

Coevolution in Variable Mutualisms

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ABSTRACT: Many mutualistic interactions are probably not mutualistic across all populations and years. This article explores consequences of this observation with a series of genetic models that consider how variable mutualisms coevolve. The first models, previously introduced in a general coevolutionary context, consider two coevolving species whose fitness interactions change between beneficial and antagonistic in response to independent spatial or temporal variation in the abiotic or biotic environment. The results demonstrate that both temporal and spatial variability in fitness interactions can cause partner species with tightly matched traits favored by unconditional mutualisms to be vulnerable to evolutionary invasion by alternative types. A new model presented here shows that an additional mutualistic species can have a similar effect and can even cause fitness interactions between the other two species to evolve. Under some conditions, the pairwise interactions can change unidirectionally from mutualistic to antagonistic, with virtually no evolutionary change in either partner species. In other cases, fitness interactions between the species pair can oscillate between mutualism and antagonism as a result of coevolution in the third species. Taken as a whole, these theoretical results suggest that many features of mutualistic coevolution can best be understood by considering spatial, temporal, and community-dependent patterns of fitness interactions.

Keywords: mutualism, antagonism, spatial variation, temporal variation, three-species coevolution.

The classic examples of mutualism are of tightly coevolved interactions between pairs of species that require one another for survival or reproduction. Well-studied examples include yuccas and yucca moths (Pellmyr and Huth 1994; Pellmyr et al. 1996; Pellmyr and Krenn 2002) and figs and

fig wasps (Herre 1987; Bronstein and Hossaert-McKey 1995; Kjellberg et al. 2001). Other mutualisms, however, are more labile, with mutualistic partners varying geographically in their degree of reciprocal adaptation (Kapan 2001; Thompson and Cunningham 2002). In fact, some interactions can vary from antagonistic to commensalistic to mutualistic, depending on the local physical or biotic community in which the species pair occurs (Thompson 1988; Cushman and Whitham 1989; Thompson and Pellmyr 1992; Saikkonen et al. 1998; Thompson and Cunningham 2002). These observations suggest that the coevolution of mutualisms may depend on fitness interactions among partner species that vary across space and time.

The importance of that variation is captured in the geographic mosaic theory of coevolution, which proposes that the overall trajectory of coevolution depends fundamentally on the geographic structure and dynamics of variable interspecific fitness effects. Two of the central components of this theory, selection mosaics and coevolutionary hotspots, capture the central role of variable selection in coevolutionary dynamics. When coevolution is driven by spatially variable interspecific fitness interactions and by the remixing of local populations through gene flow and metapopulation dynamics, novel coevolutionary dynamics may emerge (Thompson 1994, 1999; Nuismer et al. 1999, 2000, 2003a, 2003b; Gomulkiewicz et al. 2000).

Here we consider genetic models to explore how mutualisms coevolve when interspecific fitness interactions vary from antagonistic to mutualistic across space and time. The models we examine are all motivated by the well-studied interaction between the moth *Greya politella* and its primary host plant *Lithophragma parviflorum*. Much as with its close relatives the yucca moths, *G. politella* is a pollinating seed parasite of its host plant (Thompson and Pellmyr 1992; Pellmyr and Thompson 1996; Thompson and Cunningham 2002; see also Bronstein et al. 2003, in this issue). Unlike the yuccas, however, *L. parviflorum* can be pollinated by several other nonspecialist insect species, many of which pollinate the host without harming the plant or its seeds. The mutualism between *Greya* and *Lithophragma* can therefore be swamped by the presence of effective co-pollinators in some habitats. The role of

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the co-pollinators varies among habitats, and multiyear studies have shown that the interaction varies among populations from mutualism to commensalism to antagonism. Moreover, even within habitats where the usual outcome is either mutualistic or antagonistic, these outcomes are evident in only some years (Thompson and Cunningham 2002). In other years, the interaction is commensalistic. Consistent with the focus of this symposium (Stanton 2003, in this issue), fitness interactions between *G. politella* and *L. parviflorum* can thus grade from mutually beneficial to unilaterally antagonistic as the composition of the mutualist community changes (Thompson and Cunningham 2002; Thompson and Pellmyr 1992).

Although we would like to base our models entirely on the precise biology of *G. politella* and *L. parviflorum*, little is known about the genetic architecture of interactions between these species. Much more is known about the geographic structure of outcomes and its ecological causes, and it is known that populations of the moths and the plants vary in traits involved in the interaction (Janz and Thompson 2002). Studies on the population and evolutionary genetics of the interactions, however, are only now under way.

Our models will minimize the issue of genetics by draping the main ecological features of the *Greya-Lithophragma* system over the simplest of possible genetic frameworks. This general modeling approach necessarily restricts the precision of our exploration of coevolution. However, the models will provide a plausible set of qualitative predictions for future empirical work on this and similar mutualisms and will also serve as an important baseline for more elaborate theoretical treatments. Given the formidable challenges of empirical work on coevolutionary questions that span large temporal and spatial scales, we are particularly interested in discovering coevolutionary patterns that distinguish among different modes of spatial and temporal variability in interspecific fitness interactions.

To this end, we describe results from existing and new genetic models that incorporate variable interspecific fitness interactions over space or time. We use these results to address the following questions: How do episodes of antagonism influence coevolution in otherwise mutualistic interspecific interactions? Do different forms of variable fitness interactions (i.e., spatial vs. temporal variability) lead to consistently different coevolutionary patterns? Can the addition of other mutualist partner species allow the interspecific fitness interactions within a pairwise mutualism to coevolve? To answer most of these questions, we apply results from our previous analyses of the geographic mosaic theory of coevolution (Nuismer et al. 1999, 2000, 2003a, 2003b; Gomulkiewicz et al. 2000) to mutualisms. To address the last question, however, we analyze a new

model of coevolution in which two alternative mutualist partners of a host species coexist. The model makes some surprising predictions.

Matching-Alleles Model

The specific mechanisms that drive fitness interactions between *Lithophragma parviflorum* and *Greya politella* are still under investigation. However, for the purposes of modeling, a plausible hypothesis is that pollination of *L. parviflorum* and oviposition by *G. politella* are jointly enhanced when floral and moth traits such as corolla depth and abdomen length are closely matched. If other pollinators were absent from the community, fitness interactions between *L. parviflorum* and *G. politella* would thus be reciprocally positive, and the benefits to both partners would increase with the degree of matching. If benign co-pollinators were abundant, however, the pollinating services of *G. politella* would be superfluous to *L. parviflorum*, whose seeds nonetheless are devoured by the moth's larvae. In this community setting then, the relative harm to a host plant would intensify with the degree to which its floral traits match corresponding traits in the moth; interactions between *L. parviflorum* and *G. politella* would favor interspecific trait matching in the moth and mismatching in the plant.

A convenient genetic framework for analyzing the evolutionary consequences of our hypothetical scenario is the matching-alleles model of coevolution, which we now describe. The matching-alleles framework has several advantages for present purposes. The primary one is that the model is relatively tractable and thus has well-known mathematical properties (Seger 1988; Gavrillets and Hastings 1998). Another advantage is that the framework is biologically plausible. For instance, many ecologically important mutualisms appear to be mediated by a few major genes (Parker and Wilkinson 1997; Parker 1999; Dashiell et al. 2001).

Our work builds on the following haploid, one-locus version of the matching-alleles model. This baseline model is described in several other sources (e.g., Seger 1988), so our discussion of it will be brief. Consider two haploid species, X and Y, with identical discrete generations. To reinforce the connection between our models and the *L. parviflorum*-*G. politella* system, we will refer to species X as a "host" and Y as a "moth," even though our results would apply to any species with comparable fitness interactions.

Within each species, genetic variation in traits that determine fitness within the context of interspecific interaction segregates at a major locus with two alleles. In the host species X, alleles X_1 and X_2 might produce two different floral morphologies, such as short and long corolla

depth. In the moth species Y, the alleles Y_1 and Y_2 might produce complementary short and long abdomen lengths. Interspecific matches thus come in two flavors: X_1 with Y_1 and X_2 with Y_2 . Let x_i denote the frequency of allele X_i , and let y_i denote the frequency of Y_i for $i = 1, 2$.

We assume the expected relative fitnesses of alleles X_i and Y_i are, respectively,

$$V_i = 1 + ay_i \quad (1)$$

and

$$W_i = 1 + bx_i, \quad (2)$$

for $i = 1, 2$. The parameters a and b measure how the relative fitnesses of alleles change as allele frequencies in the partner species change. Both parameters must be > -1 to ensure that fitnesses are nonnegative. Though biologically simplistic in many ways (see Gomulkiewicz et al. 2000 for further discussion), the fitnesses, equations (1) and (2), capture crucial features of the *L. parviflorum*-*G. politella* mutualism, as we now explain.

Suppose that fitness interactions between host and moth are reciprocally positive, as when co-pollinators are absent. Recall that in this situation, both species benefit more when their respective traits match than when they do not. Assuming that interspecific encounters between individuals with mismatched traits are not entirely avoidable, then the average fitness of a given host or moth allele should increase with the frequency of its complementary allele in the other species. This occurs in equations (1) and (2) if coefficients a and b are both positive.

In contrast, consider the community context in which non-seed-eating pollinators of *L. parviflorum* are abundant. Then V_i , the relative fitness of host allele X_i , should decline with the frequency y_i of its allelic complement in the moth Y. A moth, however, continues to benefit more when matching the floral trait of its host, so W_i should again increase with x_i . This implies that a will be negative and b will be positive in equations (1) and (2), respectively, when interactions between host and moth are beneficial for the moth and harmful for the host.

If other evolutionary forces are weak and can be ignored, then the dynamics of the baseline matching-alleles model are described by two recursions (a prime indicates frequency at the start of the next generation):

$$x'_1 = x_1 \frac{V_1}{x_1 V_1 + x_2 V_2}, \quad (3)$$

$$y'_1 = y_1 \frac{W_1}{y_1 W_1 + y_2 W_2}. \quad (4)$$

These equations suffice to describe the dynamics of evolution since allele frequencies must always sum to 1 within species.

The coevolutionary dynamics of equations (3) and (4) have been well-studied by Seger (1988) and Gavrillets and Hastings (1998). For present purposes, we highlight two of their findings. First, if both a and b are positive, then either x_1 and y_1 both approach 1 or else x_2 and y_2 both approach 1, depending on initial allele frequencies. That is, matching alleles coevolve to fixation within the partner species whenever fitness interactions are positive between them. Second, if the interaction is such that $a < 0$ and $b > 0$, then allele frequencies cycle in both species. The amplitudes of these cycles grow over time.

Our main interest will be on the coevolutionary stability of host and moth populations in which a pair of complementary traits (X_1 - Y_1 or X_2 - Y_2) predominates everywhere. By "coevolutionary stability," we mean that the alternative alleles cannot spread when rare in either species; complementary matching traits that are common in both species will maintain their numerical dominance. Technically, we mean that the equilibria $\hat{x}_1 = \hat{y}_1 = 1$ and $\hat{x}_2 = \hat{y}_2 = 1$ of equations (3) and (4) are locally stable. It turns out (Seger 1988) that if a and b are both positive, then both fixed matches are coevolutionarily stable, essentially because rare alleles cannot overcome the mutually reinforced interspecific fitness advantages of the common matching alleles. Populations fixed for matching traits are unstable, however, if $a < 0$ and $b > 0$ (Seger 1988). In this case, a common host allele is at a severe selective disadvantage when its matching allele in the moth is also common.

The coevolutionary patterns just described hold provided the coefficients a and b are constant over space and time, akin to assuming that interspecific fitness interactions between host X and moth Y are likewise constant. In the next sections, we consider extensions of this model in which between-species fitness interactions vary from mutually beneficial to unilaterally negative, like the community context-dependent mutualism between *L. parviflorum* and *G. politella* that we described above. Our main concern will be the coevolutionary stability of systems with fixed matching alleles when the moth can be antagonistic to the host in an otherwise beneficial interaction.

Fitness Interactions That Vary across Space

Suppose first that host X and moth Y are distributed across a landscape in which the occurrence of non-seed-eating pollinators of X varies from place to place, making fitness interactions between X and Y mutualistic in some localities and antagonistic by the moth in others. As above, assume that interactions between host and moth are positive in

the local communities lacking benign co-pollinators; a and b are both positive in these habitats. Elsewhere, we assume that other harmless pollinators are abundant, making the moth a relative antagonist of the host, with $a < 0$ and $b > 0$ in such localities. For further simplicity, we assume that b is the same in all habitats, regardless of the moth's effect on its host's fitness, which implies that the moth benefits by its interaction with the host equally throughout the region. Let a_M and a_A denote the respective positive or negative value of a in equation (1), corresponding to habitats in which the moth is mutualistic or antagonistic to the host. Assume that a constant fraction f of all local communities lack non-seed-eating pollinators; these co-pollinators occur in the remaining fraction $1 - f$ of the landscape. Species X and Y can coevolve in direct response to both community contexts provided that either the host or moth migrates between them. We will describe patterns of coevolution that emerge under this scenario of spatial variation at the migratory extremes of unlimited and restricted gene flow.

Unlimited Gene Flow

Suppose that genes of both species X and Y flow freely among mutualistic and antagonistic habitats. The life cycle is as follows. At the start of each generation, intraspecific allele frequencies are uniform over all habitats. Local selection alters these frequencies according to interspecific fitness interactions within each community type. After selection, individuals of a species from the different habitats contribute gametes to a global "mating pool" within which random mating and reproduction occurs. The zygotes produced then settle at random among the different communities.

Gene flow is unlimited in the sense that, in each generation, gametes from all community types are mixed in the global mating pool. However, the specific contributions of different localities to the mating pool may depend on local fitnesses (Dempster 1955; Christiansen 1975). At one extreme ("hard selection"), the relative contribution of a local population depends on the number of survivors, as if population sizes were regulated globally. At the other extreme ("soft selection"), local populations contribute a fixed fraction of gametes to the mating pool regardless of local numbers of individuals within the populations, as though population sizes are regulated locally.

The model just described is a special case of one considered by Nuismer et al. (2003b). The interested reader may consult Appendix 2 of that article for mathematical details underlying the results that we now apply to our host-moth mutualism.

Consider hard selection. Nuismer et al. (2003b) show that an equilibrium with complementary matching alleles

fixed in host and moth species ($\hat{x}_1 = \hat{y}_1 = 1$ or $\hat{x}_2 = \hat{y}_2 = 1$) is stably maintained if the global arithmetic mean interaction between X and Y, evaluated at such an equilibrium, is mutualistic. Since the moth reaps benefits from the host everywhere by assumption ($b > 0$), this coevolutionary stability condition translates into

$$f(1 + a_M) + (1 - f)(1 + a_A) > 1, \quad (5)$$

where f is the proportion of habitats in which the moth is a mutualist of the host. (That the stability criterion applies to both $\hat{x}_1 = \hat{y}_1 = 1$ or $\hat{x}_2 = \hat{y}_2 = 1$ is a consequence of the within-species symmetries built into fitnesses in equations (1) and (2).)

In the case of soft selection, the criterion for coevolutionary stability of either equilibrium with fixed matching alleles is

$$\left(\frac{f}{1 + a_M} + \frac{1 - f}{1 + a_A} \right)^{-1} > 1. \quad (6)$$

That is, the global harmonic mean interaction must be mutualistic at a fixed matching equilibrium for matching alleles in host and moth populations to be stably maintained by selection (Nuismer et al. 2003b).

Figure 1 shows that the occurrence of communities with non-seed-eating pollinators ($f < 1$) can affect the coevolutionary stability of fixed, matching alleles between the host and moth. Indeed, rare alternative alleles can spread under a wide variety of conditions, including when the moth is a mutualist in most regions ($f > 1/2$). There are two other broad patterns. The first one we anticipate is that fewer combinations of host selection parameters a_A and a_M are consistent with the coevolutionary stability of fixed matching traits as f , the proportion of habitat in which the moth is a mutualist to the host, shrinks. Second, for a given value of f , coevolutionary stability occurs for a broader range of conditions under hard selection (fig. 1, *dashed lines*) than under soft selection (fig. 1, *solid lines*; Nuismer et al. 2003b). Hence, a given pair of fixed matching alleles in host and moth populations should be more impervious to the introduction of alternative alleles under hard selection (eq. [5]) than soft selection (eq. [6]), all else being equal.

What happens when alternative alleles can invade when rare because of antagonistic effects of the moth on the host? Several novel patterns of coevolution are possible, of which two are displayed in figure 2. The panels differ only in the fraction f of habitats in which host and moth both benefit from their interaction. In the left-hand panel, allele frequencies converge to a stable equilibrium at which the host is polymorphic. In effect, traits in the host that do not match the predominant moth abdomen type are

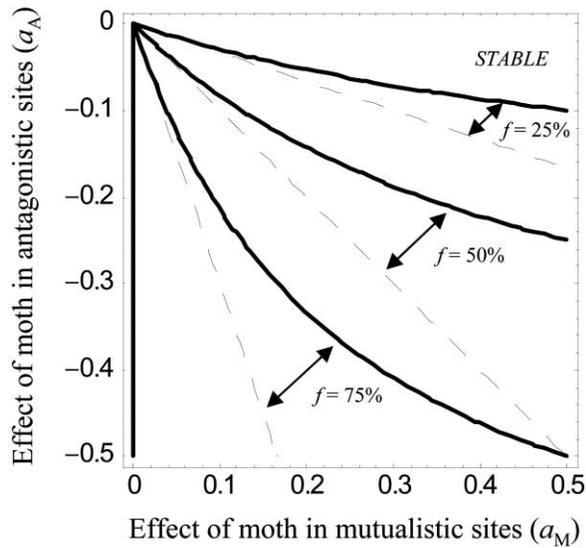


Figure 1: Coevolutionary stability of populations with fixed matching alleles ($\hat{x}_1 = \hat{y}_1 = 1$ or $\hat{x}_2 = \hat{y}_2 = 1$) in models of unlimited gene flow between habitats where moth species Y is beneficial or antagonistic to its host X. Shown are combinations of selection intensities on the host (a) in habitats where the moth is mutualistic ($a = a_M > 0$) or antagonistic ($a = a_A < 0$) and for which coevolutionary stability (area above curve) or instability (area below curve) occurs. For each proportion f of mutualistic habitat, the corresponding broken line separates parameter regions of coevolutionary stability and instability of fixed matches under hard selection (eq. [5]); solid curves separate these regions for soft selection (eq. [6]).

maintained at equilibrium by their relative selective advantage in communities containing abundant non-seed-eating pollinators. The right two panels show that allele frequency cycles within both species are also possible. Note that in the middle panel, both species' allele frequencies remain bounded away from 0 and 1, in contrast to the cycles that arise when the host is mostly (right-hand panel) or always antagonistic to its host (Seeger 1988). In the middle panel, both moth and host remain polymorphic such that different alleles perpetually rise and fall in prevalence without disappearing or becoming completely dominant within a species.

Limited Gene Flow

The model described in the previous section is based on the extreme assumption that barriers to gene flow between different communities are completely absent for host and moth. To what extent do the same coevolutionary patterns hold when gene flow is restricted? The question has already been addressed for the matching-alleles framework, including scenarios with spatially explicit landscapes (Nuismer et al. 1999, 2000). In particular, those studies show

that the more gene flow is limited, the less likely it is that a single pair of matching alleles can remain as the dominant types over the entire range of habitats.

Consider the results of Nuismer et al. (1999), as applied to the spatial scenario of the previous subsection. That article considers a landscape consisting of two equal-sized demes, one in which the moth is a mutualist and the other in which it is an antagonist of the host. In the notation of the previous section, $f = 1/2$. In contrast to the model with unrestricted migration, only a limited number of either the moth or host species are assumed to move among communities in which the moth is a mutualist or an antagonist. Specifically, demes exchange a fraction m of their respective populations following local selection. The model assumes soft selection and that gene flow rates are the same in both species.

The condition for coevolutionary stability of host and moth populations that are globally fixed for the same pair of matching traits with limited migration turns out to be (Nuismer et al. 1999)

$$\frac{1}{|a_A|} - \frac{1}{a_M} > \frac{1}{m}. \tag{7}$$

Recall that a_A and a_M represent the intensity of negative and positive effects that a matching allele in the moth has on the fitness of the host (see eq. [1]). Criterion equation (7) then states, in effect, that a globally dominant pair of matching host and moth alleles can be maintained if the intensity of positive effects provided by the moth exceeds in magnitude the intensity of its negative effects on host fitness by an amount that depends on the level of gene flow m . The condition (7) becomes less restrictive as gene flow increases (fig. 3), and as $m \rightarrow 0.5$, equation (7) is numerically similar to the stability condition for the model with unlimited migration, $f = 1/2$, and soft selection, or equation (6). However, in the case of very limited migration (i.e., as $m \rightarrow 0$), fixed matches are never stable. This is simply because gene flow from habitats in which the moth is a mutualist is far too weak to counter the inherently unstable coevolutionary patterns that occur in communities where the moth is antagonistic to the host. The same conclusions hold qualitatively for spatially explicit models of landscapes that include local communities in which the moth is either a mutualist or antagonist of the host (Nuismer et al. 2000).

Fitness Interactions That Vary through Time

Fitness interactions between species can change over time as well as space (Barton 1986; Thompson 1988; Cushman and Whitham 1989; Thompson and Pellmyr 1992; Del-Claro and Oliveira 2000; van Ommeren and Whitham

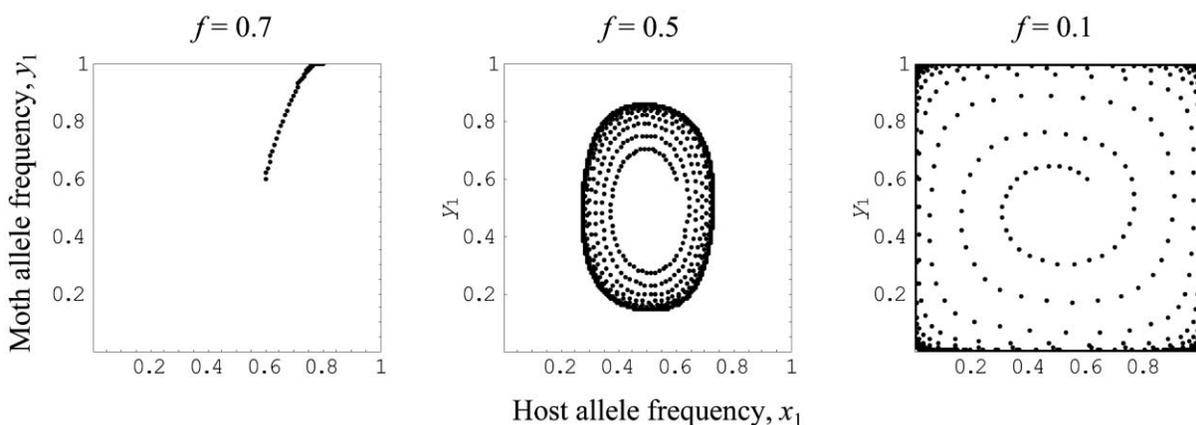


Figure 2: Examples of coevolutionary dynamics in a model with unlimited gene flow and soft selection among habitats in which the moth is either beneficial or harmful to its host (on the basis of models presented in Nuismer et al. 2003b). The coordinates of each point indicate the joint frequencies of host allele X_1 and moth allele Y_1 in successive generations. Each plot shows 5,000 iterations of the same unlimited migration model with soft selection (parameter values: $a_M = b = 0.5$, $a_A = -0.5$; initial frequencies: $x_1 = y_1 = 0.6$) for a different proportion f of mutualistic habitat.

2002). For example, in the *Lithophragma parviflorum*–*Greya politella* system, the abundance of non-seed-eating pollinators at a locality may change considerably from one season to the next. The moth would then be a mutualist of the host during years in which co-pollinators are rare and a relative antagonist when they are common, as appears to occur in some regions of the northern Rocky Mountains (Thompson and Cunningham 2002). This section focuses on how such temporal changes in interspecific fitness interactions can affect patterns of coevolution between two mutualists.

Independent Fluctuations

Nuismer et al. (2003b) analyze an extension of the baseline matching-alleles model (eqq. [3], [4]) in which fitness interactions between host X and moth Y are mutually beneficial in some generations and harmful to the host in others. The model assumes that the temporal sequence of fitness interactions is determined separately from coevolutionary dynamics of the moth and host. This could occur if abundances of benign co-pollinators were determined by factors other than the host and moth (e.g., annual rainfall). Selection within a generation is determined as before by fitness equations (1) and (2), with parameter values that reflect either mutually beneficial ($a = a_M > 0$ and $b > 0$) or antagonistic interaction ($a = a_A < 0$ and $b > 0$).

As in the spatial models above, the Nuismer et al. (2003b) model of temporally variable interactions assumes that the intensity b with which moth fitness increases because of matching alleles in the host is constant; only the

selection intensity parameter a for the host varies. Their formulation allows a to take on any value between -1 and 1 . We adapt their results for our simplified scenario in which a can take on only the two values a_M or a_A . We assume that, in a given generation, other non-seed-eating pollinators are absent with probability f (in which case

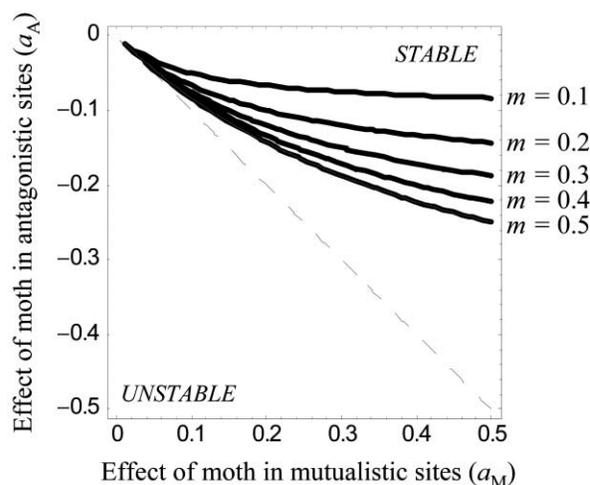


Figure 3: Effects of limited gene flow between habitats in which the moth is either beneficial or harmful to its host on the coevolutionary stability of populations fixed for matching alleles (eq. [7]). Areas above (below) each curve indicate combinations of interaction coefficients consistent with stability (instability) of fixed matching alleles for the given gene flow rate m . The curve for the model with unlimited migration, hard selection (eq. [5]), and $f = 0.5$ is shown by the broken line. The analogous curve for soft selection (eq. [6], $f = 0.5$) is visually indistinguishable from that of the limited migration model with $m = 0.5$.

$a = a_M > 0$) and present (implying $a = a_A < 0$) with probability $1 - f$.

How do such temporal fluctuations affect the coevolutionary maintenance of a species pair fixed for complementary matching alleles? It turns out that the equilibria $\hat{x}_1 = \hat{y}_1 = 1$ and $\hat{x}_2 = \hat{y}_2 = 1$ are both stable to the introduction of alternative alleles, provided that the geometric mean interaction is mutualistic (Nuismer et al. 2003b):

$$(1 + a_M)^f(1 + a_A)^{1-f} > 1. \tag{8}$$

This criterion resembles the analogous condition for the spread of an allele to fixation within a single species (Gillespie 1973). Since the geometric mean is sandwiched between the harmonic and arithmetic means of a set of numbers (e.g., see Roughgarden 1979, pp. 233–234), the stability condition shown in equation (8) is intermediate to the spatial criteria in equations (5) and (6). This implies that conditions that preserve species pairs with fixed matching traits, given temporally variable fitness interactions, are neither broader nor narrower than the corresponding conditions for spatially variable interactions (fig. 4).

Coevolution in a Multispecies Mutualism

Up to this point, pollinator communities have been included only implicitly in our models via their effects on the interspecific fitnesses of our host and moth species. We now describe a new model of coevolution that explicitly incorporates a community of benign co-pollinators that coevolves along with the moth and host whose fitness interactions it directly affects. As inspiration, imagine a three-way interaction between *L. parviflorum*, *G. politella*, and a nonspecialist pollinator such as *Bombyllius major* (Thompson and Pellmyr 1992). To model this system, we extend the baseline matching-alleles model (eqq. [3], [4]) to include a “co-pollinator” species Z. We assume that the co-pollinator pollinates without harming the host X. We also assume that the community is closed, such that the co-pollinator coevolves locally with X and the moth Y. Further, we assume that the co-pollinator’s fitness is not affected by the moth, and vice versa. The likely ecological importance of competition in mutualist communities (Bronstein et al. 2003, in this issue; Hoeksema and Kummel 2003, in this issue; Palmer et al. 2003, in this issue; Stanton 2003, in this issue), however, suggests that relaxing the latter assumption should be given high priority in future theoretical work on multispecies coevolution.

As a starting point for modeling the interactions between our three species, we assume that the same host floral variants are important in fitness interactions with

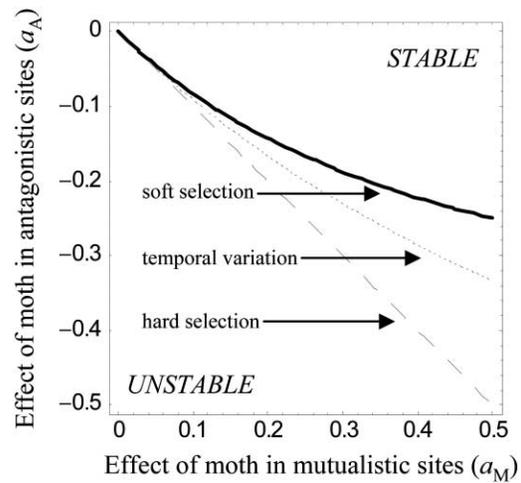


Figure 4: Stability conditions for populations of hosts and moths with fixed matching alleles, comparing temporally versus spatially variable fitness interactions. The curve for independent temporal variation in fitness interactions (dotted line) lies beneath that for unlimited migration and soft selection (solid line) and above that for unlimited migration and hard selection (broken line). The probability that the local interaction is mutualistic is $f = 0.5$ in all three models.

both the moth and co-pollinator. Like the host and moth, the co-pollinator is haploid with alleles Z_1 and Z_2 . Let z_i denote the frequency of allele Z_i .

We assume that both the moth and co-pollinator benefit from interacting with the host and that the benefit of bearing a particular allele in either species increases with the prevalence of its complementary allele in the host. A rationale similar to that used in the sections above leads to fitness definition (eq. [2]) for moth allele Y_i and the following fitness for co-pollinator allele Z_i :

$$U_i = 1 + dx_i, \tag{9}$$

where $i = 1, 2$. The parameters b in equation (2) and d in equation (9) are both positive and indicate the rates at which the fitnesses of alleles in moth and co-pollinator increase with the frequency of their complementary matching allele in the host.

The fitness of host allele X_i now depends on the frequencies of its matching alleles in the moth and co-pollinator species:

$$V_i = 1 + [a_M(1 - z_i) + a_A z_i]y_i + cz_i, \tag{10}$$

where $i = 1, 2$. The coefficient c is a positive constant that reflects the overall beneficial effects that co-pollinator alleles are assumed to provide their host counterparts.

The bracketed term in equation (10) indicates the rate

at which a host allele's relative fitness changes with the frequency of its matching allele in the moth Y . In contrast to the models considered above, this rate can take on any value between the a_A and a_M inclusive, depending on the frequency of the complementary matching allele in the co-pollinator, z_i . We set $a_A < 0$ and $a_M > 0$ to reflect the respective negative and positive impacts that the moth has on host relative fitness. Note that the net fitness effect of a moth allele Y_i on its matching host type X_i is positive or negative, depending on whether the frequency of the complementary allele Z_i is, respectively, below or above $z_i = a_M/(a_M - a_A)$. In effect, this model of fitness presumes that benefits that the co-pollinator provides substitute for those that the moth would otherwise offer to the host. If enough matching co-pollinator alleles are present, the harmful effects of seed parasitism overwhelm any fitness benefits that a moth allele provides to its match in the host.

An important feature of our model is that evolutionary changes in the co-pollinator can drive temporal changes in the fitness interactions between the host and moth. Indeed, the moth may change from a mutualist of the host to an antagonist along the way. Although this was also possible in the above model of temporal variability, here changes in fitness interactions are intrinsic to the dynamics of the community.

Recalling that $z_1 + z_2 = 1$, the evolutionary dynamics of the co-pollinator species Z are represented by

$$z'_1 = z_1 \frac{U_1}{z_1 U_1 + z_2 U_2}, \quad (11)$$

where z'_1 is the frequency of allele Z_1 in the next generation. Recursions shown in equations (3), (4), and (11), employing fitnesses shown in equations (2), (9), and (10), together describe the joint coevolution of species X , Y , and Z . The dynamics of this system are quite rich, so we will concentrate on just two questions of present interest: How does evolution in the co-pollinator affect coevolutionary stability of host and moth populations with high frequencies of complementary matching alleles? How do fitness interactions between the host and moth change over time because of the presence of a coevolving co-pollinator?

Consider, for example, the coevolutionary stability of an equilibrium community in which the matching host and moth alleles X_1 and Y_1 are fixed (i.e., $\hat{x}_1 = \hat{y}_1 = 1$), and the matching allele Z_1 is absent ($\hat{z}_1 = 0$). If the co-pollinator allele Z_1 was permanently excluded from the community, then the moth and host populations would be mutualists, and this mutualism would be stable to the introduction of the variants X_2 and Y_2 . However, if rare variants were introduced in all three species, the fitness interactions between alleles X_1 and Y_1 may undergo striking

changes. Indeed, it can be shown (by a local stability analysis) that the three-species equilibrium $\hat{x}_1 = \hat{y}_1 = 1$, $\hat{z}_1 = 0$, is always unstable, essentially because Z_1 alleles in the co-pollinator species have a large relative fitness advantage over Z_2 alleles because of the initial predominance of host allele X_1 .

If co-pollinator allele Z_1 climbs to sufficiently high frequencies ($z_1 > a_M/[a_M - a_A]$), fitness interactions between moth allele Y_1 and host allele X_1 would turn negative. This raises two additional questions: Will these host-moth fitness interactions remain negative permanently? What patterns of coevolution emerge in the host and moth species? The answer to both questions depends on how strong an antagonist the moth can be to the host.

Figure 5 shows a case in which co-pollinator allele Z_1 spreads following introduction. Notice that z_1 evolves to fixation (fig. 5A). Consequently, the fitness effect of the moth allele on its matching host allele (as indicated by the bracketed term for $i = 1$ in eq. [10]) changes from highly positive to strongly—and permanently—negative (fig. 5B). What about coevolution in the host and moth? The alleles X_1 and Y_1 hardly budge from their high initial frequencies throughout this process. This can be traced to the assumption $c > |a_A|$ for the scenario illustrated in figure 5, that is, that the benefits provided by the matching co-pollinator allele (as indicated by c) always compensate for the increasingly harmful effects of the moth (measured by $|a_A|$). The result is coevolutionary stasis in the host and moth.

One might imagine that in the scenario of figure 5, the host and moth are long-standing partners when the matching allele Z_1 first appears in the co-pollinator. Suppose instead that the long-term associates are the matching host and co-pollinator alleles, X_1 and Z_1 . Would the matching allele Y_1 be able to invade when rare in the moth population? This is tantamount to asking about the stability of an equilibrium community in which $\hat{x}_1 = \hat{z}_1 = 1$ and $\hat{y}_1 = 0$. It turns out that Y_1 will always invade when rare. This occurs because Y_1 has a large fitness advantage over its alternate form Y_2 , since X_1 is the predominant host allele (see eq. [2]). Although Y_1 is antagonistic to the host, it would eventually spread to fixation because its antagonistic effects on host fitness never exceed the benefits provided by the co-pollinator (by assumption); X_1 would maintain its relative dominance, thereby securing a consistent fitness advantage for Y_1 .

Turning again to figure 5, it is interesting to recast its dynamics in phenotypic terms. Given the assumptions of that case, one would observe almost no change in the prevalence of, say, short corollas in the host plant and short abdominal segments in the moth as a co-pollinator evolved to match host traits. However, if fitness effects of the moth on its host were also monitored, one would find

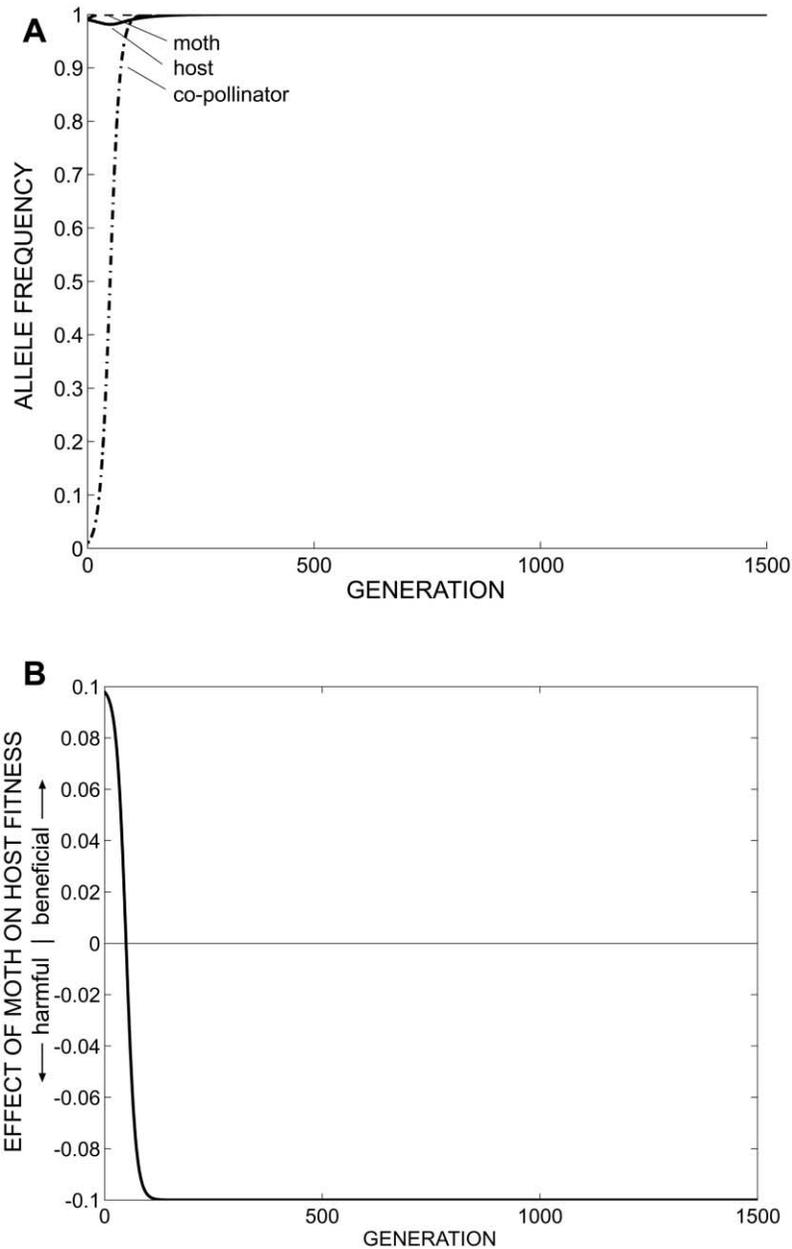


Figure 5: Coevolution in a three-species mutualist community with a stable equilibrium of fixed matching alleles. In this scenario, the beneficial effects of matching alleles with the co-pollinator exceed the negative effects of matching alleles with the moth (i.e., $c > |a_x|$). *A*, Evolution of allele frequencies in the host (x_i ; solid curve), moth (y_i ; dashed curve), and co-pollinator (z_i ; dot-dashed curve). *B*, Corresponding evolution of the fitness interactions between moth allele Y_i and host allele X_i , as indicated by the fitness intensity factor ($a_M z_i + a_x [1 - z_i]$; see eq. [10]). Allele Y_i benefits host allele X_i when the fitness intensity factor is positive and is antagonistic otherwise. Parameter values: $a_M = 0.1$, $a_x = -0.1$, $c = 0.12$, $b = d = 0.1$. Initial allele frequencies: $x_i = y_i = 0.99$ and $z_i = 0.01$.

that this close matching of corolla depth with abdomen length at first benefits, but later harms, the host. This example highlights the potentially dramatic impact of community context on local adaptation in a pairwise interaction; although host and moth have closely matched

traits, the moth is, in the end, really an antagonist. It also demonstrates the problem of automatically presuming that the widespread occurrence of tightly matched traits between two species implies that they are mutualists.

The evolutionary spread of Z_1 when rare need not lead

to its complete fixation, as occurred in the previous scenario. An illustrative example is shown in figure 6. In fact, it is possible to show (via local stability analysis) that an equilibrium community in which all three species are fixed for the same matching allele (e.g., $\hat{x}_1 = \hat{y}_1 = \hat{z}_1 = 1$) is unstable when $c < |a_A|$. Intuitively, in this community context, the co-pollinator does not provide sufficient host ben-

efits to override the negative fitness effects of the moth. The result is that X_2 alleles are at a fitness advantage in the host population when rare. A reciprocal conclusion holds for rare X_1 alleles. Fixation of complementary matching alleles in all three species is thus precluded when $c < |a_A|$.

What coevolutionary dynamics are possible when the

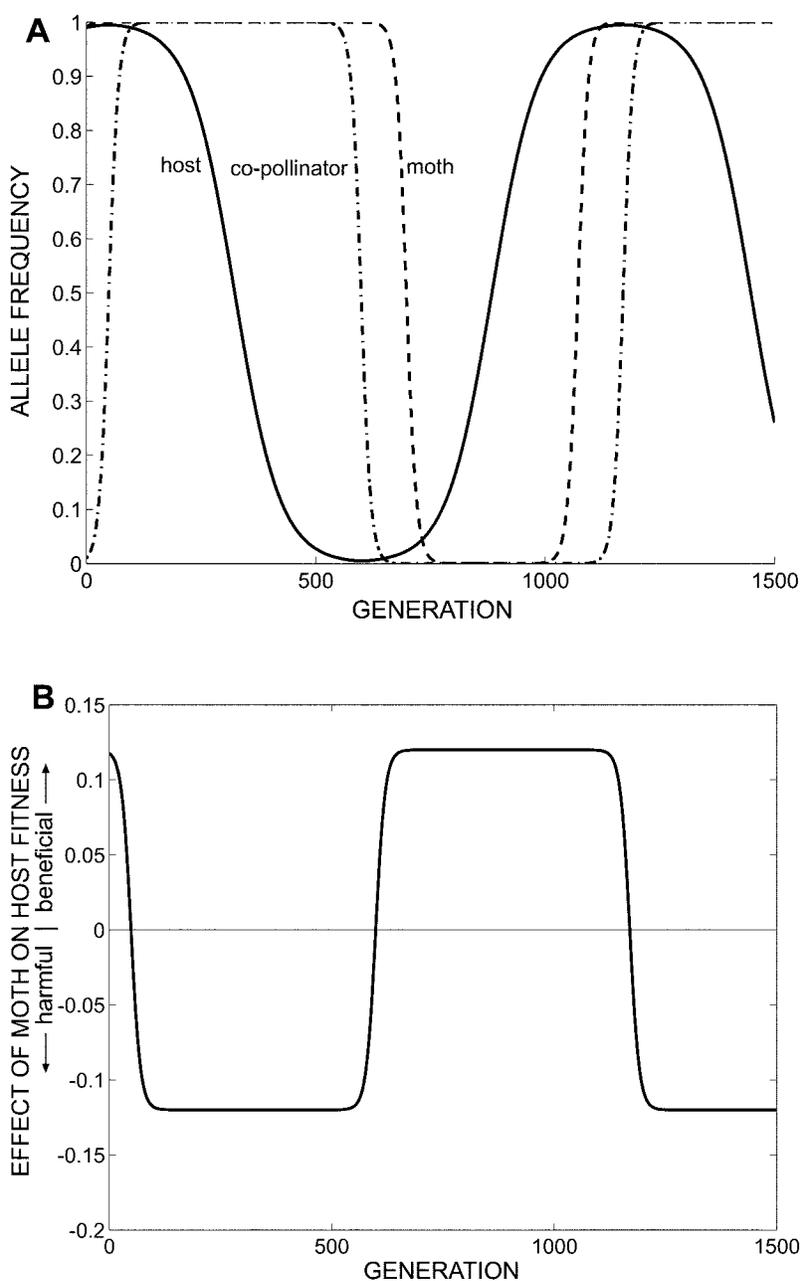


Figure 6: Unstable coevolutionary dynamics and host-moth fitness interactions in a three-species mutualist community. In contrast to figure 5, $c < |a_A|$ in this scenario. Caption details are the same as for figure 5, except for the parameter values $a_M = 0.12$, $a_A = -0.12$, and $c = 0.1$.

moth's negative effects on host fitness can eclipse the fitness benefits provided by the co-pollinator? Figure 6 illustrates one outcome. In the case shown, co-pollinator allele Z_1 spreads from an initially low frequency (as in fig. 5A). Although Z_1 becomes common, its frequency eventually declines. The later decline of Z_1 alleles can be traced to the decay of the frequency of its matching allele in the host X_1 , which is itself driven by the negative effects of the moth allele Y_1 that emerged as Z_1 spread (fig. 6B). Ultimately, allele frequencies repeatedly rise and fall in all three species (fig. 6A), and fitness interactions between host and moth alleles oscillate between mutualistic and antagonistic (fig. 6B). As this example makes clear, the existence of multiple partner species can simultaneously alter the nature of fitness interactions between two species and the coevolutionary trajectories of populations.

So far, discussion of the dynamics of our three-species model has not mentioned the role of benefits that the moth can provide to the host. Indeed, the conditions for coevolutionary stability of the moth-host-co-pollinator communities described above hold regardless of any positive effects that the moth might have on host fitness. One interesting implication of this is that both a moth allele with initially positive effects and its partner host allele can be dislodged from high frequencies by the introduction of a matching co-pollinator allele with weaker beneficial impacts on the host (specifically, with $c < a_M$). This will occur, provided that the moth allele's effects on its match in the host can become sufficiently harmful when the co-pollinator allele reaches high frequencies (this requires that $c < |a_A|$). Figure 6 represents an example of this scenario.

Why do a moth allele's beneficial effects play no apparent role in maintaining itself and its partner allele in the host at high frequencies? The answer is that high frequencies in the host population inevitably lead to the spread of the complementary matching allele in the co-pollinator, thereby causing even the most beneficial moth allele to become a relative antagonist of the very same host allele to which it was formerly a mutualistic partner. It is always at this later stage that the coevolutionary fate of the three-species community is decided (e.g., fig. 5A vs. fig. 6A), depending on the relation between c and $|a_A|$.

Discussion

We have shown that negative fitness interactions between two potentially mutualistic species can lead to different patterns of coevolution than predicted if one assumes constantly beneficial fitness interactions. For instance, if fitness interactions between potential mutualists can be antagonistic at certain locations or at particular times, then the coevolutionary persistence of tightly matched phenotypes

in the two species is not guaranteed (figs. 1, 3, 4), in contrast to mutualists whose interactions are unconditionally positive. In more extreme cases, when periods or regions of antagonistic fitness interactions are prevalent, unexpected patterns of coevolution can emerge. For example, under some conditions, traits central to fitness interactions between two potentially mutualistic species may have cyclical coevolutionary dynamics (figs. 2, 6).

We have also seen that, in terms of maintaining patterns of trait matching between two species or of promoting genetic polymorphism, there are no consistent differences between spatial and temporal variation in interspecific fitness interactions. Compare, for instance, two species with unlimited migration across a landscape over which their fitness interactions vary to two species whose interactions vary comparably but over time. The conditions under which matching traits are stably maintained in both species may be broader or narrower for spatial than temporal variation (fig. 4), depending on details such as the mode of density regulation (figs. 1, 4) and the rate of gene flow between communities in which the moth is either a mutualist or an antagonist (fig. 3). In addition, we found similar novel patterns of coevolution (e.g., allele frequency oscillations) when populations fixed for matching traits are unstable, given spatial or temporal variation (figs. 2, 6).

Our perhaps most surprising results were found in a new model of three coevolving species. In this model, fitness interactions between a host and a moth species depend on a third "co-pollinator" species that is benign to the host. We showed that if beneficial fitness effects of the co-pollinator can compensate for negative effects of the moth on its host, an interaction between the host and moth might change from beneficial to permanently antagonistic for the host, albeit with virtually no evolutionary change in either the host or the moth (fig. 5). At equilibrium, previously fixed matching traits persist in the host and moth, even though the moth becomes an antagonist when a suitable alternative partner is available. This implies that two species with closely matching traits need not be mutualists.

Our analyses also showed that if the beneficial effects of the co-pollinator on host fitness cannot compensate for the negative effects of the moth, allele frequencies can change cyclically in all three species (fig. 6A). As a consequence, fitness interactions between host and moth fluctuate between mutualism and antagonism over time, with evolution in the co-pollinator species driving changes in the interaction (fig. 6B). Although substantial evidence exists that fitness interactions between two species can fluctuate over time between mutualism and antagonism (Cushman and Whitham 1989; Thompson and Pellmyr 1992; van Ommeren and Whitham 2002), it is unknown

whether any of these cases are due to adaptation in an alternative partner species.

We emphasize that our conclusions are based on models with numerous simplifying assumptions. Some of these are not expected to affect our main results, at least qualitatively. For example, the results for spatial variability and independent temporal variability in fitness interactions focused exclusively on scenarios in which the effect of the moth on host fitness assumed one level each of mutualism and antagonism (represented respectively by the constants a_M and a_A). However, the main qualitative results also hold for fitness interactions that vary continuously from negative to positive (Nuismer et al. 2003b). Similarly, relaxing the perfect intraspecific symmetries inherent in fitness equations (1) and (2) would not substantively affect the conclusions.

Another seemingly restrictive assumption of our models is the rudimentary one-locus haploid genetic architecture. We first note that one-locus haploid models of selection are mathematically equivalent to one-locus diploid models with multiplicative fitnesses (e.g., Crow and Kimura 1970), so our results do not pertain exclusively to haploids. We have also found that qualitatively similar dynamics obtain in polygenic models of coevolution, provided that interspecific fitness interactions correspond in both frameworks (S. L. Nuismer, unpublished results).

We expect, however, that some of our assumptions, when violated, are likely to produce qualitatively different predictions about coevolution in communities of mutualists. For instance, interactions based on genetic systems with strong epistasis, such as multilocus matching-alleles models (Peters and Lively 1999) or gene-for-gene models (Thompson and Burdon 1992; Thrall and Burdon 1999), could alter our conclusions. Another potentially important limitation of our models is that the host species is not allowed to exclude interactions with undesirable partners (such as a matching moth type when matching co-pollinator alleles abound). An interesting future direction for theoretical work would be to model the simultaneous evolution of partner choice (Bull and Rice 1991) and the traits involved in fitness interactions between species. Likewise, evolutionary models that account for ecological competition among mutualists (Hoeksema and Kummel 2003, in this issue; Palmer et al. 2003, in this issue; Stanton 2003, in this issue), or between mutualists and antagonists (Bronstein et al. 2003, in this issue), could conceivably change some of our qualitative findings. Without incorporating such assumptions into more detailed models, it is difficult to predict whether they would modify our results in important ways. Given the scarcity of data for even well-studied interactions, developing detailed models based on realistic ecological, behavioral, and genetic assump-

tions will be a joint challenge for empiricists and modelers.

Despite the biological simplicity of our models—indeed, perhaps because of this simplicity—the results we have discussed point to an inescapable and sobering message for empirical studies of coevolution involving variable fitness interactions. In particular, our findings suggest that one cannot pinpoint the process responsible for a coevolutionary pattern based solely on observations of the pattern itself. For example, a stable community of closely interacting species possessing fixed matching traits is logically consistent with either spatially or temporally variable fitness interactions that include one-sided antagonism. Evidently, the next generation of empirical work on variable interactions will need to measure interaction-based selection across multiple locations and generations rather than simply document patterns of interaction. In addition, these studies may need to move beyond pairs of species to make sense of observations. In particular, it will be important to discover how interactions between different genotypes within closely associated species pairs depend on and affect other partner species with which they interact (Stanton 2003, in this issue). These challenges are obviously daunting, but we hope they will guide future empirical and theoretical research on coevolution in communities with variable fitness interactions.

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