is expressed in its total growth rate form, i.e., the change in the plant population's total nectar volume):

$$\begin{aligned}\frac{1}{R_1}\frac{dR_1}{dt} &= (c_1 - \gamma_{\mathrm{NPR}}z_{\mathrm{NPR}}^2 - \gamma_{\mathrm{RV}}z_{\mathrm{RV}}^2) - d_1R_1 \\ &\quad + \frac{\dfrac{a_{11}S_1}{\vartheta_{11} + S_1}N_1}{1 + \dfrac{a_{11}S_1}{\vartheta_{11} + S_1}\phi_1 N_1} - \psi_1 z_{\mathrm{NPR}}\left(1 - \frac{S_1}{z_{\mathrm{RV}}}\right), \\ \frac{d(R_1S_1)}{dt} &= R_1 z_{\mathrm{NPR}}\left(1 - \frac{S_1}{z_{\mathrm{RV}}}\right) - \frac{a_{11}S_1}{\vartheta_{11} + S_1}R_1S_1N_1, \\ \frac{1}{N_1}\frac{dN_1}{dt} &= b_{11}\frac{a_{11}S_1}{\vartheta_{11} + S_1}R_1S_1 - f_1.\end{aligned} \tag{7}$$

In the pollinator equation, b_{11} is the conversion efficiency describing the rate at which pollinators convert consumed nectar into pollinator offspring.

The per capita population growth equation for the plant species in (7) also expresses the average per capita fitness of the plant with mean trait values of z_{NPR} and z_{RV} (Lande 1982, 2007). In other words, this equation defines the fitness topography against which the plant population evolves. The various terms in (7) define how z_{NPR} and z_{RV} influence fitness components that act in combination to determine the plant's total fitness. However, the equation given in (7) only explicitly relates the relationships of these traits to the fitness costs. The relationships of these traits to the benefits of nectar production for the plant are not apparent because they are embedded in the dynamic variable for standing nectar volume, S_1.

To incorporate both the fitness benefit and cost relationships with the two quantitative plant traits into the plant equation, we assume that standing nectar volume is always at equilibrium with plant and pollinator population size (i.e., $d(R_1S_1)/dt = 0$) and solve the nectar dynamics equation for the equilibrium standing nectar volume. This results in a quadratic function, and the root associated with positive equilibrium standing nectar volume is

$$S_1^+ = z_{\mathrm{NPR}}\left(\frac{z_{\mathrm{RV}} - \vartheta_{11} + \sqrt{(z_{\mathrm{RV}} + \vartheta_{11})^2 + 4z_{\mathrm{RV}}^2\vartheta_{11}a_{11}N_1/z_{\mathrm{NPR}}}}{2(z_{\mathrm{NPR}} + z_{\mathrm{RV}}a_{11}N_1)}\right). \tag{8}$$

This derivation is then substituted into the plant population dynamics equation in (7) to express the plant per capita fitness explicitly as a function of its two quantitative traits.

The resulting equation can then be used to model the evolution of nectar production rate and nectar reservoir volume in response to the various selection pressures outlined above. We follow Lande's (1982, 2007) approach to trait dynamics using the continuous time breeder's equation formulation to study the evolution of the mean nectar production phenotype in this population. We favor Lande's approach over other possible approaches (e.g., adaptive dynamics) because it is based on the breeder's equation from quantitative genetics. Thus, the evolutionary process is modeled in the same framework empiricists use to study the dynamics of selection in natural systems. The dynamics of trait evolution are then given in box 1.

A model of this complexity prohibits analytical analysis. Therefore, we use computer simulations (numerical integration of the model using the ode45 solver of Matlab) to analyze patterns emerging from interesting and biologically reasonable areas of parameter space. Matlab code is

Box 1: Dynamics of trait evolution

The two nectar dynamics traits of the plant evolve according to

$$\begin{aligned}
\frac{dz_{\mathrm{NPR}}}{dt} &= G_{\mathrm{NPR}}\frac{\partial\dfrac{dR_1}{R_1dt}}{\partial z_{\mathrm{NPR}}}\\
&= G_{\mathrm{NPR}}\left(-2\gamma_{\mathrm{NPR}}z_{\mathrm{NPR}}+\frac{a_{11}\vartheta_{11}N_1\dfrac{\partial S_1^+}{\partial z_{\mathrm{NPR}}}}{(\vartheta_{11}+S_1^+)^2\left(1+\dfrac{a_{11}S_1^+}{\vartheta_{11}+S_1^+}\phi_1N_1\right)^2}-\psi_1\left(1-\frac{S_1^+}{z_{\mathrm{RV}}}-\frac{z_{\mathrm{NPR}}\dfrac{\partial S_1^+}{\partial z_{\mathrm{NPR}}}}{z_{\mathrm{RV}}}\right)\right),\\
\frac{dz_{\mathrm{RV}}}{dt} &= G_{\mathrm{RV}}\frac{\partial\dfrac{dR_1}{R_1dt}}{\partial z_{\mathrm{RV}}}\\
&= G_{\mathrm{RV}}\left(-2\gamma_{\mathrm{RV}}z_{\mathrm{RV}}+\frac{a_{11}\vartheta_{11}N_1\dfrac{\partial S_1^+}{\partial z_{\mathrm{RV}}}}{(\vartheta_{11}+S_1^+)^2\left(1+\dfrac{a_{11}S_1^+}{\vartheta_{11}+S_1^+}\phi_1N_1\right)^2}-\psi_1\frac{z_{\mathrm{NPR}}}{z_{\mathrm{RV}}}\left(\frac{S_1^+}{z_{\mathrm{RV}}}-\frac{\partial S_1^+}{\partial z_{\mathrm{NPR}}}\right)\right),
\end{aligned}\tag{9}$$

where

$$\begin{aligned}
\frac{\partial S_1^+}{\partial z_{\mathrm{NPR}}} &= \frac{2z_{\mathrm{RV}}a_{11}N_1(z_{\mathrm{RV}}-\vartheta_{11})}{(2z_{\mathrm{NPR}}+2z_{\mathrm{RV}}a_{11}N_1)^2}\\
&\quad+\frac{2z_{\mathrm{RV}}a_{11}N_1(z_{\mathrm{NPR}}\vartheta_{11}^2+z_{\mathrm{NPR}}z_{\mathrm{RV}}^2+2z_{\mathrm{RV}}^2a_{11}\vartheta_{11}N_1)}{(2z_{\mathrm{NPR}}+2z_{\mathrm{RV}}a_{11}N_1)^2\sqrt{(z_{\mathrm{NPR}}z_{\mathrm{RV}}+z_{\mathrm{NPR}}\vartheta_{11})^2+4z_{\mathrm{NPR}}z_{\mathrm{RV}}^2\vartheta_{11}a_{11}N_1}},\\
\frac{\partial S_1^+}{\partial z_{\mathrm{RV}}} &= \frac{2z_{\mathrm{NPR}}(z_{\mathrm{NPR}}+\vartheta_{11}a_{11}N_1)}{(2z_{\mathrm{NPR}}+2z_{\mathrm{RV}}a_{11}N_1)^2}\\
&\quad+\frac{2z_{\mathrm{NPR}}^2(z_{\mathrm{NPR}}\vartheta_{11}+z_{\mathrm{NPR}}z_{\mathrm{RV}}+3z_{\mathrm{RV}}\vartheta_{11}a_{11}N_1-\vartheta_{11}^2a_{11}N_1)}{(2z_{\mathrm{NPR}}+2z_{\mathrm{RV}}a_{11}N_1)^2\sqrt{(z_{\mathrm{NPR}}z_{\mathrm{RV}}+z_{\mathrm{NPR}}\vartheta_{11})^2+4z_{\mathrm{NPR}}z_{\mathrm{RV}}^2\vartheta_{11}a_{11}N_1}},
\end{aligned}$$

G_{NPR} and G_{RV} are the additive genetic variances in nectar production in the two corresponding traits, and the terms in parentheses are the selection gradients on z_{NPR} and z_{RV} from the various fitness components of the plant.

provided in the Dryad Digital Repository (https://doi.org/10.5061/dryad.7m0cfxptq; McPeek et al. 2021).

Results

Defining the Fitness Surfaces of Nectar Production Traits

We first examine how the fitness landscape of the plant's two nectar production traits, maximum nectar production rate z_{NPR} and maximum nectar reservoir volume z_{RV}, define the ecological and evolutionary trajectory of the plant population R_1. We partition the plant's total fitness into three components that depend on its trait values z_{NPR} and z_{RV} (eq. [7]): the fitness contributions of the intrinsic rate of increase, of pollinators, and of nectar production.

First, consider a plant population that receives no attention from pollinators. The population's total and component fitness surfaces at ecological and evolutionary equilibrium are shown in figure 2. Without pollinators, the costs of producing nectar for no beneficial returns push the plant population to evolve to a fitness maximum at a zero nectar production rate (fig. 2*A*) and a zero nectar reservoir volume (fig. 2*B*). Notice that the plant population's total fitness surfaces for nectar production rate (fig. 2*A*) and reservoir volume (fig. 2*B*) are identical to the component surfaces measuring the cost of making nectar-secreting and nectar-holding structures on its intrinsic rate of increase $c_1(z_{\mathrm{NPR}}, z_{\mathrm{RV}})$ (fig. 2*C*, 2*D*). The other component surfaces remain completely flat because plants in this case earn no fitness benefit from making nectar

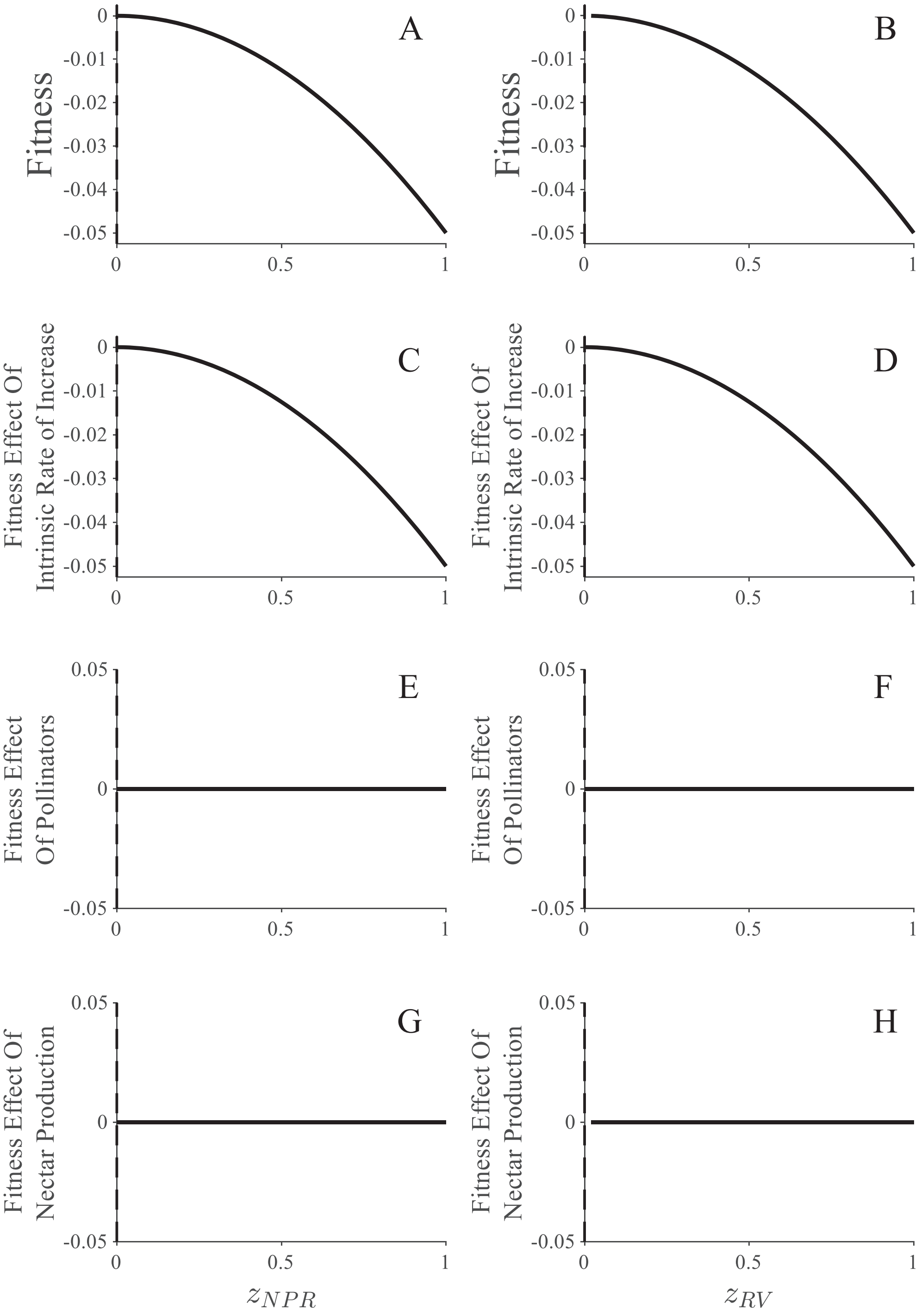

Figure 2: Determinants of plant fitness for nectar production rate and nectar reservoir volume without pollinators at evolutionary equilibrium. The top row of panels shows the topography of overall fitness for nectar production rate z_{NPR} (*A*) and reservoir volume z_{RV} (*B*). These overall fitness relationships are composed of component topographies due to the effects that each trait has on the plant's intrinsic rate of increase (*C*, *D*), the benefits accrued from pollinator visits (*E*, *F*), and the cost of nectar production (*G*, *H*). Because pollinators are absent in this example, the plants accrue neither of these benefits or production costs, so the overall fitness topography is identical to the trait effects on the intrinsic rate of increase. Model parameters are as follows: $c_1 = 2.0$, $d_1 = 0.02$, $\gamma_{\mathrm{NPR}} = \gamma_{\mathrm{RV}} = \psi_1 = 0.05$, $\phi_1 = 0.25$, $a_{11} = 0.25$, $b_{11} = 0.1$, $\vartheta_{11} = 0.05$, $f_1 = 0.15$, $G_{\mathrm{NPR}} = G_{\mathrm{RV}} = 0.2$.

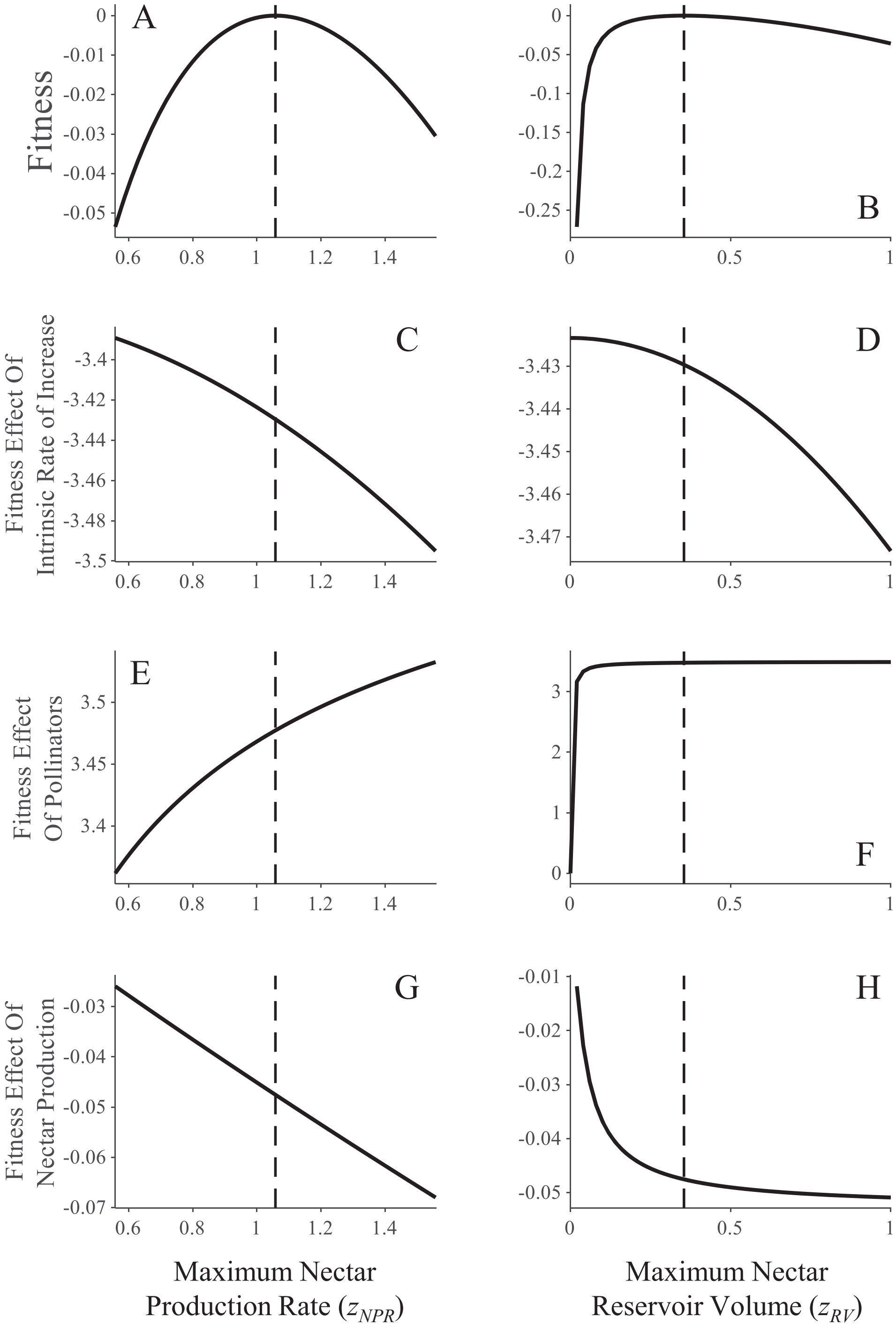

Figure 3: Determinants of plant fitness for nectar production rate and nectar reservoir volume with pollinators at evolutionary equilibrium. The panels here correspond to the same fitness topographies as shown in figure 2, but now with the pollinator population present and at its equilibrium abundance. Parameters are also as given in figure 2.

(fig. 2*E*, 2*F*), and they pay no incremental cost ψ_1 of producing nectar because the nectar reservoir has a volume of zero (fig. 2*G*, 2*H*).

Now, consider the total and component fitness surfaces of the same plant population when pollinators are present (fig. 3). The structural costs on the plant's intrinsic rate of increase of making nectar-producing and nectar-holding structures (fig. 3*C*, 3*D*) are identical in magnitude to those experienced by an abiotically pollinated plant (fig. 2*C*, 2*D*). However, in this population these fitness costs are offset by the direct benefits pollinators provide to plants by fertilizing ovules while they forage for nectar. Therefore, plants with faster nectar production rates (fig. 3*E*) and larger nectar reservoir volumes (fig. 3*F*) attain higher fitness benefits by inducing pollinators to consume nectar at faster rates $a_{11}(S_1)$ from larger total nectar pools S_1. Plants with faster nectar production rates also provide more food for pollinators, directly increasing pollinator population size and indirectly increasing plant fitness and plant population size by elevating the number of pollinator individuals that interact with plants (fig. 1*C*). However, this benefit saturates with higher pollinator population size because females have a finite number of ovules, and more pollinators cannot continue to confer benefits to female fitness once all plant ovules have been fertilized. Last, a plant's nectar production is further constrained by the per capita cost ψ_1 of filling a larger nectar reservoir as pollinators consume nectar at faster rates (fig. 3*G*, 3*H*).

Altering Selection on the Benefits of Nectar Production

In both previous cases, the plant population evolves to a phenotypic optimum that balances the costs and benefits of nectar production for total plant fitness. We now examine how different selective environments affect the evolution of nectar production dynamics in this pairwise plant-pollinator relationship.

Both nectar production traits generally increase in a similar manner as the maximum fitness benefit from the pollinator to the plant increases (fig. 4*A*, 4*B*). Figure 4 shows the equilibrium trait values, population sizes, and standing nectar volume along gradients of c_1, the plant's maximum intrinsic rate of increase, and $1/\phi_1$, the maximum fitness benefit a plant can earn from the actions of pollinators. The plant evolves both a faster nectar production rate and a larger nectar reservoir volume when the benefit it earns from pollinators $1/\phi_1$ is high (e.g., $1/\phi_1 = 4.0$; fig. 4*A*, 4*B*). Additionally, plants evolve larger nectar reservoir volumes and faster nectar production rates in an environment affording a lower c_1 (i.e., a lower intrinsic rate of increase independent of the actions of pollinators) compared with plants in environments with higher c_1 (fig. 4*A*, 4*B*). Below a certain level of pollinator benefit $1/\phi_1$, plants with a lower c_1 cannot maintain a population in that environment, causing plants to evolve lower and lower nectar provisioning until both the plant population and the pollinator population become extinct (fig. 4*A*, 4*B*). Likewise, a higher minimum intrinsic death rate for pollinators, f_1, which reflects ecological conditions that limit the growth of the pollinator population independent of its relationship with the plants, also causes the plant to evolve higher nectar provisioning (results not shown).

Plant and pollinator population sizes also increase with elevated fitness benefits from pollinators (fig. 4*C*, 4*E*). The pollinator population increases because the plant provides more nectar via an increased nectar production rate and a larger reservoir volume (fig. 4*E*). The plant population increases because plants receive a greater fitness benefit via the larger number of interacting pollinators (fig. 4*C*). Note that while the nectar production rate and the total nectar reservoir volume both increase with higher $1/\phi_1$, the standing nectar volume per plant decreases (fig. 4*D*) because more pollinator individuals with higher nectar consumption rates are continuously depleting the plant's standing nectar volume (fig. 4*E*).

Varying properties of the pollinators that affect the frequency of their interactions with plants also cause corresponding evolutionary responses in the plant's nectar production rate and nectar reservoir volume (fig. 5*A*, 5*B*). Figure 5 depicts the effects of these interaction-limiting factors, the pollinator's maximum nectar consumption rate a_{11} and its maximum nectar conversion efficiency b_{11}, on plant traits, population sizes, and standing nectar volume, with fitness benefits $1/\phi_1$ and fitness costs γ_{NPR}, γ_{RV}, and ψ_1 held constant. When the pollinator's maximum nectar consumption rate is low (i.e., low a_{11}), the plant evolves a larger nectar reservoir volume (fig. 5*B*) and produces nectar to fill that reservoir at a faster rate (fig. 5*A*), both of which cause the plant to supply nectar to the pollinator at a faster rate. Likewise, when the pollinator's maximum nectar conversion efficiency is low (i.e., low b_{11}, meaning that each pollinator must consume more nectar to produce one offspring), plants that supply nectar at faster rates and have larger reservoir volumes earn higher fitness benefits by increasing the number of pollinators, thereby also increasing the number of interactions they receive (fig. 5*A*, 5*B*).

Plant population size and standing nectar volume respond identically to a pollinator with a higher nectar consumption rate and a higher nectar conversion efficiency, while pollinator population size responds differently to these interaction-limiting factors (fig. 5*C*, 5*D*). Plant population sizes are largest when their pollinator's nectar conversion efficiency and nectar consumption rate are high because plants receive a greater number of visits from a larger population of pollinators while also experiencing weaker selection to produce more nectar, thus paying

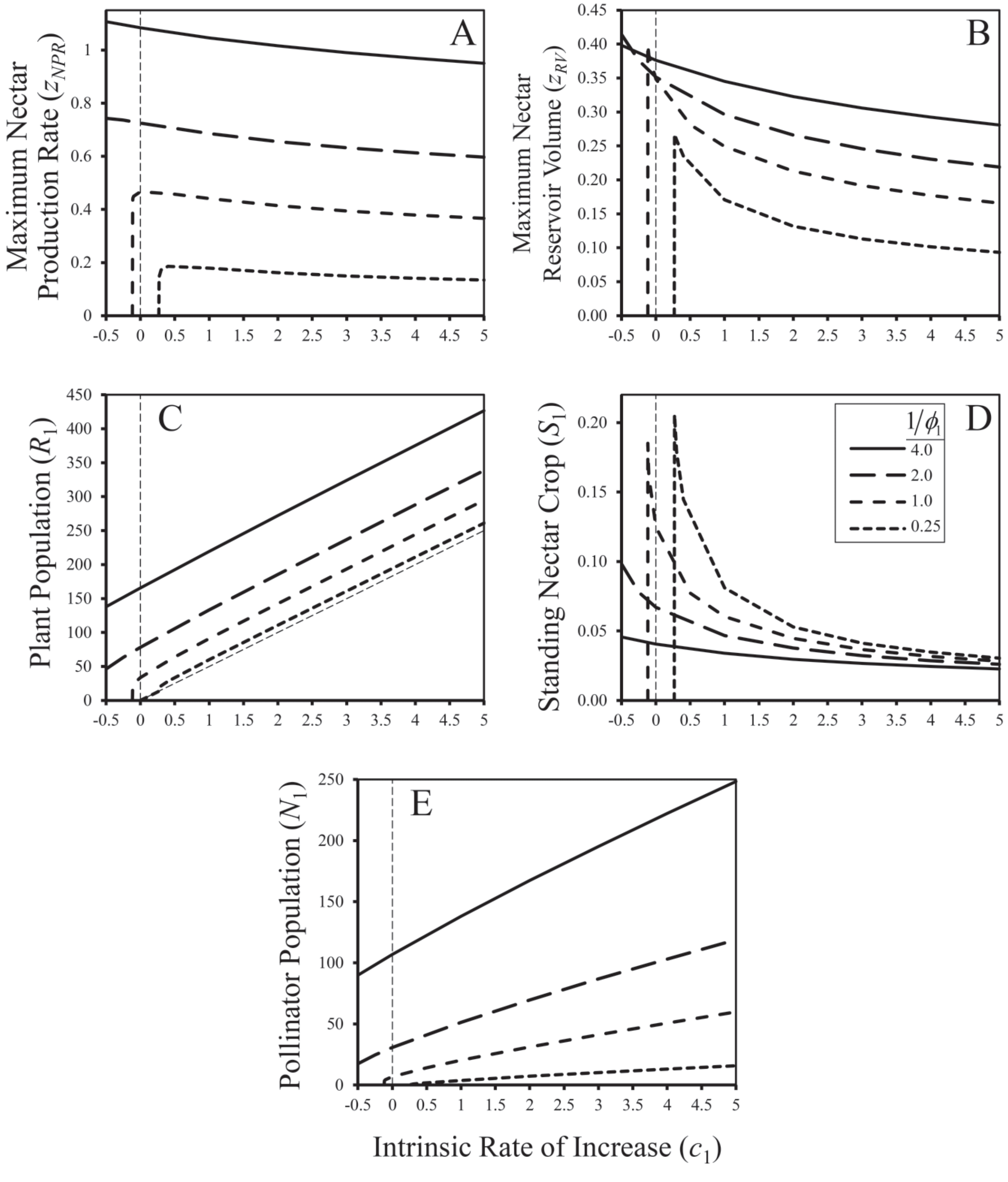

Figure 4: Plants evolve trait combinations that increase nectar provisioning when their maximum intrinsic rate of increase c_1 is low. Panels display the effects of plant maximum intrinsic rate of increase c_1 and maximum fitness benefit from pollinators ϕ_1 on the equilibrium values for maximum nectar production rate (*A*), maximum nectar reservoir volume (*B*), plant abundance (*C*), standing nectar volume per plant (*D*), and pollinator abundance (*E*). All other model parameters are as given in figure 2.

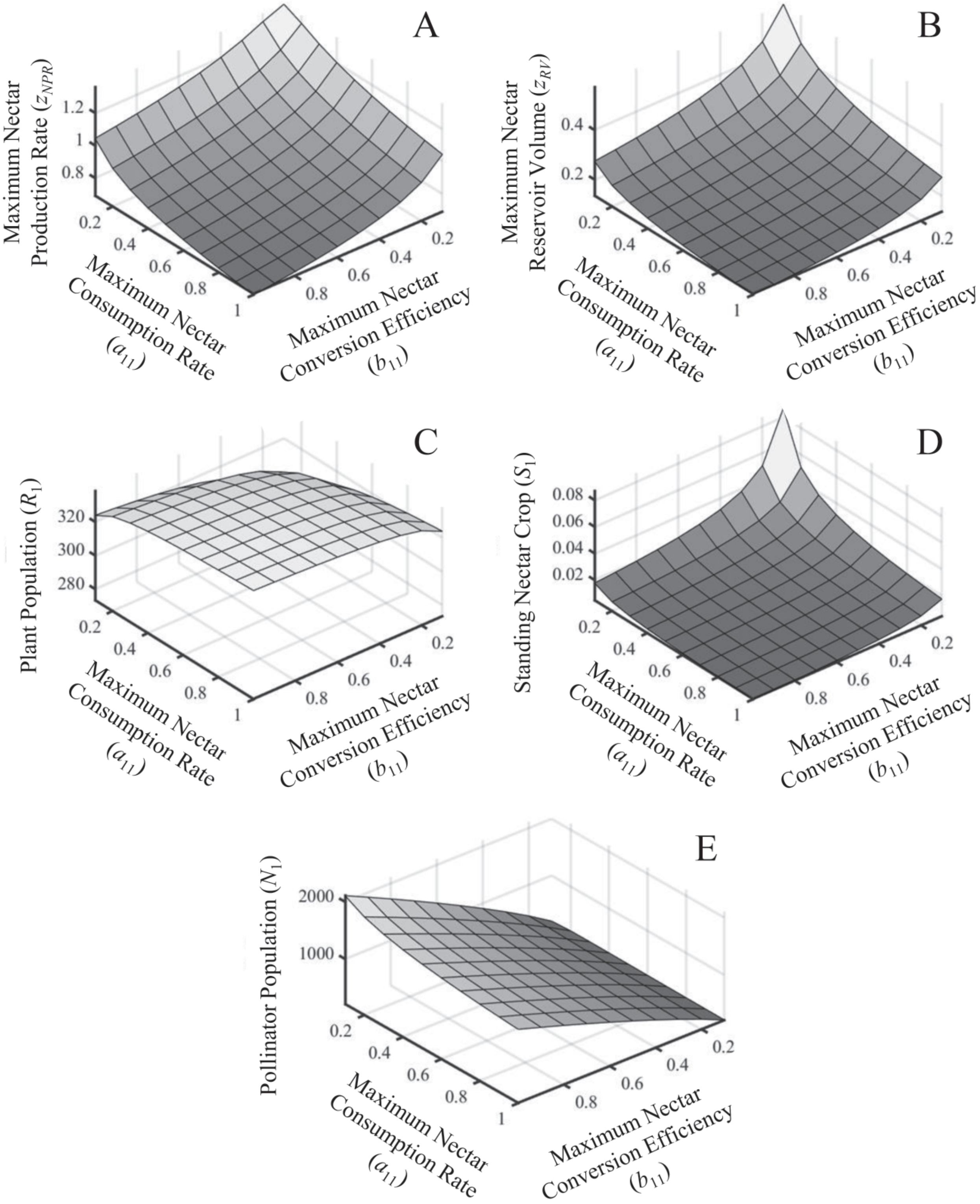

Figure 5: Plants evolve trait combinations that provision more nectar to poorer nectar foragers. Phenotypic (*A*, *B*) and population (*C*–*E*) surfaces display the effects of pollinator nectar consumption rate a_{11} and pollinator conversion efficiency b_{11} on the equilibrium values for maximum nectar production rate (*A*), maximum nectar reservoir volume (*B*), plant abundance (*C*), standing nectar volume per plant (*D*), and pollinator abundance (*E*). All other model parameters are as given in figure 2.

lower production costs (fig. 5*C*). Correspondingly, the standing nectar volume per plant is highest when the opposite is true: when the pollinator's nectar conversion efficiency and nectar consumption rate are low there are fewer pollinators consuming plant nectar, and each is consuming nectar at a slower rate (fig. 5*D*). Pollinator population sizes are largest when their nectar conversion efficiency is high and their nectar consumption rate is low (fig. 5*E*) because individual pollinators deplete less of the nectar resource pool but produce more offspring.

Modulating Selection on the Costs of Nectar Production

In contrast to changes in the benefits from pollinators, nectar production rate and nectar reservoir volume respond differently to changes in the various nectar production costs. The surfaces in figure 6 display how the plant traits, population sizes, and standing nectar volume change with varying fitness costs of nectar production traits (i.e., various combinations of γ_{NPR} and γ_{RV}) on the plant's intrinsic rate of increase. High fitness costs on the plant's intrinsic rate of increase resulting from higher costs of making larger nectar-secreting structures (i.e., larger values of γ_{NPR}) select for a slower nectar production rate (fig. 6*A*). Additionally, at high costs for increasing production rate but low costs for increasing nectar reservoir volume (i.e., small γ_{RV}), the plant evolves a larger reservoir volume that compensates for a slower production rate (fig. 6*B*). In contrast, increasing the fitness cost of a larger nectar reservoir volume has almost no effect on the evolution of a plant's maximum nectar production rate (fig. 6*A*).

The per capita cost of replenishing nectar ψ_1 affects the evolution of the two plant traits in a similar way, but responses to this cost vary between the two traits depending on the fitness cost of increasing nectar production rate (γ_{NPR}) on the plant's intrinsic rate of increase (fig. 7). Overall, a higher incremental cost of replenishing nectar at a given rate (i.e., larger ψ_1) selects for both a slower nectar production rate (fig. 7*A*) and a smaller reservoir volume (fig. 7*B*). The plant evolves the largest reservoir volume when the cost of replenishing nectar at a given rate (ψ_1) is low and the cost of a faster nectar production rate on the plant's intrinsic rate of increase (γ_{NPR}) is high (fig. 7*B*), again demonstrating a compensatory evolutionary response of increasing reservoir volume when nectar production costs are high. The plant evolves the fastest nectar production rate when both costs are low (fig. 7*A*). Interestingly, the cost of replenishing nectar at a given rate (ψ_1) has a greater effect on the evolution of a plant's maximum nectar reservoir volume than it does on a plant's maximum nectar production rate. This further supports the evolution of trait combinations that cause an increase in standing nectar volume in compensation for high nectar production rate costs (fig. 7*D*).

Varying the costs of nectar production also has differential impacts on equilibrium population sizes. Steeper production costs on either nectar production rate (larger γ_{NPR}) or nectar reservoir volume (larger γ_{RV}) reduce plant population size (fig. 6*C*) and pollinator population size (fig. 6*E*) and increase the standing nectar volume available from each plant individual (fig. 6*D*). However, population sizes and standing nectar volumes respond much more strongly to increasing costs of nectar production rate than they do to the cost of a larger reservoir volume. Standing nectar volume primarily increases when nectar production rate decreases because there are fewer pollinators to deplete the plant's nectar pool when plants provide fewer resources (fig. 6*D*, 6*E*). Plant population size generally decreases as any of these costs increase (figs. 6*C*, 7*C*). Pollinator population size increases when both production costs are low because the plants provide the most nectar under these conditions (figs. 6*E*, 7*E*).

Discussion

The contemporary ecology of consumer-resource mutualisms is shaped by past selection on a species' resource-provisioning dynamics (Parachnowitsch et al. 2019). In this article, we explicitly model how ecological processes generate natural selection on two plant resource-provisioning traits to shape the evolutionary trajectory of the plant's interaction with a pollinator. We show that consumers with low functional or numerical responses (i.e., lower nectar-foraging rates or lower nectar conversion efficiencies) select for increased nectar provisioning by plants, which has the effect of boosting their population size (fig. 5). Additionally, high nectar production costs select for suites of nectar traits that minimize the effects of these costs on the level of resource provisioning, thus increasing the plant's population by maintaining high levels of pollination interactions (figs. 6, 7). In particular, selection against larger values of one trait may cause a compensatory increase in the other. These model results extend existing theories of consumer-resource mutualisms into an evolutionary framework and provide testable predictions that can guide empirical research on the evolution of consumer-resource mutualisms in nature.

Providers Evolve Resource Production Dynamics That Increase Interactions with Consumers

Several researchers have shown that consumer functional and numerical responses play a key role in shaping the consumer-resource dynamics of mutualisms (e.g., Holland et al. 2005; Holland and DeAngelis 2009; Valdovinos et al.

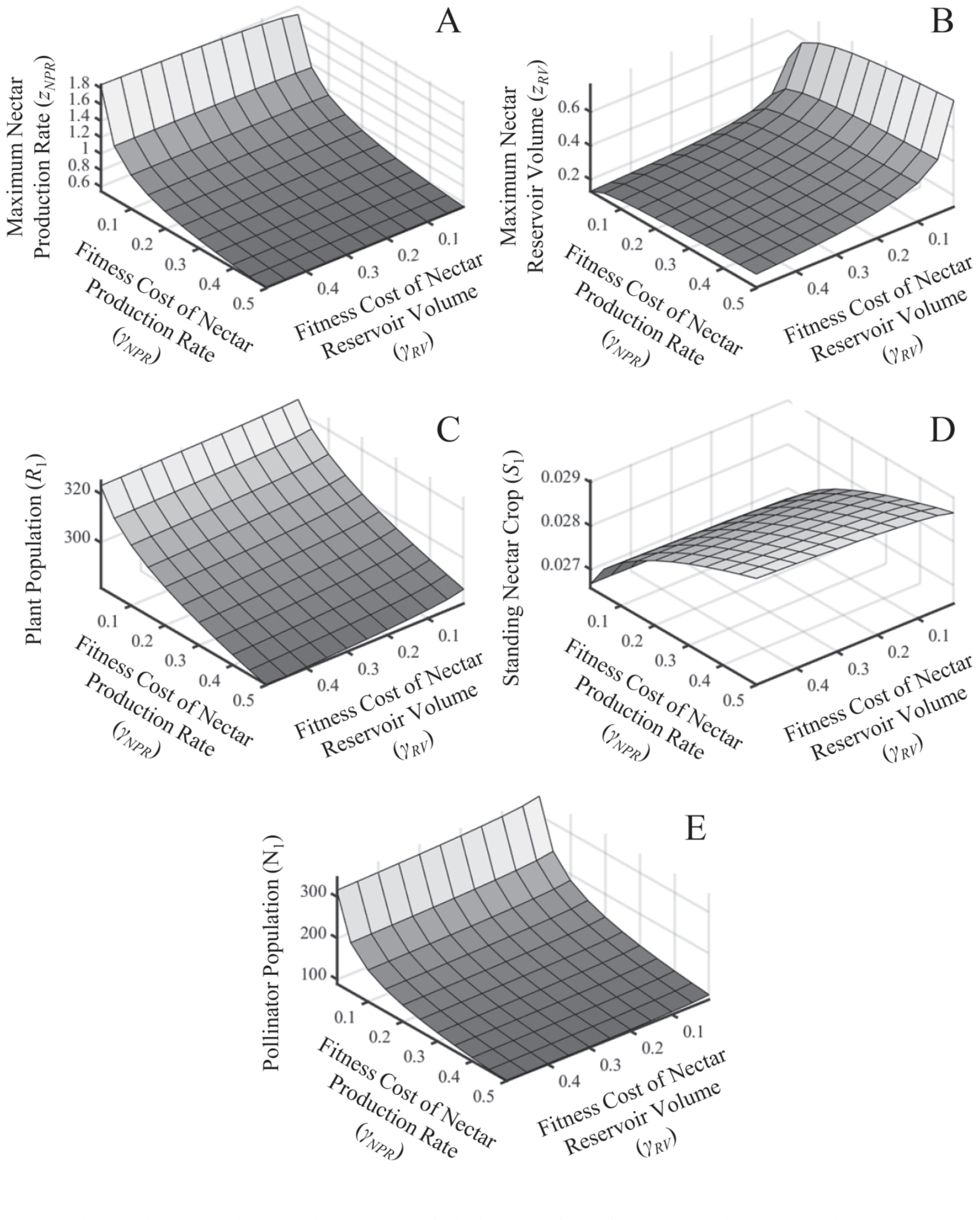

Figure 6: Plants evolve trait combinations that compensate for higher costs of one of the nectar production traits. Phenotypic (*A*, *B*) and population (*C–E*) surfaces display the effects of the selection strengths (γ_{NPR} and γ_{RV}) on the plant intrinsic rate of increase on the equilibrium values for maximum nectar production rate (*A*), maximum nectar reservoir volume (*B*), plant abundance (*C*), standing nectar volume per plant (*D*), and pollinator abundance (*E*). All other model parameters are as given in figure 2.

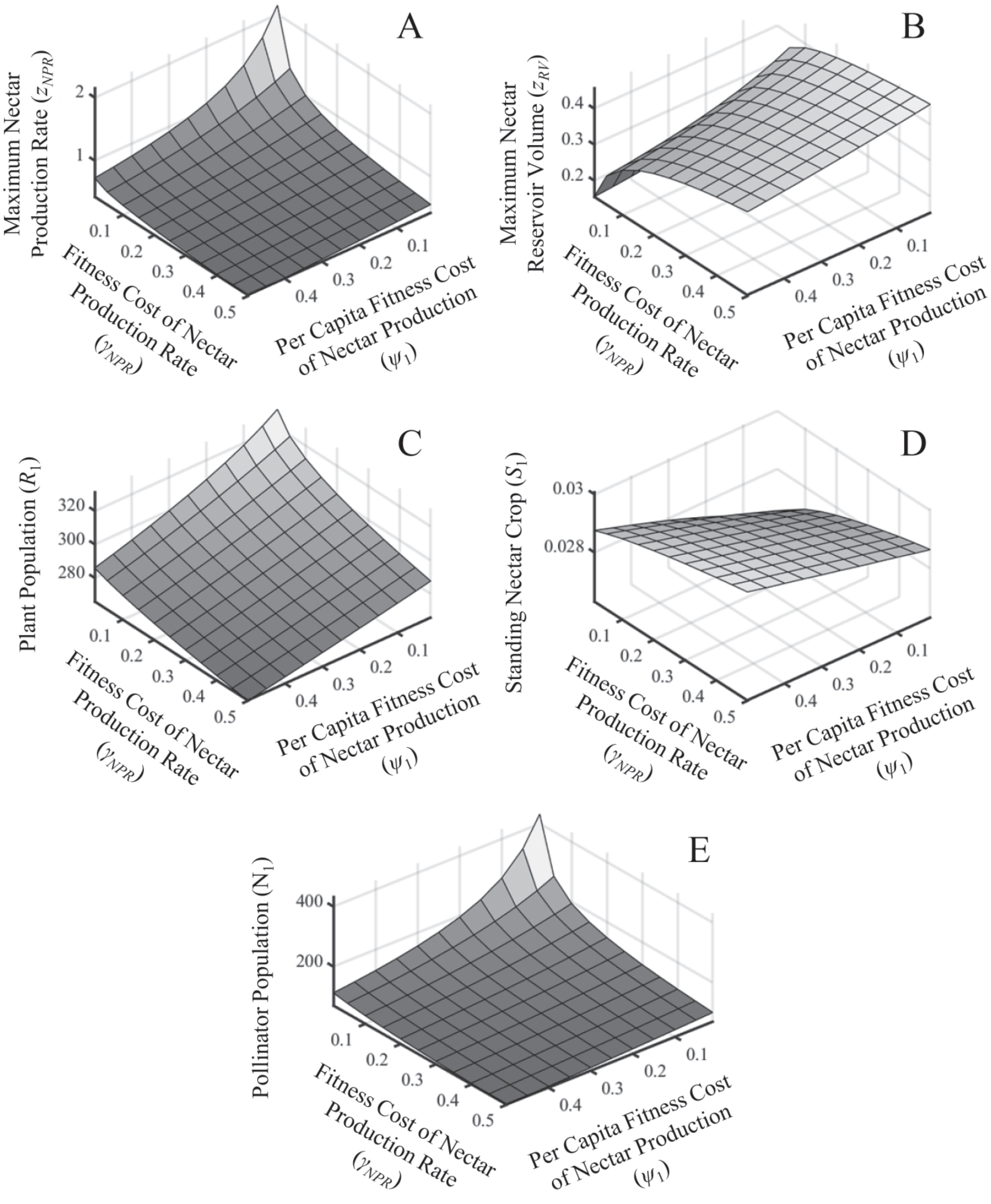

Figure 7: Plants evolve trait combinations that compensate for greater per capita costs of producing nectar. Phenotypic (*A*, *B*) and population (*C*–*E*) surfaces display the effects of the selection strength on plant intrinsic rate of increase γ_{NPR} and incremental cost of nectar production ψ_1 on the equilibrium values for maximum nectar production rate (*A*), maximum nectar reservoir volume (*B*), plant abundance (*C*), standing nectar volume per plant (*D*), and pollinator abundance (*E*). All other model parameters are as given in figure 2.

2013; Revilla 2015; Hale et al. 2020). Our findings demonstrate how these consumer characteristics may also serve as agents of natural selection on resource-provisioning traits. The model results show how pollinators' behavioral (e.g., traits that influence nectar-foraging rate a_{11}) and physiological (e.g., traits that influence nectar conversion efficiency b_{11}) properties have identical effects on nectar trait evolution (fig. 5*A*, 5*B*), but the effects of these two different selective agents are mediated through distinct indirect pathways.

First, our model predicts that plants evolve trait combinations that provide more resources for consumers with lower intrinsic functional responses (i.e., lower a_{11}; fig. 5*A*, 5*B*) via a trait-mediated indirect effect (Abrams 1995; Werner and Peacor 2003). Specifically, plants that provision more nectar enact a trait-mediated indirect effect on their own fitness by causing pollinators to consume nectar at faster rates. Increasing the pollinator's nectar-foraging rate indirectly enhances the plant's own fitness by increasing the frequency and duration of its interactions with pollinators. Furthermore, a plant earns a greater fitness benefit from increasing its nectar production when pollinator foraging rates are low (fig. 5*A*, 5*B*). If pollinators already forage frequently from the plants and pollinate most of a plant's ovules in the process, individuals earn only a marginally greater benefit by provisioning more nectar and in fact evolve to provision less nectar, causing a slight decrease in pollinator abundance (fig. 5*E*). One empirical prediction emerging from this result is that plants with generalist pollinators that visit infrequently may evolve to produce more nectar than plants with pollinators that forage exclusively on that species. Indeed, Johnson and Nicolson (2008) found this exact pattern in bird-pollinated plants: species that interact with a large group of generalist pollinators produce up to 10 times more nectar than those with highly specialized pollinators. These patterns are typically attributed to larger body sizes of generalist species, but our results suggest an alternative explanation: by increasing their resource supply, generalist-pollinated plants garner higher visitation rates and thus higher fitness benefits, whereas specialist-pollinated plants earn only a marginal fitness increase from provisioning more resources for an already active consumer. We note that while our model assumes saturating pollinator foraging on the plant's resource, the same qualitative evolutionary patterns will hold for pollinators with linear functional responses (e.g., Feldman 2006).

Second, our model predicts that plants should evolve trait combinations that provision more resources for consumers with lower intrinsic numerical responses (lower b_{11}; fig. 5*A*, 5*B*) via an abundance indirect effect. High-provisioning plants generate a positive indirect effect on their own abundance via their effect on the consumer's abundance (fig. 5*C*, 5*E*). Specifically, plants increase the consumer's population size by increasing its food supply, thus indirectly enhancing the plant's own fitness benefit and increasing its population growth rate. As evidence for positive effects of resource provisioning on small pollinator populations, Crone (2013) found that abundant floral resources increase pollinator population sizes from one flowering season to the next. This effect was especially pronounced for solitary species over social species, perhaps because solitary foragers must accumulate all of the energy required for reproduction while social foragers share energetic resources to grow their colony (Crone 2013; Maia et al. 2019). Furthermore, this model result is consistent with a widespread natural pattern: plants visited by pollinators that have higher energy needs, such as bats, hawkmoths, and birds, produce larger volumes of nectar than plants with small insect pollinators that have lower energy requirements (Heinrich and Raven 1972; Cruden et al. 1983). This relationship would not evolve unless plants earn some fitness benefit from provisioning more nectar for more needy consumers. Here we have demonstrated a potential mechanism for that benefit that merits further investigation in empirical systems: enhancing the pollinator's abundance by provisioning more nectar may enhance the plant's own fitness benefit. Although our model collapses many biological properties of pollinators (e.g., specificity, metabolic efficiency, sociality) into a few parameters describing consumer population growth, it points to specific pollinator traits that may be important selective agents on a plant's resource-provisioning traits.

Providers Evolve Trait Combinations That Lower the Demographic Consequences of Costly Production

Costs of provisioning can substantially impact ecological consumer-resource dynamics in mutualisms (Revilla 2015; Bachelot and Lee 2018; Cropp and Norbury 2018, 2019). Our model further highlights how production costs can shape the form of stabilizing selection on resource traits, which will in turn affect the ecological dynamics of consumer-resource interactions. In previous ecological models, a slight imbalance of provisioning costs over benefits often resulted in mutualism collapse (Holland and DeAngelis 2009, 2010). By allowing resource traits to evolve in response to these trade-offs, plants in our model sustain nectar production over a wide range of fitness costs. In fact, our model predicts that resource-provisioning traits evolve in ways that minimize these trade-offs between resource production and individual growth (figs. 6, 7). This response is possible because the model treats resource provisioning as a suite of traits that can each respond independently to production costs. Thus, plants can still evolve higher provisioning via the less costly trait, thereby compensating for limitations affecting the more costly trait. This theoretical result presents a potential explanation for why some plants replenish large volumes of nectar slowly and others replenish small volumes of nectar rapidly (e.g., Luo et al. 2014): contrasting values of a plant's nectar production traits may result in part from differential costs of making nectaries and nectar-holding structures. Some empirical evidence suggests that high nectar production rates can impose fecundity costs (e.g., Pyke 1991; Rutter and Rausher 2004; Whitehead et al. 2012), potentially influencing selection on nectar production in the ways our model predicts. Evaluating these predictions in nature will require more studies that examine the individual and demographic costs of various nectar production traits in a wide range of plant systems (Pyke 1991; Whitehead et al. 2012; Parachnowitsch et al. 2019).

Mechanisms that minimize resource production costs will likely be favored in environments with harsh abiotic conditions, such as those characterized by water, nitrogen, or other nutrient limitations. Our model predicts that plants evolve higher nectar provisioning when their intrinsic rate of increase (c_1) is low (fig. 4*A*, 4*B*) because allocating more resources toward the pollinator boosts the plant's abundance by greatly increasing the pollinator's population size and foraging rate (fig. 4*C*, 4*E*). As a caveat, abiotic resource limitations may constrain a plant's ability to produce nectar (e.g., Shuel 1955, 1957; Dudley 1996; Boose 1997). However, these populations may also experience lower growth rates when pollinators are scarce, potentially favoring a higher proportional investment in resource provisioning despite higher individual costs. Alternatively, the costs of provisioning may themselves evolve via selection on traits that are not modeled here, such as water uptake capacity or nutrient use efficiency (e.g., Brodribb et al. 2009), particularly in nutrient-limited environments. This may be the case in desert honey mesquite, where Golubov et al. (2004) found no measurable fitness differences between nectar-producing individuals and nectarless individuals. Absence of evidence for resource production costs is not necessarily evidence of their absence in an evolutionary sense. Instead, we suggest that selection may act on nonresource traits that affect nutrient uptake or nutrient metabolism, thus indirectly lowering the costs of resource production.

Dynamic Resource Provisioning in an Evolving Community

Our model explores the evolutionary response of two plant nectar-provisioning traits that determine the standing nectar volume available to the pollinators. Since we are principally concerned with the evolution of traits that impact average resource provisioning in a plant population, our model does not capture the full intricacy of pollinator foraging observed in nature (e.g., Conner and Rush 1996; Zimmerman 1983; Makino and Sakai 2007; Knauer and Schiestl 2015). For example, the spatial patterning of nectar distribution among flowers may particularly impact a plant's male fitness, which we do not explicitly model here, by affecting how pollinators move pollen between flowers and plants (Klinkhammer and de Jong 1993; Pyke 2016*a*; Pyke et al. 2020). We expect spatial complexity to affect the quantitative but not qualitative patterns of provisioning dynamics observed in our model. Additionally, the foraging strategies of pollinators will shape patterns of natural selection on resource provisioning if individuals in the focal plant population compete with other nectar-producing species. Several empirical studies have found that high plant density contributes to increasing pollinator visitation to all species in the patch (e.g., Moeller 2004; Mesgaran et al. 2017). Our results suggest that resource provisioning among co-occurring species will play a key role in shaping community dynamics by impacting not only pollinator behavior (e.g., Valdovinos et al. 2013, 2016) but local pollinator abundance as well. Sharing the burden of supporting a pollinator population may lessen the selective pressure for increased provisioning by each individual species. Hence, plant species with higher production costs may have higher likelihoods of persisting in communities with multiple high nectar-producing species. Alternatively, competition for optimally foraging pollinators may increase the fitness benefits of producing more nectar, initiating an evolutionary race for higher and higher resource production. If nectar is costly to make, intense competition for forager attention may also drive selection for traits that lower the costs of resource provisioning.

The insights of our evolutionary model stem from its explicit examination of how two plant traits that determine the nectar supply available to pollinators interact to generate a plant's resource-provisioning dynamics. It would also be valuable to develop models that ask the same questions about resource quality, such as the sugar or amino acid content of nectar. For instance, while the model of total nectar quantity finds that populations of both species respond more strongly to provisioning rates than they do to provisioned volumes, incorporating nutritional content may increase the value of holding larger volumes of nectar, particularly if sugar is costly. Studies of nectar concentration often find an inverse relationship between nectar volumes and sugar concentrations (Johnson and Nicolson 2008; Pyke 2016*a*). Costs of sugar production are one hypothesis for this pattern, while others include the biophysical limitations of different nectar-sipping morphologies (e.g., Kim et al. 2011) or evolved behavioral manipulations by plants that force pollinators to visit more plants and thus transfer more pollen to meet their energy needs (Pyke 2016*a*, 2016*b*). In general, we expect that sugar concentrations will follow similar evolutionary patterns as nectar production rates and volumes because nutrient content will also impact the population dynamics of pollinators.

By linking population and trait dynamics with consumer-resource ecology, our evolutionary model provides testable predictions about how natural selection from pollinators and other ecological sources may affect the evolution of a provider species' resource provisioning. Furthermore, our model highlights how the mechanics of natural selection acting on quantitative traits, often via indirect pathways, can produce observed but little understood patterns of consumer-resource trait dynamics, such as the close covariation between a plant's nectar volume and its pollinators' energy requirements (Heinrich and Raven 1972; Cruden et al. 1983; Johnson and Nicolson 2008) and the growing mosaic evidence of varying nectar production costs in different plant species (Pyke 1991; Rutter and Rausher 2004; Golubov et al. 2004; Whitehead et al. 2012). While we focus on nectar here, our modeling framework could be modified to explore trait evolution and its ecological consequences in other unidirectional consumer-resource mutualisms, such as seed-dispersal and defense mutualisms, as well as bidirectional consumer-resource mutualisms, such as plant-mycorrhizal and by-product mutualisms. Overall, the core insight of the evolutionary model is this: ecological dynamics define the evolution of resource provisioning in consumer-resource mutualisms. The rest, as with all patterns in nature, depends on ecological context.

Acknowledgments

We thank Christopher Moore, Jessamyn Manson, Michael Cortez, and two anonymous reviewers for their insightful comments on the manuscript. We also thank Edmund Brodie III, Savanna Cabrera, Phoebe Cook, Robin Costello, Hannah Donald, Vincent Formica, Anthony Gilbert, and Liza Mitchem for helpful conversations about the model and its predictions.

Statement of Authorship

S.J.M. and M.A.M. developed the project ideas and the corresponding modeling framework. S.J.M. analyzed the model. S.J.M. wrote the manuscript with input from M.A.M. and J.L.B. J.L.B. assisted in building the theoretical and empirical context for the work.

Data and Code Availability

The Matlab code for the model can be accessed via the Dryad Digital Repository (https://doi.org/10.5061/dryad.7m0cfxptq; McPeek et al. 2021).

Literature Cited

Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. American Naturalist 146:112–134.

Abrams, P. A., and X. Chen. 2002. The evolution of traits affecting resource acquisition and predator vulnerability: character displacement under real and apparent competition. American Naturalist 160:692–704.

Ashman, T. L. 1994. Reproductive allocation in hermaphrodite and female plants of *Sidalcea oregana* ssp. *spicata* (Malvaceae) using four currencies. American Journal of Botany 81:433–438.

Bachelot, B., and C. T. Lee. 2018. Dynamic preferential allocation to arbuscular mycorrhizal fungi explains fungal succession and coexistence. Ecology 99:372–384.

Boose, D. L. 1997. Sources of variation in floral nectar production rate in *Epilobium canum* (Onagraceae): implications for natural selection. Oecologia 110:493–500.

Brodribb, T. J., S. A. McAdam, G. J. Jordan, and T. S. Feild. 2009. Evolution of stomatal responsiveness to CO_2 and optimization of water-use efficiency among land plants. New Phytologist 183:839–847.

Bronstein, J. L. 2015. The study of mutualism. Pages 3–19 *in* J. L. Bronstein, ed. Mutualism. Oxford University Press, Oxford.

Cohen, D., and A. Shmida. 1993. The evolution of flower display and reward. Pages 197–243 *in* Evolutionary biology. Springer, Boston.

Conner, J. K., and S. Rush. 1996. Effects of flower size and number on pollinator visitation to wild radish, *Raphanus raphanistrum*. Oecologia 105:509–516.

Crawley, M. J. 1989. Insect herbivores and plant population dynamics. Annual Review of Entomology 34:531–562.

Crone, E. E. 2013. Responses of social and solitary bees to pulsed floral resources. American Naturalist 182:465–473.

Cropp, R., and J. Norbury. 2018. Linking obligate mutualism models in an extended consumer-resource framework. Ecological Modelling 374:1–13.

———. 2019. Resource-based models of mutualism. Environmental Modeling and Assessment 24:405–420.

Cruden, R. W., S. M. Hermann, and S. Peterson. 1983. Patterns of nectar production and plant-pollinator coevolution. Pages 80–125 *in* B. Bentley and T. Elias, eds. The biology of nectaries. Columbia University Press, New York.

Dudley, S. A. 1996. Differing selection on plant physiological traits in response to environmental water availability: a test of adaptive hypotheses. Evolution 50:92–102.

Feldman, T. S. 2006. Pollinator aggregative and functional responses to flower density: does pollinator response to patches of plants accelerate at low-densities? Oikos 115:128–140.

Goldberg, D. E. 1990. Components of resource competition in plant communities. Pages 27–49 *in* J. B. Grace and J. Tilman, eds. Perspectives on plant competition. Blackburn, Caldwell, NJ.

Golubov, J., M. C. Mandujano, C. Montaña, J. López-Portillo, and L. E. Eguiarte. 2004. The demographic costs of nectar production in the desert perennial *Prosopis glandulosa* (Mimosoideae): a modular approach. Plant Ecology 170:267–275.

Gutschick, V. P. 1981. Evolved strategies in nitrogen acquisition by plants. American Naturalist 118:607–637.

Hale, K. R., F. S. Valdovinos, and N. D. Martinez. 2020. Mutualism increases diversity, stability, and function of multiplex networks that integrate pollinators into food webs. Nature Communications 11:1–14.

Heinrich, B., and P. H. Raven. 1972. Energetics and pollination ecology. Science 176:597–602.

Herre, E., N. Knowlton, U. Mueller, and S. Rehner. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. Trends in Ecology and Evolution 14:49–53.

Holland, J. N., and D. L. DeAngelis. 2009. Consumer-resource theory predicts dynamic transitions between outcomes of interspecific interactions. Ecology Letters 12:1357–1366.

———. 2010. A consumer-resource approach to the density-dependent population dynamics of mutualism. Ecology 91:1286–1295.

Holland, J. N., J. H. Ness, A. L. Boyle, and J. L. Bronstein. 2005. Pages 17–33 *in* I. Castellanos and P. Barbosa, eds. Mutualisms as consumer-resource interactions. Ecology of predator–prey interactions. Oxford University Press, Oxford.

Johnson, N. C. 2015. Mutualisms and ecosystem-level processes. Pages 221–238 *in* J. L. Bronstein, ed. Mutualism. Oxford University Press, Oxford.

Johnson, S. D., and S. W. Nicolson. 2008. Evolutionary associations between nectar properties and specificity in bird pollination systems. Biology Letters 4:49–52.

Jones, E. I., J. L. Bronstein, and R. Ferriere. 2012. The fundamental role of competition in the ecology and evolution of mutualisms. Annals of the New York Academy of Sciences 1256:66–88.

Karban, R., A. A. Agrawal, and M. Mangel. 1997. The benefits of induced defenses against herbivores. Ecology 78:1351–1355.

Kim, W., T. Gilet, and J. W. Bush. 2011. Optimal concentrations in nectar feeding. Proceedings of the National Academy of Sciences of the USA 108:16618–16621.

Klinkhamer, P. G., and T. J. de Jong. 1993. Attractiveness to pollinators: a plant's dilemma. Oikos 66:180–184.

Knauer, A. C., and F. P. Schiestl. 2015. Bees use honest floral signals as indicators of reward when visiting flowers. Ecology Letters 18:135–143.

Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology 63:607–615.

———. 2007. Expected relative fitness and the adaptive topography of fluctuating selection. Evolution 61:1835–1846.

Luo, E. Y., J. E. Ogilvie, and J. D. Thomson. 2014. Stimulation of flower nectar replenishment by removal: a survey of eleven animal-pollinated plant species. Journal of Pollination Ecology 12:52–62.

Maia, K. P., C. Rasmussen, J. M. Olesen, and P. R. Guimarães Jr. 2019. Does the sociality of pollinators shape the organisation of pollination networks? Oikos 128:741–752.

Makino, T. T., and S. Sakai. 2007. Experience changes pollinator responses to floral display size: from size-based to reward-based foraging. Functional Ecology 21:854–863.

McPeek, M. A. 2017*a*. The ecological dynamics of natural selection: traits and the coevolution of community structure. American Naturalist 189:E91–E117.

———. 2017*b*. Evolutionary community ecology. Vol. 58. Princeton University Press, Princeton, NJ.

———. 2019. Limiting similarity? the ecological dynamics of natural selection among resources and consumers caused by both apparent and resource competition. American Naturalist 193:E92–E115.

McPeek, S. J., J. L. Bronstein, and M. A. McPeek. 2021. Data from: The evolution of resource provisioning in pollination mutualisms. American Naturalist, Dryad Digital Repository, https://datadryad.org/stash/share/hq9AyOsQ4HLI_9UgS1M0464KVDyK-6fZ9NQiKkYd-sk.

Mesgaran, M. B., J. Bouhours, M. A. Lewis, and R. D. Cousens. 2017. How to be a good neighbour: facilitation and competition between two co-flowering species. Journal of Theoretical Biology 422:72–83.

Michaelis, L., and M. L. Menten. 1913. Die Kinetik der Invertinwirkung. Biochemische Zeitschrift 49:333–369.

Moeller, D. A. 2004. Facilitative interactions among plants via shared pollinators. Ecology 85:3289–3301.

Monod, J. 1949. The growth of bacterial cultures. Annual review of microbiology 3:371–394.

Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 2003. Consumer-resource dynamics. Princeton University Press, Princeton, NJ.

Nicolson, S. W., M. Nepi, and E. Pacini, eds. 2007. Nectaries and nectar. Vol. 4. Springer, Dordrecht.

Nobel, P. S. 1977. Water relations of flowering *Agave deserti*. Botanical Gazette 138:1–6.

Parachnowitsch, A. L., J. S. Manson, and N. Sletvold. 2019. Evolutionary ecology of nectar. Annals of Botany 123:247–261.

Pearl, R., and L. J. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proceedings of the National Academy of Science 6:275–288.

Pianka, E. R. 1972. *r* and *K* selection or *b* and *d* selection? American Naturalist 106:581–588.

Pierce, N. E., M. F. Braby, A. Heath, D. J. Lohman, J. Mathew, D. B. Rand, and M. A. Travassos. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology 47:733–771.

Pyke, G. H. 1981. Optimal nectar production in a hummingbird pollinated plant. Theoretical Population Biology 20:326–343.

———. 1991. What does it cost a plant to produce floral nectar? Nature 350:58–59.

———. 2016*a*. Floral nectar: pollinator attraction or manipulation? Trends in Ecology and Evolution 31:339–341.

———. 2016*b*. Plant–pollinator co-evolution: it's time to reconnect with optimal foraging theory and evolutionarily stable strategies. Perspectives in Plant Ecology, Evolution and Systematics 19:70–76.

Pyke, G. H., J. R. Kalman, D. M. Bordin, L. Blanes, and P. A. Doble. 2020. Patterns of floral nectar standing crops allow plants to manipulate their pollinators. Scientific Reports 10:1–10.

Revilla, T. A. 2015. Numerical responses in resource-based mutualisms: a time scale approach. Journal of Theoretical Biology 378:39–46.

Roughgarden, J. 1972. Evolution of niche width. American Naturalist 106:683–718.

Rutter, M. T., and M. D. Rausher. 2004. Natural selection on extrafloral nectar production in *Chamaecrista fasciculata*: the costs and benefits of a mutualism trait. Evolution 58:2657–2668.

Schaffer, W. M. 1981. Ecological abstraction: the consequences of reduced dimensionality in ecological models. Ecological Monographs 51:383–401.

Schaffer, W. M., and E. G. Leigh. 1976. The prospective role of mathematical theory in plant ecology. Systematic Botany 1:209–232.

Schoener, T. W. 1973. Population growth regulated by intraspecific competition for energy or time: some simple representations. Theoretical Population Biology 4:56–84.

Shuel, R. W. 1955. Nectar secretion in relation to nitrogen supply, nutritional status, and growth of the plant. Canadian Journal of Agricultural Science 35:124–138.

———. 1957. Some aspects of the relation between nectar secretion and nitrogen, phosphorus, and potassium nutrition. Canadian Journal of Plant Science 37:220–236.

Simmons, B. I., W. J. Sutherland, L. V. Dicks, J. Albrecht, N. Farwig, D. García, P. Jordano, and J. P. González-Varo. 2018. Moving from frugivory to seed dispersal: incorporating the functional outcomes of interactions in plant–frugivore networks. Journal of Animal Ecology 87:995–1007.

Slatkin, M. 1980. Ecological character displacement. Ecology 61:163–177.

Soberon, J. M., and C. Martinez del Rio. 1981. The dynamics of a plant-pollinator interaction. Journal of Theoretical Biology 91:363–378.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities: positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. BioScience 51:235–246.

Taper, M. L., and T. J. Case. 1985. Quantitative genetic models for the coevolution of character displacement. Ecology 66:355–371.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

Valdovinos, F. S. 2019. Mutualistic networks: moving closer to a predictive theory. Ecology Letters 22:1517–1534.

Valdovinos, F. S., B. J. Brosi, H. M. Briggs, P. Moisset de Espanés, R. Ramos-Jiliberto, and N. D. Martinez. 2016. Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. Ecology Letters 19:1277–1286.

Valdovinos, F. S., P. Moisset de Espanés, J. D. Flores, and R. Ramos-Jiliberto. 2013. Adaptive foraging allows the maintenance of biodiversity of pollination networks. Oikos 122:907–917.

Vasseur, D. A., and J. W. Fox. 2011. Adaptive dynamics of competition for nutritionally complementary resources: character convergence, displacement, and parallelism. American Naturalist 178:501–514.

Venable, D. L. 1996. Packaging and provisioning in plant reproduction. Philosophical Transactions of the Royal Society B 351:1319–1329.

Verhulst, P. F. 1838. Notice sur la loi que la population poursuit dans son accroissement. Correspondance Mathématique et Physique 10:113–121.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.

Whitehead, M. R., R. D. Phillips, and R. Peakall. 2012. Pollination: the price of attraction. Current Biology 22:R680–R682.

Willmer, P. 2011. Pollination and floral ecology. Princeton University Press, Princeton, NJ.

Zimmerman, M. 1983. Plant reproduction and optimal foraging: experimental nectar manipulations in *Delphinium nelsonii*. Oikos 41:57–63.

Associate Editor: Michael H. Cortez
Editor: Jennifer A. Lau

Nectar presentation of *Amianthium muscaetoxicum* at Mountain Lake Biological Station, Giles County, Virginia. Photo taken by Sarah J. McPeek.