

Plant–animal mutualism in biological markets: Evolutionary and ecological dynamics driven by non-heritable phenotypic variance



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ABSTRACT

Mutualism between plants and animals, such as in pollination and seed dispersal, is a fundamental mechanism facilitating the productivity and biodiversity of ecosystems, and it is often considered as an analog of a free-market economy. The coevolution of plant reward and animal choosiness, however, involves an apparent paradox due to incomplete information and limited mutation rates: plant rewards evolve only when animals are choosy, but choosy animals purge the heritable variations of plants, which then favors less choosy animals. Here we use a two-species mathematical model to illustrate how non-heritable phenotypic variances of plants may facilitate the coevolution of rewards and choosiness and solve the paradox with low mutation rates. We simultaneously track the ecological and evolutionary dynamics and show that the population ratio links the two processes and tunes the stable eco-evolutionary equilibrium. Numerical simulations confirm the analytic prediction with varying mutation rates (heritable variance). The efficiency of a biological market is generally suboptimal due to the information constraint and individual competition.

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1. Introduction

Mutualism often involves interactions between members of different kingdoms that provide complementary services that appear to be of mutual benefit (Leigh, 2010). One prominent class of examples is the “brief-exchange” mutualism between animals and plants. Plants are the primary producers in many ecosystems and provide food and other resources for animals, but this interaction is often bidirectional as mobile animals may disperse pollen or seeds of the immobile plants they visit; they may therefore facilitate the reproduction and contribute to the genetic diversity of plants. Nearly three-quarters of all extant flowering plants (angiosperms) receive pollination services from animals (National Research Council, 2007), and animal pollination is considered the ancestral form of pollination in angiosperms (Hu et al., 2008). A large number of plant species rely on animal-mediated seed dispersal as seedling growth is inhibited near the parent plants (Howe and Smallwood, 1982), and the absence of animal dispersers would greatly reduce seedling species richness (Wang and Smith, 2002).

Analogous to a market with producers and consumers (Noë and Hammerstein, 1994), plants offer rewards to animals, and animals choose among offers and pay with delivery service. As Smith (1776)

noted, market-based mutualism does not result from the “benevolence of individuals”, but “from their regard to their own interest”. And Darwin (1859) echoed, “...I do not believe that any animal in the world performs an action for the exclusive good of another of a distinct species, yet each species tries to take advantage of the instincts of others...” A free market is expected to be self-organized with evolving mutualism, but the efficiency of the “invisible hand” depends on a series of conditions, one of which is the availability of information. A perfect market with Pareto efficiency, where no one can become better off without making at least one individual worse off, requires complete information so that all individuals will always make their best choices without any cost (Arrow and Debreu, 1954). Furthermore, perfect competition also assumes instant transactions so that the market reaches an instantaneous equilibrium where supply equals demand. These assumptions are, however, far from fulfilled in real economies, and it has been shown that incomplete information almost always leads to compromised efficiency (Greenwald and Stiglitz, 1986). Similarly, animals in a biological market probably have very little information about the spacial distribution of the plant rewards and have to spend time searching and comparing offers, and this may hinder the evolution of mutualism. Animals also have to spend non-trivial time traveling between individual plants, and therefore, the market never reaches a complete saturation as a participant always benefits from a higher trading rate, despite a diminishing marginal effect. Accordingly, we need to address these ecological and evolutionary constraints to explain the evolutionary outcomes of plant–animal mutualism in what is effectively a biological market.

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First, unlike selection pressures directly driven by an independent environment, the evolution of inter-specific mutualism in a biological market is a process of coevolution of two (or more) species, driven by each other. This is a type of niche construction (see also Odling-Smee et al., 2003), where each species constructs its environment (positively or negatively) by driving the evolution of the partner species in the market. On the one hand, since rewards are often costly to produce, plants offering more generous rewards might be expected to evolve only if they were to receive more visits in return. This requires that animals be sufficiently choosy to differentiate among the available offers by plants. On the other hand, searching, sampling and comparing rewards cost time and energy if animals are choosy and information is limited. Therefore, there must be sufficient variation among the offers that choosy animals obtain better rewards. These two conditions result in an apparent paradox if the heritability of the reward trait is high, because choosy animals should select for higher rewards, purging variation among plants through time, which in turn would favor less choosy animals. One solution to this paradox is to introduce frequent mutation or dispersal to counteract the selection and maintain sufficient genetic variations in the reward trait (Foster and Kokko, 2006; McNamara et al., 2008). This solution, however, does not often apply to plant–animal mutualism as the mutation rate is generally much lower than required in those models, and most mutations are deleterious. The persistence of a large source plant population with low rewards but sufficiently high dispersibility is also questionable.

However, heritability is often variable and much lower in natural environments as phenotypes are mostly co-determined by genotypes and environment (Charmantier and Garant, 2005). Quantitative traits, such as nectar concentration and fruit size, are well-known to be plastic and subject to developmental plasticity as well as environmental stochasticity and heterogeneity (Wheelwright, 1993; Sultan, 2000). For example, rewards per flower may vary greatly between plants of a single species and between flowers on a single plant in response to the pattern of depletion of rewards by foragers (Waser and Mitchell, 1990). Therefore, even with low genetic variance of a strongly selected trait, the phenotypic variance may be large. Since it is the phenotypic variation that immediately drives partner choice, it seems plausible that provided there is at least some heritability, increased developmental variation will amplify the selection pressure on cooperation (McNamara and Leimar, 2010). The non-heritable phenotypic variation due to heterogeneous environmental factors and phenotypic plasticity may contribute significantly in driving the evolution of mutualism between plants and animals in the context of a biological market. To the best of our knowledge, no theoretical work has been done so far to address this issue.

Second, an invisible hand is expected to function by simultaneously regulating both the quantity (ecological) and the quality (evolutionary) of transactions in a free market. Similarly, the value of rewards and the “price” of dispersal services depend on the ratio of demand and supply in a biological market (Noë and Hammerstein, 1994). When plants are relatively rare, animals have to compete for access to them so that even the lowest offers may be accepted; on the contrary, when plants are relatively abundant, they have to compete for animals’ visits. If the two interacting populations share identical payoff functions and demographic characteristics, e.g., they are from the same species, and the trade is strictly pairwise, the feedback could balance demand and supply in the market, and select for fairness (André and Baumard, 2011). However, plant–animal interactions are not pairwise; an animal can visit many plants, and a plant can also receive visits from numerous animals. The participants are unable to enter or exit the market freely but are subject to the population dynamics. As a result, the supply–demand ratio may vary over a large range even at

an equilibrium. This ecological feedback changes the fitness, and hence the selection pressure, on both participants. Mutualism in ecology is defined in general terms, requiring only that all participants benefit from the interaction, with no necessity of symmetry in exchange of benefit. Consequently, the evolutionary equilibrium, if it exists, is determined by the interaction of the ecological and evolutionary dynamics, as the fitness of a genotype not only depends on the genotype frequencies in a population but also depends on the plant–animal population ratio, which changes through ecological dynamics (Holland et al., 2004). Therefore, generating predictions and testing them correctly requires that this ecogenetic feedback loop be included in the analysis (Laland et al., 1999; Kokko and López-Sepulcre, 2007).

Third, the relationship between conspecific individuals in a biological market is more complex than mere competition, when population dynamics are taken into consideration. On the one hand, conspecific individuals directly compete for resources; on the other hand, they cooperatively maintain the population of the partner species as a common good which benefits all conspecific individuals, irrespective of their relatedness. This latter point is often neglected in evolutionary analyses using fixed-size population models, but has important implications for understanding the significant role of evolution of mutualism in shaping ecosystems and building ecosystem services (Leigh, 2010). The overall effect of intra-specific competition and cooperation determines the efficiency of a biological market.

In this study, we address the three issues introduced above with a two-species (plant and animal) interaction model. We model the searching and choosing behavior of animals based on the model of Foster and Kokko’s (2006) and incorporate the dynamic population ratio as a constraint on the efficiency of choice. Population densities of genotypes in both populations are tracked so that the feedbacks between ecological and evolutionary dynamics can be analyzed. The evolutionary and ecological dynamics are first studied analytically, assuming rare mutations. Then we use simulations to test the analytic prediction with broader parameter sets and to analyze the dynamics assuming that choosiness is a learned strategy. We show that the non-heritable phenotypic variance can be the main driving force facilitating the evolution of plant–animal mutualism. We also find that the dynamic population ratio links the evolutionary and ecological dynamics and regulates the biological market. The efficiency of the biological market and the evolutionary response to environmental change are also investigated.

2. Models

Here we construct a model to describe the mutualistic interaction between a plant species and an animal species in a biological market, where the plants offer rewards to visiting animals, and animals selectively collect rewards and provide dispersal service to the plants. This model applies to the common animal-mediated pollination or seed dispersal, but it may also apply to other types of mutualism between less mobile and more mobile partners, e.g., cleaner fish and their clients (Bshary and Grutter, 2006).

2.1. The behavior model

According to optimal foraging theory (MacArthur and Pianka, 1966; Stephens and Krebs, 1987), organisms selectively forage to maximize their net energy intake per unit time. While animal foragers may easily learn to recognize different plant species by their morphological characteristics, it is relatively difficult to differentiate the rewards from individuals of the same species. They often have to visit an individual plant first before deciding to stay or continue searching (Goulson, 2010).

We use B ($B_0 \leq B \leq 1$) to designate the plant genotype that determines the resource invested in producing reward (B_0 is the lowest investment), and b the corresponding reward phenotype that animals perceive. A plant with genotype B offers a reward b with the probability $\alpha(b, B)$, where $\int \alpha(b, B)db = 1$, and receives a benefit $1 - B$ on average. The frequency of genotype B in the whole plant population is $\beta(B)$, and $\int \beta(B)dB = 1$. Assume that an animal with genotype c spends a fraction c ($0 \leq c \leq 1$) of its foraging time on choosing the rewards and uses $1 - c$ of its foraging time to collect them. With $c > 0$, it tends to visit plants offering higher rewards more often; otherwise it makes random visits. Since plants do not choose animals, the non-heritable variance of animal choosiness has no qualitative effect on the evolution of mutualism, and for the sake of simplicity, we assume that an animal's choosiness is solely determined by its genotype whose frequency is $\gamma(c)$, where $\int \gamma(c)dc = 1$. We will also analyze the model with the assumption that an animal is able to optimize its choosiness quickly by individual learning.

The frequency of an animal's visitation to a plant depends on its relative reward trait rather than its absolute value (Biernaskie and Gegeer, 2007). As in Foster and Kokko's (2006) model, we assume that this frequency q is a function of the focal animal's choosiness, the focal plant's reward as well as the reward traits of the whole plant population as the background. However, it is also constrained by the availability of choice, measured by the plant relative abundance $H = \frac{P}{P + (1 - \bar{c})A}$, where $\bar{c} = \int c\gamma(c)dc$ is the average choosiness over the whole animal population, P and A are total population densities of plants and animals, respectively, and $(1 - \bar{c})A$ is the density of animals that are visiting plants. The subscript \bullet is used to label the genotype or phenotype of a focal individual plant or animal. An animal with choosiness c_\bullet has relative preference $q(b_\bullet, c_\bullet)$ on a plant with reward b_\bullet :

$$q(b_\bullet, c_\bullet) = \frac{e^{Kb_\bullet c_\bullet}}{\int \int e^{Kbc_\bullet} \alpha(b, B) \beta(B) db dB}, \quad (1)$$

where $K = kH^s \log k$ is the coefficient of choice. k is determined by an animal's physical ability to detect differences among the plants, which is a constraint of information availability. s is the strength of animal competition for the reward, determined by the animals' sociality in resource sharing. A greater k means that animals have more information to make a better choice, but it also intensifies the competition between animals. A small H leads to a small K as animals have to compete against each other for limited options. In particular, K is bounded by H even if $k \rightarrow \infty$, as we can rewrite $K = k^{1+s \log H}$, and it is clear that $K < 1$ when $\log H < -1/s$, and $K \rightarrow 0$ when $H \rightarrow 0$, given any $k > 1$. For numerical calculations, we use the base-10 logarithm in this study.

The average reward that an animal with choosiness c_\bullet collects per visit is thus

$$\bar{b}(c_\bullet) = \int \int b q(b, c_\bullet) \alpha(b, B) \beta(B) db dB, \quad (2)$$

and the rate that a plant of genotype B_\bullet is visited by animals is

$$G(B_\bullet) = \frac{A \int \int (1 - c) q(b, c) \alpha(b, B_\bullet) \gamma(c) db dc}{P + (1 - \bar{c})A}, \quad (3)$$

which is the integration of the product of animal relative abundance ($\frac{A(1-c)}{P + (1-\bar{c})A}$) and the attractiveness of the plant ($q(b, c)$). Clearly, the rate increases with the animal population density.

2.2. The population model

An animal is often able to visit a number of plants, and a plant may receive multiple visits from animals and also be subject to

Table 1
Variables and parameters.

Symbols	Description	Default/initial value
A	Animal population density	
B	Plant genotype (the mean individual reward)	0.01
b	Reward phenotype of a plant	
c	Choosiness of an animal	0
D	Dispersion index ($= \sigma^2/B$) of plant genotype B	
G	Visitation rate of a plant	
H	Plant relative density	
K	Coefficient of choice	
k	Discrimination efficiency	10
M_p, M_a	Mortality rates of plants and animals	
P	Plant population density	
r_a	Animal fertility rate	1
r_p, r_s	Plant fertility rates with/without animal-mediated dispersal	1, 0.01
s	Strength of animal competition	
$u_{a\bullet}, u_{p\bullet}$	Animal/plant fitness of genotype B_\bullet/c_\bullet	
$\alpha(b, B)$	Frequency of reward phenotype b given genotype B	
$\beta(B)$	Frequency of genotype B in plants	
$\gamma(c)$	Frequency of genotype c in animals	
σ	Standard variation of reward phenotype	
μ	Mutation rate	

abiotic dispersal. Therefore, the reproduction rate of an animal is proportional to the rate of collecting rewards, with the scale factor r_a , and that of a plant is proportional to the rate of total dispersal (mediated by animals or by abiotic forces, with the scale factors r_p and r_s , respectively). We assume that the animal species have no alternative food resource in this community. The mortality rates of plants (M_p) and animals (M_a), due to some environmental capacity limit, can both be density-dependent. Here we use linear functions $M_p = m_{p0} + m_{p1}P$ and $M_a = m_{a0} + m_{a1}A$.

Based on a general model of plant–pollinator population dynamics (Fishman and Hadany, 2010), the subpopulation dynamics for plants with genotype B_\bullet and animals with choosiness c_\bullet are

$$\dot{P}_\bullet = (1 - B_\bullet) [r_p G(B_\bullet) + r_s] P_\bullet - M_p P_\bullet, \quad (4a)$$

$$\dot{A}_\bullet = r_a H \bar{b}(c_\bullet) (1 - c_\bullet) A_\bullet - M_a A_\bullet, \quad (4b)$$

where A_\bullet and P_\bullet are the densities of the two focal subpopulations, respectively. The plant fitness $u_{p\bullet}$ of genotype B_\bullet and the animal fitness $u_{a\bullet}$ of genotype c_\bullet are measured by the relative population density change between two generations: $u_{p\bullet} = \dot{P}_\bullet/P_\bullet$ and $u_{a\bullet} = \dot{A}_\bullet/A_\bullet$. Clearly, the relative fitness depends not only on the genotype frequencies but also the plant relative abundance H .

If the density of animals is constrained to be low (A is small) such that most plants do not receive any animal visits, i.e., $H \approx 1$ and $G(B_\bullet) \approx 0$ for any B_\bullet , the ecological dynamics can be neglected and the relative fitness of a mutant plant genotype B' against the resident genotype B can be simplified from (4a) approximately: $u_{p'} = r_s(B - B') - M_p$. It is clear that $du_{p'}/dB' < 0$ for any B' , so that no mutant genotype $B' > B_0$ can invade the resident population with the lowest reward trait B_0 . This is not surprising because the contribution of animals is limited to be small relative to the cost of reward. In contrast, if the animal population density were to fluctuate in a wide range as a response to the food resource availability, the relative fitness of a genotype could change significantly as a result of the population dynamics. Here we focus on the latter case. Refer to Table 1 for a full list of variables and parameters used in our model.

3. Results

To illustrate the results of our model explicitly, we assume that the reward phenotype b of a plant is a random variable with a normal distribution $N(B, \sigma^2)$ whose mean value equals its genotypic

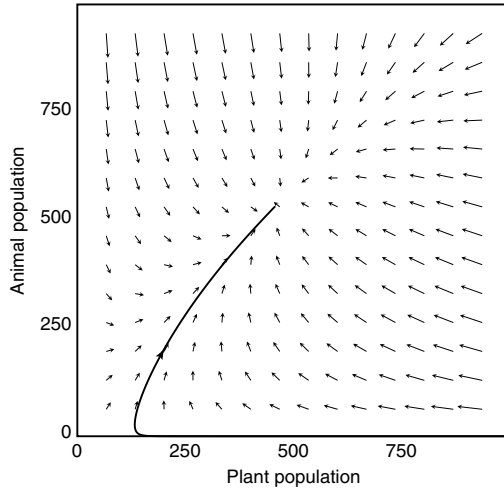


Fig. 1. The vector field of ecological dynamics when an interior equilibrium exists. The parameters are used as $B = 0.5$, $c = 0.3$, $D = 0.5$, $k = 10$, $s = 1$, $M_p = 0.0005P$ and $M_a = 0.0005A$.

trait value B so that $\alpha(b, B) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(b-B)^2}{2\sigma^2}}$. Empirical studies on plants indicate that the phenotypic variance is often correlated with the mean of the trait. Accordingly, here we assume that the variance is linearly correlated with the mean value, with the index of dispersion (D), which is independent of the mean value, i.e., $\sigma^2 = BD$. We assume that the plant reward and animal choosiness are both quantitative traits with low mutation rates so that it is much faster to reach an ecological equilibrium than to reach an evolutionary equilibrium, if both exist.

3.1. The ecological equilibrium

Due to low mutation rates and strong selection, the two-species community mostly consists of plants of a single genotype B and animals of a single genotype c , we can simplify an animal's relative preference from Eq. (1),

$$q(b, c) = \exp[Kc(b - B - KBcD/2)],$$

and derive an animal's mean benefit from Eq. (2),

$$\bar{b}(c) = B(1 + KcD). \quad (5)$$

And the visitation rate of any plant is simply $G(B) = 1 - H$ as all plants have the same genotype. See Appendix A for the algebraic details.

Thus, we can simplify the population dynamics from Eqs. (4a) and (4b) to

$$\dot{P} = (1 - B)[r_p(1 - H) + r_s]P - M_pP, \quad (6a)$$

$$\dot{A} = r_a(1 - c)HB(1 + KcD)A - M_aA. \quad (6b)$$

At an ecological equilibrium, the population densities of plants and animals do not change, i.e., $\dot{P} = 0$ and $\dot{A} = 0$. Clearly, $(0, 0)$ is always an equilibrium, and it is stable if and only if the density-independent mortality rates m_{p0} and m_{a0} are sufficiently high that it is the only equilibrium. Alternatively, if m_{a0} is high but m_{p0} is lower than r_s , $([r_s(1 - B) - m_{p0}]/m_{p1}, 0)$ is the only stable equilibrium, and $(0, 0)$ is an unstable equilibrium. Otherwise, if m_{p0} and m_{a0} are both sufficiently low, (\hat{B}, \hat{A}) is the only stable equilibrium, where $\hat{B} > 0$ and $\hat{A} > 0$ can be found by solving $\dot{P}/P = 0$ and $\dot{A}/A = 0$, and $(0, 0)$ is an unstable equilibrium. Therefore, \hat{B} can be derived as a function of \hat{A} and \hat{c} at the ecological equilibrium. The local stability of an equilibrium is verified by computing the

Jacobian matrix at the equilibrium (Appendix B). Graphical analysis shows that this ecological equilibrium (\hat{B}, \hat{A}) is also globally stable and there is no limit cycle (Fig. 1). We focus on this situation in the evolutionary analysis.

3.2. The evolutionary equilibrium

For mutant genotypes B' and c' introduced into a population of resident genotypes B and c , respectively, $G(B')$ is derived from Eq. (3):

$$G(B') = (1 - H)e^{Kc(1 + KcD/2)(B' - B)}. \quad (7)$$

Substituting Eqs. (5) and (7) in Eq. (4), we obtain the fitness functions of the mutants, $u_{p'}$ and $u_{a'}$:

$$u_{p'} = (1 - B') \left[r_p(1 - H)e^{Kc(1 + KcD/2)(B' - B)} + r_s \right] - M_p,$$

$$u_{a'} = r_aHB(1 + Kc'D)(1 - c') - M_a.$$

We first use adaptive dynamics to investigate weak mutation effects, where the difference between any mutant genotype and the resident genotype is vanishingly small, i.e., $B' \approx B$ and $c' \approx c$. The selection gradients for the mutants are

$$\left. \frac{du_{p'}}{dB'} \right|_{B'=B} = r_p(1 - H) [Kc(1 + KcD/2)(1 - B) - 1] - r_s, \quad (8a)$$

$$\left. \frac{du_{a'}}{dc'} \right|_{c'=c} = r_aHB(KD - 2KcD - 1). \quad (8b)$$

An evolutionarily stable equilibrium is reached when no mutants are able to invade. Note that H is a function of B and c at the ecological equilibrium, deduced from Eq. (6). Assume that plants have a minimum mean reward trait $B_0 > 0$, which is a byproduct of pollen or seed set. Depending on the values of D and k , the system converges to one of the three possible equilibria, (B^*, c^*) , (B_0, c^*) and $(B_0, 0)$. First, the system converges to an interior equilibrium if $B^* > B_0$ and $c^* > 0$ exist as a solution of $\left. \frac{du_{p'}}{dB'} \right|_{B'=B} = 0$ and $\left. \frac{du_{a'}}{dc'} \right|_{c'=c} = 0$, with the additional condition $0 \leq H \leq 1$ (Fig. 2(a)). If the solution (B^*, c^*) does not exist, $B = B_0$ must be stable. Then we solve $\left. \frac{du_{a'}}{dc'} \right|_{c'=c} = 0$ to get c^* . If $0 < c^* < 1$ does not exist, the equilibrium $(B_0, 0)$ is globally stable (Fig. 2(b)). Then the population densities at the eco-evolutionary equilibrium can be derived as \hat{B} and \hat{A} evaluated at the evolutionary equilibrium. Since there is always only one equilibrium, allowing animals to optimize their choosiness by quick learning does not change the evolutionary equilibrium, though the transient dynamics are different.

The stability of the interior equilibrium (B^*, c^*) can be examined by the following steps: first, it is easy to show that the second-order derivatives $\left. \frac{d^2u_{p'}}{dB'^2} \right|_{B'=B}$ and $\left. \frac{d^2u_{a'}}{dc'^2} \right|_{c'=c}$ (for any c') are negative.

This means that if there is a singular point (B^*, c^*) , it is a local fitness maximum. Second, given $B = B^*$ and $c = c^*$, we relax the assumption of weak mutation effects, and $B' = B^*$ is the only solution of $du_{p'}/dB' = 0$ in the space $(0, 1)$. Since $u_{p'}$ is a continuous function of B' , the equilibrium is globally evolutionarily stable. Graphical analyses (Fig. 2(a)) suggest that it is also a global attractor (convergence-stable). As a result, the equilibrium (B^*, c^*) is continuously stable (Eshel and Motro, 1981; Geritz et al., 1997).

Eq. (8b) indicates that the efficiency of choice depends on DK . If D is very small, there is little variance to choose from when the mean reward trait B is low. Consequently, no choosiness evolves, and the reward trait remains at the lowest level. As D increases slightly beyond a threshold, higher choosiness starts to evolve, but higher reward does not evolve until animals are sufficiently

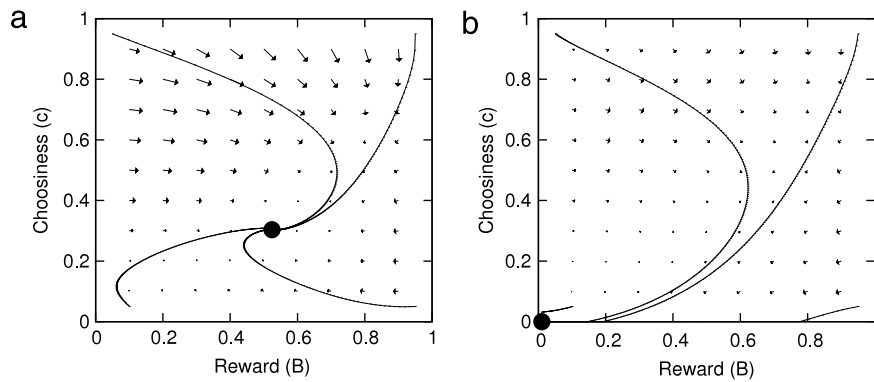


Fig. 2. The vector field of selection gradients and the evolutionary trajectories of Eq. (8). (a) The system converges to an interior equilibrium, given $D = 0.5$. (b) The system converges to a boundary solution, given $D = 0.05$. $B_0 = 0.01$, $s = 1$ and $k = 10$. The arrows indicate the directions of selection, and the length of an arrow indicates the strength of selection.

choosy. It is clear that B^* and c^* are both increasing functions of D (Fig. 3(a) and (b)). This is consistent with our intuition that greater variance of rewards encourages higher choosiness, which in turn favors higher rewards. This positive feedback, however, slows down as D increases, due to the density-dependent mortality and the decreasing coefficient of choice, K (Fig. 3(f)), which reduces the efficiency of choosiness.

Reward variance also has a strong effect on population densities at the equilibrium. When D is too low for mutualism to evolve, both animal and plant population densities are low. If D is above a threshold, the animal population grows as an increasing function of D (Fig. 3(d)), with a diminishing marginal effect. The effect of D on the plant population at the equilibrium is less straightforward, appearing as an S-shape or bell-shape curve. An intermediate D facilitates the growth of the plant population due to the increase of animals. The marginal effect of reward variance diminishes as D increases, due to the density-dependent mortality. A high D may lead to over-competition between plant individuals, causing a drop of the plant population density, due to the growing choosiness of animals, if the competition between animals is limited (s is small).

Similar to D , the coefficient of choice, K , tunes the selection pressures on both traits by modulating the efficiency of choice. A greater K amplifies the effect of reward variance, causes all these curves to shift to the left, corresponding to a lower D . As K is an increasing function of H , given $s > 0$, a high plant–animal ratio leads to a greater efficiency of choice, i.e., strong selection, while a low plant–animal ratio lowers the selection pressures. As a result, while a greater D directly raises the efficiency of choice on the one hand, it indirectly lowers the plant–animal ratio through the ecological dynamics on the other (Fig. 3(e)), weakening the selection by reducing K (Fig. 3(f)). The strength of the ecological feedback on selection is tuned by s . A greater s means that animals have to compete and compromise their choices more frequently, resulting in lower reward and choosiness at the equilibrium (Fig. 3(a) and (b)), but it increases the plant population density with a high D as it mitigates the competition between plants (Fig. 3(c)). The information availability, k , has a double-edged effect on K (Fig. 3(f)): first, greater k increases the efficiency of choice; second, it also intensifies the competition between animals as animals with better information aggregate and confront each other more frequently. The two effects may cancel out when H is small.

3.3. Simulations

In our simulations, we kept the mutation rate and size relatively low so that the genetic variance is a minor component of the phenotypic variance, but it is sufficiently high for the concurrence of multiple mutants (Fig. 4(a) and (c)). The range of reward is set

between 0.05 and 1, and the range of choosiness is set between 0 and 1. The initial reward and choosiness genotypes are 0.05 and 0, respectively. Mutations are assumed to be discrete with small mutation changes (≤ 0.01). Truncated normal distributions are used to produce the phenotypes of any given genotype of plants. Instead of assuming an ecological equilibrium at any moment when studying the evolutionary dynamics, we allow the two dynamics to occur together and interact with each other.

Given a sufficiently large D , a nonzero baseline reward from plants first stimulates the evolution of choosiness among animals, and once choosiness is sufficiently high, higher reward genotypes start to evolve. The equilibrium of the mutualism fits our analytical prediction well (Fig. 4(a) and (c)). The variances of B and c are greater around the equilibrium because the selection is weaker in the neighborhood of the equilibrium (Fig. 2(a)). In general, the population densities of both species increase as mutualistic traits evolve (Fig. 4(e)), which indicates that the evolution of mutualism benefits both species, in spite of the intra-specific competition. We tested the model with mutation rates as high as 0.01, and the results remain consistent, suggesting that we can generalize our results with a broad range of mutation rates.

We also tested the model with an alternative assumption that animals are able to optimize their choosiness by individual learning, which occurs significantly faster than the population dynamics. For simplicity, we let all animals learn the choosiness value at the competitive equilibrium immediately at the beginning of each season (Akçay et al., 2009), and the equilibrium of choosiness in each season is therefore history-independent. This individual optimal choosiness may not maximize the population productivity. We used the same parameters and initial values in this new simulation. Compared to the previous model, the learning model converges to the same eco-evolutionary equilibrium (Fig. 4(b), (d) and (f)) but at a faster rate. In particular, choosiness drops as reward rises because the plant relative density decreases. Note that there may be coexisting optimal choosiness values even without mutation (Fig. 4(d)). This is because we have to use discrete units in numerical simulations.

3.4. Ecological implications

An evolutionary equilibrium does not often lead to Pareto efficiency, where no species can continue to grow without reducing the other (Fig. 5), due to incomplete information or over-competition. Animals are under information constraint, if k is small, which can be overcome only by high choosiness. When D is limited, high choosiness does not evolve, and consequently, the market efficiency is far from the Pareto front, which is the set of Pareto efficient points, due to weak mutualism (Fig. 5(a)). The evolutionary equilibrium moves closer to the Pareto front when D

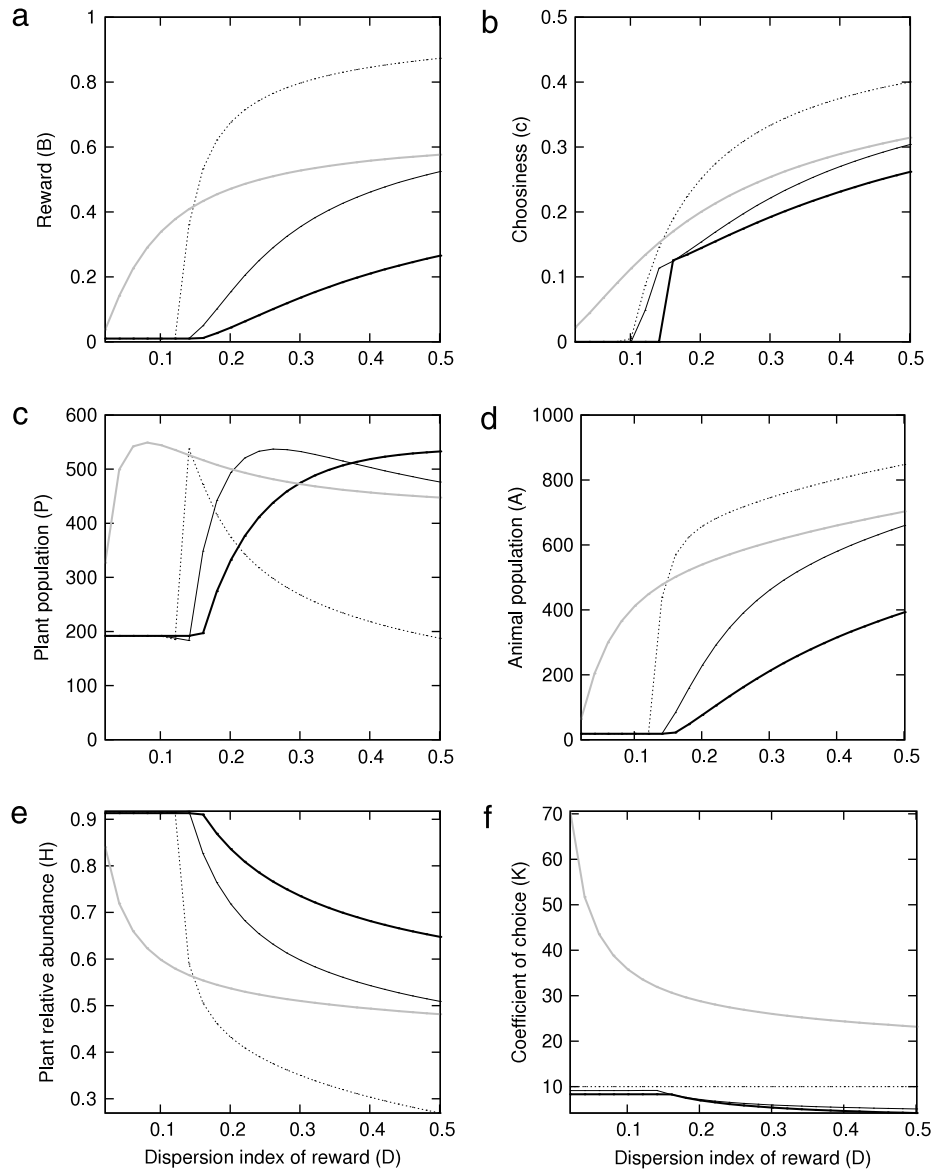


Fig. 3. Analytic predictions of evolutionary equilibrium and ecological equilibrium, for the given dispersion index of the plant reward trait D , the strength of animal competition, s , and the physical limit of information availability, k . (a) Mean reward (genotype); (b) choosiness; (c) plant population densities; (d) animal population densities; (e) plant relative abundance; (f) coefficient of choice. All the equilibria are derived from Eq. (8). Black lines indicate $k = 10$, and gray lines indicate $k = 100$. Different line types indicate s values: dotted lines for $s = 0$, thin solid lines for $s = 1$, and thick solid lines for $s = 2$. Other parameters: $B_0 = 0.01$, $M_p = 0.0005P$ and $M_a = 0.0005A$.

increases, as high choosiness and stronger mutualism evolve. However, the evolutionary equilibrium is still often below the Pareto front (Fig. 5(b)) even if the information constraint is relaxed (k and D are sufficiently large), due to the over-competition between plants (if s is small) or between animals (if s is large).

We also tested the eco-evolutionary response to an increased animal mortality (Fig. 6), which is a common consequence of overuse of pesticides, outbreak of animal diseases, or defaunation. In the short run, without immediate evolutionary change, the system simply converges to a new ecological equilibrium with a lower plant population density, due to the decrease of animals. In the long run, the system converges to a new evolutionary equilibrium, and as the plant–animal population ratio increases, the competition between plants is intensified. The evolutionary response partly compensates the loss of animals (Fig. 6(a)), and the plant population may partly recover with under-competition or drop further with over-competition (Fig. 6(b)).

4. Discussion

In this study, we showed that non-heritable phenotypic variance may be the key to the evolution of plant–animal mutualism in a biological market, when genetic variance is limited on the selected trait. Unlike selection driven by an independent, abiotic environment, partner choices in a biological market are maintained by the total phenotypic variance of rewards, which is the sum of heritable and non-heritable variances (McNamara and Leimar, 2010). As less fit genotypes are purged by partner choices, heritable variance of the selected reward trait can only be limited if the mutation rate is not very high. Both our mathematical analyses and simulations confirm that the evolutionary and ecological dynamics lead to a unique stable equilibrium with low heritable variance, whether choosiness is an evolving genetic trait or a learned strategy. In contrast, non-heritable variance can be maintained under selection and, thus, may contribute a greater component to the total variance of rewards that is the basis of the

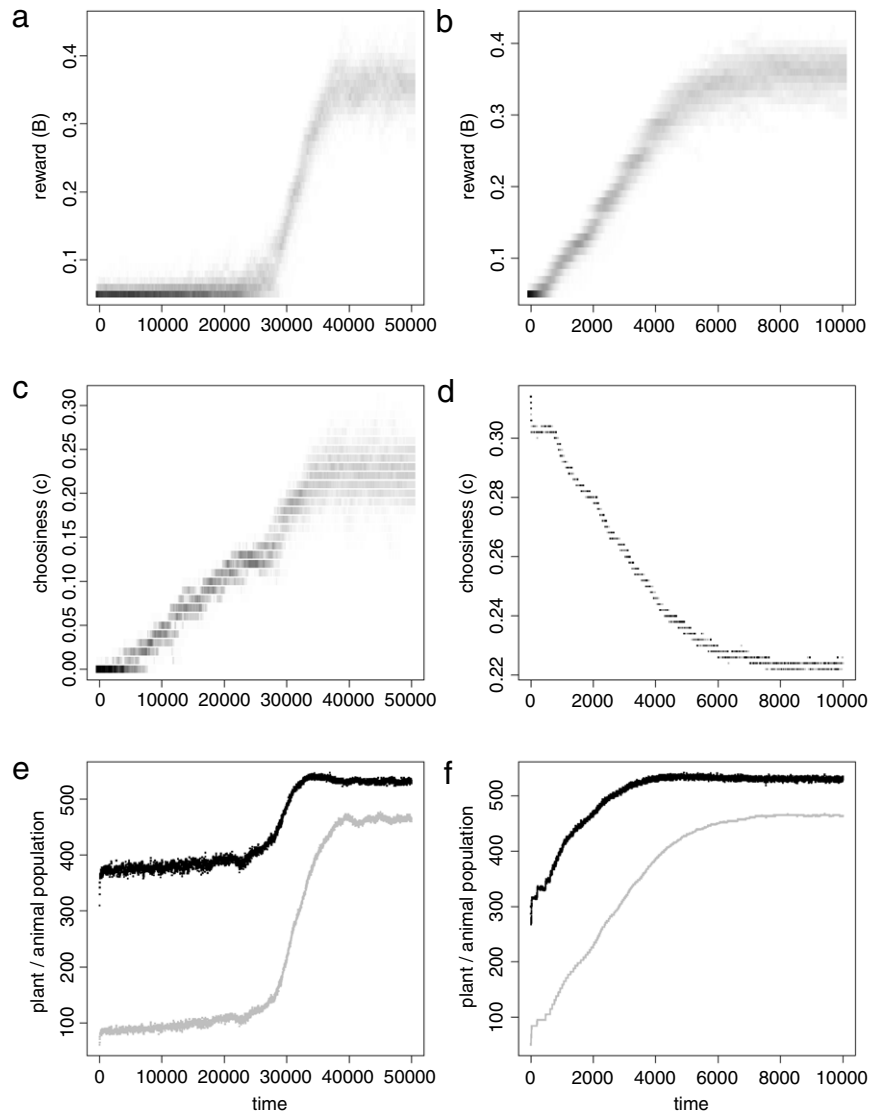


Fig. 4. The result of two simulation runs: (left) choosiness evolves as a genetic trait; (right) choosiness is a learned strategy. The evolutionary equilibria of plant reward genotype (a and b), animal choosiness (c and d) and population densities (e and f; black: plant; gray: animal) are identical for the two cases, but the dynamics are different. The darkness of dots reflects the corresponding genotype frequencies in (a, b and c). $s = 1$, $k = 10$, $D = 0.3$, $B_0 = 0.05$, $\mu = 0.01$, $M_p = 0.0005P$ and $M_a = 0.0005A$.

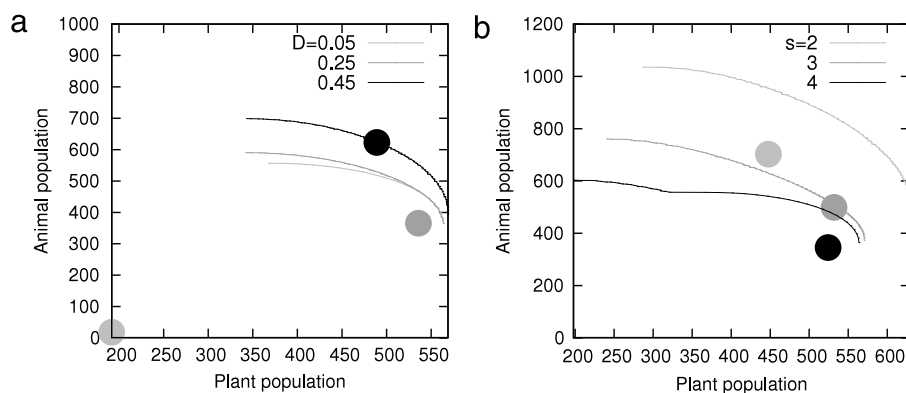


Fig. 5. Comparing the population densities on Pareto fronts (solid lines) and at evolutionary equilibria (filled circles) numerically computed with the parameter sets: (a) $s = 1$, $k = 10$ (b) $D = 0.5$, $k = 100$.

evolution of plant–animal mutualism, which determines the productivity of the biological market. In addition, phenotypic plasticity may amplify or reduce the phenotypic variance, change the ecological and evolutionary dynamics (Mougi et al., 2011; Scheiner

and Holt, 2012), and have an impact on the evolution of cooperation (Leimar, 1997; Andrré, 2010). Further studies are needed to investigate the effect of phenotypic plasticity on the evolution of the plant–animal mutualism.

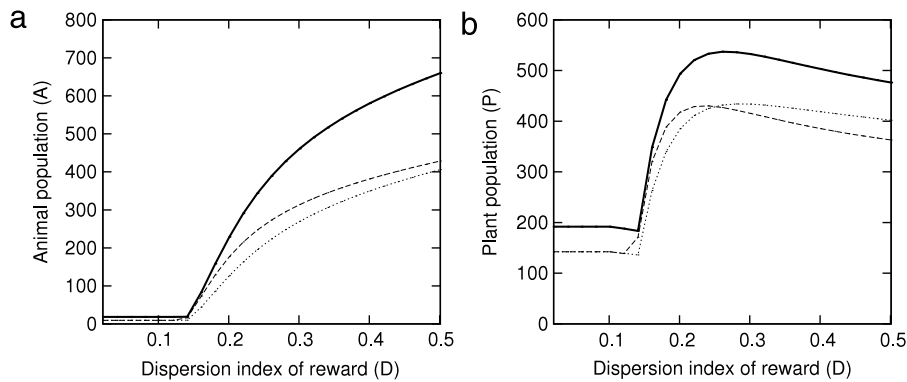


Fig. 6. The short-term ecological response (without evolutionary change) and long-term evolutionary response to an increase in animal mortality (from 0.0005 to 0.001). (a) Animal population; (b) plant population. Solid line: pre-change; dashed line: evolutionary response; dotted line: ecological response. $k = 1$, $s = 1$.

On the other hand, we do not exclude the possibility of maintaining large heritable variance of a trait against strong selection. In this study, we use a quantitative genetic model, which approximately applies to many quantitative traits, but if the reward trait is determined by a small number of alleles at a single locus with strong genetic effects, polymorphic genotypes may coexist stably, resulting in large stable genetic variance. Polymorphism may also evolve if the environment is a mosaic of distinct habitat patches with sufficient migration between subpopulations, or the environment condition fluctuates sufficiently through time that there is no single evolutionarily stable genotype. Both heritable and non-heritable variance of rewards add to the total variance that drives partner choice, facilitating evolution of mutualism. Empirical studies are needed to estimate both the heritable and non-heritable variances of rewards in order to understand the driving and limiting forces of plant–animal mutualism in each special case.

In principle, mutualism cannot evolve if the initial mean reward level B_0 is near 0, which leads to limited variance when the mean and variance are positively correlated. However, this is not an empirical obstacle for plant–animal mutualism to evolve as studies on insect fossils indicate that the earliest pollinators were pollen-consumers (Labandeira, 1998; Willmer, 2011), and nectar rewards evolved later (Bronstein et al., 2006). Similarly, the earliest seed dispersers probably foraged on seeds before edible fruits evolved. As pollen and seeds are necessary products of plant reproduction, this suggests that there was a nontrivial minimal reward for the evolution of plant–animal mutualism to begin.

Typical plant–animal mutualism involves continuous many-to-many “brief exchanges” (Leigh, 2010), where no stable pairwise partnership exists, and both of the participant populations are only subject to relative saturation because the interaction rate is always an increasing function of the relative density of the partner population, despite the declining marginal effect. By tracking the evolutionary and ecological dynamics simultaneously, we found that selection changes the population ratio at the ecological equilibrium, which in turn changes the selection pressures, forming a feedback loop that links ecological and evolutionary dynamics. This feedback may significantly change the evolutionary equilibrium if the strength of competition between animals, s , is not very low. Both plants and animals compete intra-specifically, and the balance of the evolutionary equilibrium depends on the relative strength of the two competitions. If s is small, e.g., when animals are able to share an offer, the competition between animals is limited, and consequently, plants may over-compete when the variance of reward is large. If s is large, e.g., when an animal can defend its resource, the competition between animals is intensified when the plant relative abundance is low, and the competition between plants is reduced (Fig. 3(c)).

The evolution of a biological market is a process of niche construction for all participant species (Odling-Smee et al., 2003). Each

species can shape its environment by driving the ecological and evolutionary change of the partner species. By investing in reward, a plant may not only help itself by attracting animal visits, but also generate the common good by increasing the total population of animals through the population dynamics. Therefore, the competition driven by self-interest also generates indirect cooperation, and offering reward may improve the niche at the population/species level. Similarly, animals build their ecological niches by visiting the plants and increasing the plant population (Kylafis and Loreau, 2011), and they may also build their evolutionary niches by being choosy, which induces the evolution of higher rewards from plants. In general, the relative strength of competition and cooperation depends on the supply–demand ratio in the biological market.

The competition between individuals, however, does not often lead to Pareto efficiency of the biological market. While animals may use visual and olfactory signals, or even floral electric fields (Clarke et al., 2013), to detect the reward differences between plant individuals, the efficiency of choice is subject to physical constraints when the plant population is large. If the efficiency of choice is low, due to information or variance constraint, low choosiness evolves and leads to under-competition between plants, resulting in a below-optimal reward level. Even when the efficiency of choice is high and choosy animals evolve, the market efficiency at the evolutionary equilibrium is still often suboptimal, as over-competition may occur between plants or animals, depending on the social tolerance of animals.

Previous modeling studies on the evolution of mutualism or cooperation with partner choice have paid little attention to this dynamic population ratio. Many evolutionary models fixed the population ratio to be 1 in one-to-one interactions (McNamara et al., 2008), or infinity in many-to-one interactions (Foster and Kokko, 2006). These models only have limited application to typical plant–animal mutualism. As an exception, one model including the dynamic supply–demand ratio shows that the offer balancing supply and demand evolves as long as the probability to be chosen increases sufficiently strongly with the size of the offer, even if choices are made with limited precision (e.g. André and Baumard, 2011). But this study did not take into account the relationship between the dynamic population ratio and the efficiency of choice, which may dramatically change the selection pressure. On a different path, ecological dynamics are explicitly modeled in a study on the evolution of mutualism in a cactus-moth system (Holland et al., 2004), where the dynamic ratio of pollinators and flowers was shown to regulate the evolution of the cactus flower production strategy. In this mutualism, however, moths do not choose rewards as they benefit from laying eggs in the flowers instead of collecting direct rewards. Similarly, a theoretical study on the evolution of resource trading takes into account the demographic feedback (De Mazancourt and Schwartz, 2010), but partner choice

is absent in their model. Our study suggests that models tracking the feedback between ecological and evolutionary dynamics are important to understand the evolution of plant–animal mutualism in a biological market.

For the sake of simplicity, we assume in this study that the distribution of reward among plants remains constant. In a real biological market, however, the distribution of reward often changes as a result of the nonrandom visitations of animals. For a simple pollination system with two plant species and one pollinator species, the optimal foraging strategies of the pollinators have been modeled by integrating the animal locomotive pattern and the plant reward production rate (Goulson, 1994; Kunin and Iwasa, 1996). Based on these studies, it is possible to add a dynamic reward distribution to the current model, given a specific biological system. Alternatively, agent-based simulations with spatial structures can also be used to study the evolution of a biological market at a finer time scale.

Furthermore, our study may shed some light on the evolutionary transition between generalized brief-exchange mutualism (e.g. honeybee–plant mutualism) to more specialized, even obligate mutualism (e.g., fig–wasp mutualism Machado et al., 2005 and ant–Acacia mutualism Palmer et al., 2008). Our model suggests that a stronger mutualism could evolve if the plants offered the reward with a greater phenotypic variance, which might subsequently evolve to a specialized mutualism as stable partnership co-evolves (Song and Feldman, 2013). Therefore, phenotypic variance of rewards, together with other mechanisms such as geographical isolation, may have facilitated and stabilized specialized mutualism. On the other hand, a reduced reward variance may lead to a reversal of this, resulting in an evolutionary transition toward weaker mutualism.

As the ecological and evolutionary dynamics are interlinked, any environmental disturbance that causes a shift of the ecological equilibrium in the short run may also lead to an evolutionary change in the long run, resulting in a different eco-evolutionary equilibrium. In particular, a rise in the animal mortality, for example due to overuse of pesticides, overhunting, or climate change, may first cause a quick decline in the partner plant population as an ecological response. In the long run, the intensified competition between plants will lead to the evolution of higher reward genotypes, which may result in a partial recovery or a further decline in the plant population. The evolutionary change may be rapid if it is subject to strong selection (Hairston et al., 2005; Ellner et al., 2011) and if the animals can learn their foraging strategies on the behavioral time scale. This evolutionary response, either buffering or enhancing the ecological change (Olsen et al., 2004; Osmond and de Mazancourt, 2013), requires attention in ecological management.

We have modeled a simple two-species mutualistic system, which could be one component of a large plant–animal mutualistic network. Since the animal participant species are often generalists, the plant species in the network may compete with or facilitate each other (Feldman et al., 2004), which would result in different network structures (Bascompte and Jordano, 2007; Guimarães et al., 2011). While environmental variation may affect the coexistence of competing species directly (Snyder and Chesson, 2004; Mathias and Chesson, 2013), our study suggests that it might also affect the coexistence of plant species in a mutualistic network indirectly by inducing phenotypic variation, which may drive the evolution of mutualistic interactions.

In conclusion, our study has shown that non-heritable variance of the plant reward trait may greatly contribute to the evolution of plant–animal mutualism, as the evolutionary dynamics converge to a unique monomorphic equilibrium with limited genetic variance. As the efficiency of choice is often sensitive to the plant–animal population ratio, the population dynamics are not only driven by evolution, but also drive the evolutionary dynamics. It is thus important to integrate the two interactive dynamic

processes. Our model also applies to other types of mutualism between participants with one-sided partner choice. The efficiency of a biological market is generally inferior to Pareto efficiency due to information constraint and individual competition.

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Appendix A. Algebra to derive the ecological equilibrium

Given $\alpha(b, B) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(b-B)^2}{2\sigma^2}}$, we can derive

$$\begin{aligned} e^{Kbc} \alpha(b, B) &= \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(b-B)^2}{2\sigma^2} + Kbc} \\ &= \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{[b-B+Kc\sigma^2]^2}{2\sigma^2} + KBc + K^2c^2\sigma^2/2} \\ &= \alpha(b, B + KcBD) e^{KBc + K^2c^2BD/2}. \end{aligned} \quad (\text{A.1})$$

Note that $\int \alpha(b, B + KcBD) db = 1$ and $\int b \alpha(b, B + KcBD) db = B + KcBD$. At an evolutionary equilibrium with plants of a single genotype B and animals of a single genotype c , we simplify $q(b_*, c)$, $\bar{b}(c)$ and $G(B)$ by substituting Eq. (A.1) in Eqs. (1)–(3), respectively:

$$\begin{aligned} q(b_*, c) &= \frac{e^{Kb_*c}}{\int e^{Kbc} \alpha(b, B) db} \\ &= \frac{e^{Kb_*c - KBc - K^2c^2BD/2}}{\int \alpha(b, B + KcBD) db} \\ &= \exp[Kc(b_* - B - KBcD/2)], \\ \bar{b}(c) &= \frac{\int b q(b, c) \alpha(b, B) db}{\int e^{Kbc} \alpha(b, B) db} \\ &= \frac{\int b \alpha(b, B + KcBD) db}{\int \alpha(b, B + KcBD) db} \\ &= B(1 + KcD), \\ G(B) &= \frac{A \int (1 - c) q(b, c) \alpha(b, B) db}{P + (1 - c)A} \\ &= \frac{(1 - c)A}{P + (1 - c)A} \\ &= 1 - H. \end{aligned}$$

Appendix B. Ecological stability analysis

The local stability of an equilibrium can be verified by computing the Jacobian matrix

$$J = \begin{pmatrix} \frac{\partial \dot{P}}{\partial P} & \frac{\partial \dot{P}}{\partial A} \\ \frac{\partial \dot{A}}{\partial P} & \frac{\partial \dot{A}}{\partial A} \end{pmatrix}$$

at the equilibrium. The sufficient conditions for stability are $|J| > 0$ and $\text{Tr}(J) < 0$.

For $P > 0$ and $A > 0$, we first derive the following results from Eqs. (6):

$$\frac{\partial H}{\partial P} = \frac{(1-c)A}{[P + (1-c)A]^2} > 0$$

$$\frac{\partial H}{\partial A} = -\frac{(1-c)P}{[P + (1-c)A]^2} < 0.$$

Then we have

$$\frac{\partial(\dot{A}/A)}{\partial A} = r_a(1-c)B [1 + kcD(1 + s \log k)H^{s \log k}] \times \partial H/\partial A - m_{a1} < 0,$$

$$\frac{\partial(\dot{A}/A)}{\partial P} = r_a(1-c)B [1 + kcD(1 + s \log k)H^{s \log k}] \times \partial H/\partial P > 0,$$

$$\frac{\partial(\dot{P}/P)}{\partial A} = -r_p(1-B)\partial H/\partial A > 0,$$

$$\frac{\partial(\dot{P}/P)}{\partial P} = -r_p(1-B)\partial H/\partial P - m_{p1} < 0.$$

We use the results above to derive the signs of the entries of the Jacobian matrix at the internal equilibrium where $P = \hat{P}$ and $A = \hat{A}$,

$$\frac{\partial \dot{A}}{\partial A} = A \frac{\partial(\dot{A}/A)}{\partial A} + \dot{A}/A = A \frac{\partial(\dot{A}/A)}{\partial A} < 0$$

$$\frac{\partial \dot{A}}{\partial P} = A \frac{\partial(\dot{A}/A)}{\partial P} > 0$$

$$\frac{\partial \dot{P}}{\partial A} = P \frac{\partial(\dot{P}/P)}{\partial A} > 0$$

$$\frac{\partial \dot{P}}{\partial P} = P \frac{\partial(\dot{P}/P)}{\partial P} < 0.$$

As a result, the sufficient conditions for stability hold, as $\text{Tr}(J) < 0$ and

$$\begin{aligned} |J| &= \frac{\partial \dot{P}}{\partial P} \frac{\partial \dot{A}}{\partial A} - \frac{\partial \dot{P}}{\partial A} \frac{\partial \dot{A}}{\partial P} \\ &= PA \left[\frac{\partial(\dot{P}/P)}{\partial P} \frac{\partial(\dot{A}/A)}{\partial A} - \frac{\partial \dot{P}/P}{\partial A} \frac{\partial \dot{A}/A}{\partial P} \right] \\ &> 0. \end{aligned}$$

The local stability of other ecological equilibria can be examined similarly.

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