

Coevolution in Temporally Variable Environments

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ABSTRACT: Many potentially mutualistic interactions are conditional, with selection that varies between mutualism and antagonism over space and time. We develop a genetic model of temporally variable coevolution that incorporates stochastic fluctuations between mutualism and antagonism. We use this model to determine conditions necessary for the coevolution of matching traits between a host and a conditional mutualist. Using an analytical approximation, we show that matching traits will coevolve when the geometric mean interaction is mutualistic. When this condition does not hold, polymorphism and trait mismatching are maintained, and coevolutionary cycles may result. Numerical simulations verify this prediction and suggest that it remains robust in the presence of temporal autocorrelation. These results are compared with those from spatial models with unrestricted movement. The comparisons demonstrate that gene flow is unnecessary for generating empirical patterns predicted by the geographic mosaic theory of coevolution.

Keywords: mutualism, conditional mutualism, antagonism, host-parasite, coevolution, local adaptation.

Many of the best examples of refined reciprocal adaptation between species arise in mutualistic interactions (e.g., Pellmyr and Krenn 2002). The yuccas and yucca moths or figs and fig wasps provide compelling illustrations. While striking, interactions exhibiting tight coadaptation comprise only a fraction of the diversity of mutualistic interactions. In other cases, mutualisms are better characterized

by spatially variable patterns of local maladaptation (Thompson 1994; Parker 1999; Kapan 2001; Thompson et al. 2002) or by selection that may be antagonistic at certain points in time or space (Barton 1986; Cushman and Whitham 1989; Thompson and Pellmyr 1992; Bronstein 1994). These observations suggest that an adequate theory of mutualistic coevolution must explain not only extreme reciprocal adaptation but also substantial local maladaptation.

Recent work in this direction has been stimulated by Thompson's geographic mosaic theory of coevolution (e.g., Thompson 1994, 1999b). This theory suggests that coevolution will commonly lead to spatially variable patterns of local maladaptation due to the interplay of local selection, gene flow, and other evolutionary forces. This may be particularly important within conditional mutualisms, where selection varies between mutualism and antagonism in response to changing ecological conditions (Cushman and Whitham 1989; Michalakis et al. 1992; Bronstein 1994, 2001). In the interaction between the pollinating seed parasite *Greya politella* and its host plant *Lithophragma parviflorum*, for instance, the ecological outcome may vary between mutualism and antagonism as the density of other pollinator species changes across time and space (Thompson and Pellmyr 1992; Thompson and Cunningham 2002). Similarly, Cushman and Whitham (1989) demonstrated temporal variability in the ecological outcome of the interaction between a membracid and its tending ant in response to changing population densities of a predatory spider. These and other examples (Schemske and Horvitz 1989; Campbell et al. 1997; Caruso 2001) suggest that for many apparently mutualistic interactions, there is abundant spatial and temporal variation in selection.

Theoretical efforts to incorporate variation between mutualistic and antagonistic selection have considered only spatial variation. This work has investigated the coevolutionary dynamics that result when mutualistic and antagonistic communities are linked by gene flow (Nuismer et al. 1999, 2000). These models demonstrate that the interplay between gene flow and spatially variable selection leads to a rich variety of possible coevolutionary dynamics. Much as predicted by the geographic mosaic theory, in-

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intermediate values of gene flow frequently generate spatial patterns of maladaptation. This work, and that of Parker (1999) and Sasaki et. al. (2002), also shows that polymorphism can be maintained for some levels of gene flow. None of these models addresses the coevolutionary dynamics that result when selection varies between mutualism and antagonism over time.

Our goal is to develop a genetically explicit model of a coevolutionary interaction that varies between mutualism and antagonism over time. We use this model to address the following questions: What conditions lead to the coevolution of matching traits rather than polymorphism and trait mismatching? How does temporal autocorrelation modify these conditions? Do spatial and temporal variability generate unique signatures that distinguish their relative importance in generating empirical patterns?

The Model

We consider the interaction between two biallelic coevolving haploid species. Species 1, the parasite/mutualist, has alleles Y_1 with frequency p_1 and Y_2 with frequency q_1 . Species 2, the host, has alleles Z_1 with frequency p_2 and Z_2 with frequency q_2 . We assume that a symmetric matching alleles model governs the interaction, such that at time t , the fitnesses of the interacting species are given by

$$W_{Y_1,t} = 1 + cp_{2,t} \quad (1a)$$

$$W_{Y_2,t} = 1 + cq_{2,t} \quad (1b)$$

$$W_{Z_1,t} = 1 + b_t p_{1,t} \quad (1c)$$

$$W_{Z_2,t} = 1 + b_t q_{1,t} \quad (1d)$$

where $W_{i,t}$ is the fitness of allele i at time t (e.g., Seger 1988; Gavrillets and Hastings 1998). The parameter c is the fitness sensitivity of species 1 to changes in the allele frequencies of species 2. Here c is assumed to be fixed and positive (i.e., $0 < c < 1$) so that the parasite/mutualist species always benefits by matching alleles with the host. This assumption is reasonable for many obligate parasite/mutualist species that rely on a single host. The parameter b_t is the fitness sensitivity of species 2 to changes in the allele frequencies of species 1. In contrast to c , b_t varies through time. We assume that the host species may benefit ($0 < b_t < 1$) or be harmed by the interaction ($-1 < b_t < 0$), depending on current local ecological conditions (e.g., Thompson 1988; Michalakis et al. 1992; Thompson and Pellmyr 1992; Bronstein 1994; Saikkonen et al. 1998). As a consequence, the host is selected to match alleles with the parasite/mutualist within some generations ($b_t > 0$) but not to match in others ($b_t < 0$). These assumptions lead

to the following equations for the allele frequencies p_1 and p_2 of the two species after one episode of selection:

$$p_{1,t+1} = \frac{p_{1,t}(1 + cp_{2,t})}{p_{1,t}(1 + cp_{2,t}) + q_{1,t}(1 + cq_{2,t})}, \quad (2a)$$

$$p_{2,t+1} = \frac{p_{2,t}(1 + b_t p_{1,t})}{p_{2,t}(1 + b_t p_{1,t}) + q_{2,t}(1 + b_t q_{1,t})} \quad (2b)$$

(e.g., Seger 1988; Gavrillets and Hastings 1998; Nuismer et al. 1999). Equations (2) ignore the effects of mutation and genetic drift.

To incorporate stochastic variation in selection, we assume that b_t is a random variable with mean μ_b and variance σ_b^2 . The form of the distribution of b_t is not important for the analytic treatment presented below. Simulations assume b_t is drawn from either a truncated normal or uniform distribution. In the case of simulations using a truncated normal distribution, values of b_t were restricted to lie between -1 and 1 , to prevent negative fitnesses. In these cases, the reported variance is that of the nontruncated distribution. All simulations followed allele frequencies of replicate communities started from random initial allele frequencies.

Results

Coevolution in Constant Environments

To establish a baseline for judging the effects of temporally variable interactions, we describe the coevolution dynamics of our model assuming a constant interaction. This case corresponds to equations (2) with the time variable fitness sensitivity b_t set to a constant value b . This model predicts different dynamics for mutualistic and antagonistic interactions (Seger 1988; Gavrillets and Hastings 1998).

If c is positive and b is negative, the interaction is antagonistic, and unstable allele frequency oscillations evolve within both species (fig. 1A). Coevolutionary dynamics approach a heteroclinic cycle where long periods near fixation are broken by bursts of rapid evolutionary change (Hofbauer and Sigmund 1988, p. 211). Ultimately, this leads to a distribution with most probability density concentrated at the four corner equilibria (fig. 1B). As a consequence, some samples drawn from purely antagonistic communities are nearly fixed for the matching alleles Y_1 and Z_1 or Y_2 and Z_2 .

The second class of dynamics occurs when c and b are positive. In this case, the interaction is mutualistic, and one of two alternative monomorphic equilibria evolves ($\hat{p}_1 = \hat{p}_2 = 0$ or $\hat{p}_1 = \hat{p}_2 = 1$; fig. 1C). These monomorphic equilibria are characterized by the fixation of the

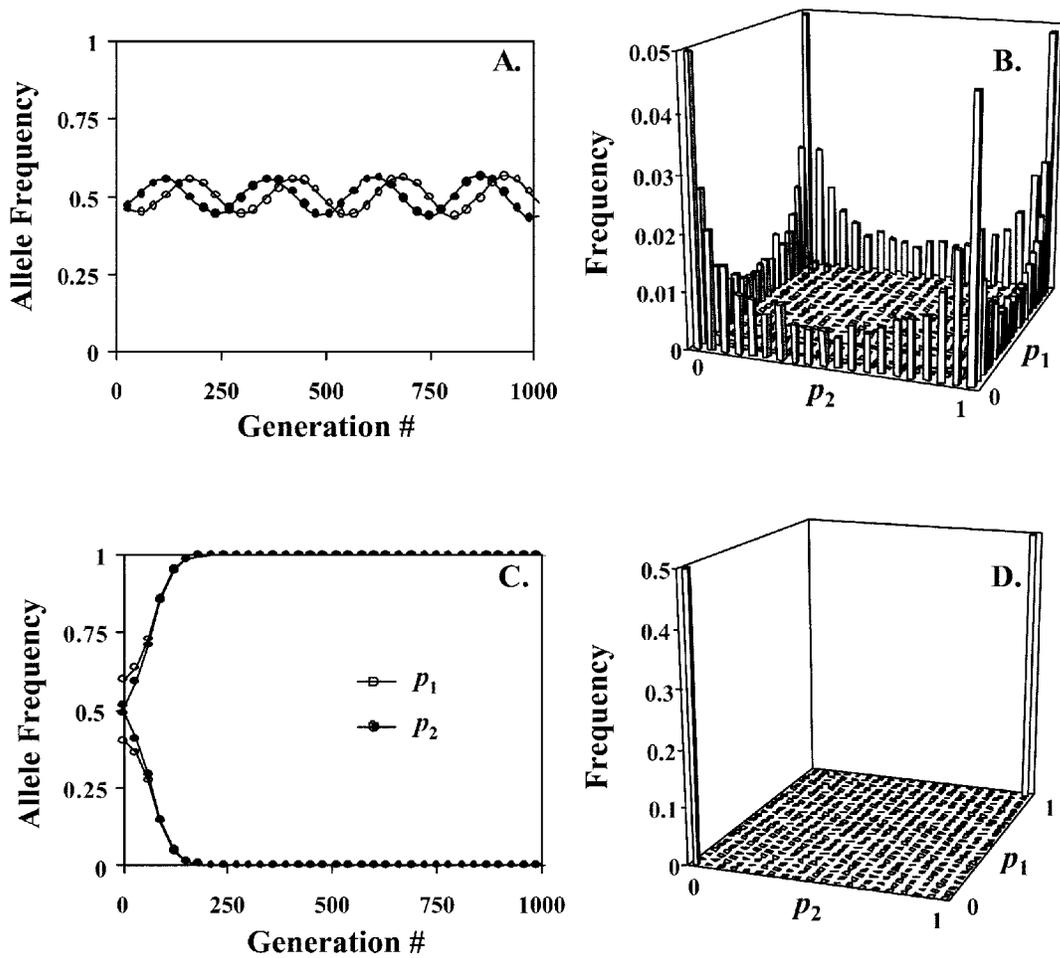


Figure 1: Coevolutionary dynamics for antagonistic and mutualistic communities in the absence of temporal variability. *A*, Cyclical allele frequency dynamics that result when selection is antagonistic. *B*, Distribution of allele frequencies that is approached by generation 10,000 when 20,000 replicate antagonistic communities are initiated from random initial allele frequencies. *C*, Fixation of either the Y_1 and Z_1 or Y_2 and Z_2 matching alleles that results as a consequence of mutualistic selection. *D*, Distribution of allele frequencies p_1 and p_2 that result by generation 10,000 when 20,000 replicate mutualistic communities are initiated from random initial allele frequencies. Parameter values in *A* and *B* were $b = -.05$ and $c = .05$, while in *C* and *D* these values were $b = .05$ and $c = .05$. Note that, for clarity, the scale of the Y -axis is not the same in *B* and *D*.

matched alleles Y_1 and Z_1 or Y_2 and Z_2 . Polymorphism cannot be maintained in a local mutualism. Given initial allele frequencies chosen as uniform random deviates from $0 < p_1 < 1$, $0 < p_2 < 1$, half of all coevolving mutualisms will fix the Y_1 and Z_1 alleles while the other half will fix the Y_2 and Z_2 alleles (fig. 1*D*). Biologically, these equilibria correspond to matching traits between species, such as the matched floral spur lengths and foreleg lengths in *Rediviva* bees and their host plants (Steiner and Whitehead 1991) or matched compatibility alleles between legume plants and rhizobia (e.g., Wilkinson et al. 1996; Parker 1999). We will refer to this mutualistic outcome as a “fixed match” throughout.

Coevolution in Temporally Variable Environments

In this section, we consider how temporal variability in an interaction affects the outcome of coevolution. In particular, we determine conditions that ensure the evolutionary stability of a fixed match when the interaction varies between mutualism and antagonism over time. We first assume the interaction varies independently from one generation to the next. This will allow us to derive an analytic expression for the stability of fixed matching.

In appendix A, we derive exact and approximate conditions for the local stability of a fixed match. The approximate condition is

$$\mu_b > \frac{\sigma_b^2}{2}. \tag{3}$$

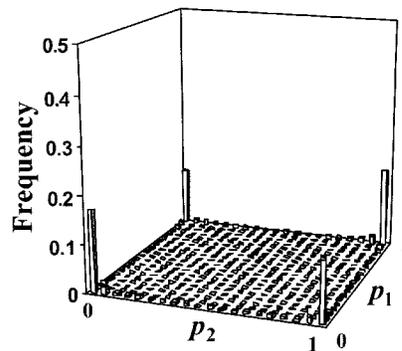
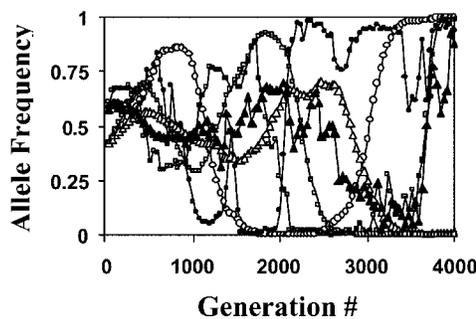
This reduces to the deterministic stability condition $b > 0$ in the absence of temporal variation. When equation (3) holds, the interacting species coevolve matching alleles, as would be expected from a purely mutualistic interaction. When equation (3) does not hold, however, polymorphism is maintained, and trait matching fails to coevolve.

Condition (3) highlights the importance of variance in determining the outcome of coevolution. The greater the variance experienced by hosts, the greater the mean must be to favor the coevolution of a fixed match. Further insight can be gained by noting that $\mu_b - \sigma_b^2/2$ is an approximation to the geometric mean of b_t . Equation (3) then implies that the geometric mean interaction rather than the arithmetic mean (i.e., μ_b) must be mutualistic,

which is the exact criterion for stability of fixed matches (app. A). An important consequence is that with temporal variability, a fixed match can be unstable even though the arithmetic mean interaction is mutualistic (i.e., $\mu_b > 0$). Condition (3) resembles the single species result for the fixation of a selectively favored allele in a temporally variable environment (e.g., Haldane and Jayakar 1963; Gillespie 1973; Karlin and Lieberman 1974).

To determine whether equation (3) is sufficient for the origination, as well as maintenance, of fixed matches, we performed extensive numerical simulations. These simulations used the discrete model given by equations (2). The results show that equation (3) is sufficient for both the maintenance and origination of fixed matching whenever the mean and variance of b_t are both small (e.g., $\mu_b < .05$; $\sigma_b^2 < .1$). As expected from equation (3), simulations show that many communities remain polymorphic

A. Average host selection below critical value



B. Average host selection above critical value

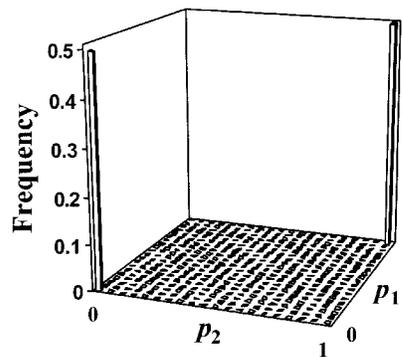
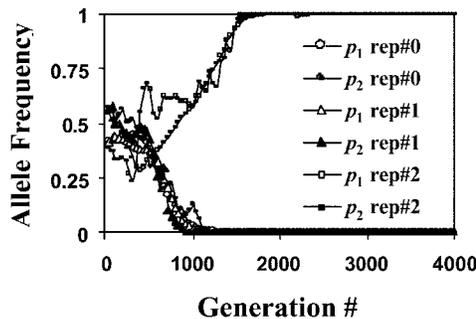


Figure 2: Temporal dynamics and allele frequency distributions for two different values of mean selection sensitivity μ_b in a temporally variable environment. In A, the mean selection sensitivity ($\mu_b = .005$) is below the critical value calculated from equation (3). As a result, not all communities coevolve fixed matches, and polymorphism is maintained. In B, the mean selection sensitivity ($\mu_b = .015$) exceeds the critical value calculated from equation (3). As predicted, this results in a rapid loss of polymorphism and the coevolution of fixed matches. Frequency distributions are shown for generation 10,000 and were generated from 5,000 replicate communities with random initial allele frequencies. Plots of temporal dynamics show only three of the 5,000 replicates, with the host marked by solid symbols and the parasite/mutualist marked by hollow symbols. In all cases, the variance was $\sigma_b^2 = .02$, and the selection sensitivity on the parasite/mutualist was $c = .01$.

when $\mu_b < \sigma_b^2/2$, even after 10,000 generations (fig. 2A). In addition, when the interaction variance becomes substantially larger than the mean ($\mu_b \ll \sigma_b^2/2$), coevolutionary cycles result. Only when $\mu_b > \sigma_b^2/2$ do all coevolving communities converge on the fixed matches expected from a purely mutualistic interaction (fig. 2B). These results do not depend on whether the values of b_t were drawn from a truncated normal or uniform distribution.

Condition (3) provides insight into the conditions that favor fixed matching but not into the rate at which fixed matching evolves. To address this issue, we used simulations of equations (2) to calculate the time until 95% of communities evolved fixed matching. Because equations (2) assume infinite population sizes, exact fixation is precluded. For this reason, we considered fixed matching to have occurred when the allele frequencies of both species were less than .001 or greater than .999. Adjusting these arbitrary thresholds does not qualitatively affect the results reported below.

Simulations show that increasing the mean selection sensitivity of the host μ_b reduces the time taken for fixed matching to coevolve (fig. 3). In contrast, increasing the variance in the selection sensitivity of the host σ_b^2 increases the time to fixation (fig. 3). Specifically, the time taken for fixed matching to evolve increases approximately exponentially with increasing variance and decreasing mean, with this time becoming very large as the variance nears the critical value given by equation (3). This result suggests that even when variance in selection is insufficient to prevent the ultimate evolution of a fixed match, it may greatly slow the approach to this equilibrium.

The foregoing assumes that the selection sensitivity of the host is independent across generations. While this may be the case for some naturally occurring interactions, others may experience temporally correlated mutualistic and antagonistic selection. Thompson and Cunningham (2002), for instance, found that the effect of *Greya politella* on *Lithophragma parviflorum* varied across time, but that in some communities this effect was similar in consecutive years.

To address this issue we incorporate temporal autocorrelation into the model by assuming that the selection sensitivity of the host b_t is given by a first-order autoregressive process:

$$b_t = \lambda b_{t-1} + z_t, \quad (4)$$

Here z_t is a discrete random variable drawn from a distribution with mean $(1 - \lambda)\mu_b$ and variance $(1 - \lambda^2)\sigma_b^2$, and λ is the autocorrelation coefficient between generations t and $t - 1$ (e.g., Roughgarden 1996). By parameterizing z_t in this way, the asymptotic mean and variance of b_t remain equal to μ_b and σ_b^2 , respectively.

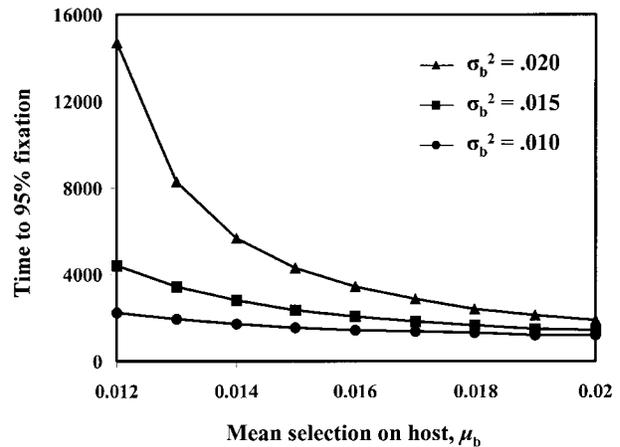


Figure 3: Time until 95% of replicate populations reach fixation as a function of mean selection sensitivity μ_b for three different values of variance σ_b^2 . Values were calculated from simulations of 40,000 replicate communities initiated from random initial allele frequencies. Any given community was considered a fixed match if the allele frequencies of both species were either less than .001 or greater than .999. The selection sensitivity of the parasite/mutualist was $c = .01$.

Assuming that autocorrelation among the selection sensitivities b_t is weak, one can argue (app. A) that the stability of fixed matches is again determined by equation (3). We assessed the impact of stronger autocorrelations using numerical simulations of equations (2). These simulations suggest that equation (3) continues to predict the stability of fixed matches quite accurately (consistently within 8%–12%) across a range of parameter values (table 1). The apparent accuracy of equation (3) suggests that temporal autocorrelation does not substantially alter the conditions under which fixed matches coevolve.

Comparing Variation in Space and Time

In this section, we compare the conditions that allow fixed matches to coevolve in spatially versus temporally variable environments. Our hope is to bridge the gap between the results of this article and those of previous articles investigating coevolution in mutualistic and antagonistic communities coupled by restricted gene flow (Nuismer et al. 1999, 2000; Gomulkiewicz et al. 2000). To simplify the comparison, we analyze a spatial scenario where both species exist in a habitat consisting of an infinite number of mutualistic and antagonistic patches connected by unlimited gene flow. To facilitate comparison with the temporal model, the selection sensitivity of the host in any habitat patch i , b_i , is assumed to be a random variable drawn independently from a distribution with mean μ_b and var-

Table 1: Critical values of mean selection sensitivity of hosts necessary for 95% fixation

λ	$\sigma_b^2 = .010$	$\sigma_b^2 = .010$	$\sigma_b^2 = .015$	$\sigma_b^2 = .015$	$\sigma_b^2 = .020$	$\sigma_b^2 = .020$
	Observed	Predicted	Observed	Predicted	Observed	Predicted
-.10	.0056	.0050	.0082	.0075	.0108	.0100
-.05	.0056	.0050	.0082	.0075	.0109	.0100
.00	.0056	.0050	.0082	.0075	.0109	.0100
.05	.0057	.0050	.0083	.0075	.0110	.0100
.10	.0057	.0050	.0084	.0075	.0110	.0100

Note: Results are based on the analytical expression (3) “predicted” or numerical simulations of expression (2) “observed.” For simulations, b_i was drawn from a uniform distribution with mean $(1 - \lambda)\mu_b$ and variance $(1 - \lambda^2)\sigma_b^2$. Simulations followed 1,000 replicate communities for 60,000 generations.

iance σ_b^2 . We consider both soft and hard selection (Levene 1953; Dempster 1955; Christiansen 1975).

Local stability analyses demonstrate that hard selection provides the most favorable conditions for fixed matching (app. B). With hard selection, matching is stable if the arithmetic mean selection sensitivity of the host is positive:

$$\mu_b > 0. \quad (5)$$

In contrast, soft selection yields the more restrictive condition that the mean selection sensitivity of the host must exceed the variance:

$$\mu_b > \sigma_b^2. \quad (6)$$

These two conditions lie on either side of the condition required for fixed matching to coevolve within temporally variable and independent environments (fig. 4).

Discussion

Our analyses suggest that temporal fluctuations in selection sensitivities determine whether and how rapidly fixed matches coevolve within conditional mutualisms. Fixed matching coevolves only when the geometric mean interaction is mutualistic. In contrast, polymorphism and imperfect matching are maintained when the geometric mean interaction is antagonistic. Since the geometric mean is necessarily bounded above by the arithmetic mean, this result demonstrates that temporal variability impedes the coevolution of tight reciprocal adaptation. Extensive numerical simulations support these results. In addition, these simulations demonstrate that maladaptation and polymorphism can persist for considerable periods of time even when the geometric mean interaction is weakly mutualistic. These results demonstrate the importance of the geometric mean for coevolutionary interactions, as has

long been realized for single species within temporally variable environments (Haldane and Jayakar 1963; Gillespie 1973; Karlin and Lieberman 1974).

Evaluating the relevance of these results for naturally occurring interactions requires data on the strength of selection sensitivities over multiple generations. Unfortunately, there are no studies of conditional mutualisms that can provide the necessary data. A number of studies document that the ecological effect of an interaction can vary between mutualism and antagonism (Cushman and Whitham 1989; Thompson and Pellmyr 1992; Thompson and Cunningham 2002). However, none of these have measured selection sensitivities or even the strength of selection. In the absence of estimates of selection, it is possible to draw only relatively weak qualitative conclusions. From this perspective, two empirical patterns are in general accord with our findings. First, many well-studied mutualistic interactions exhibit a surprising level of maladaptation or polymorphism (Spoerke et al. 1996; Kapan 2001; Thompson et al. 2002). Second, examples of tight species-level reciprocal adaptation between mutualists are relatively rare (Thompson 1994; Pellmyr 1997; Thompson et al. 2002). These observations are consistent with our findings provided naturally occurring conditional mutualisms tend to be characterized by a geometric mean that is antagonistic over time.

Critically evaluating the relevance of our results will also require the development of models with more realistic genetics. Coevolutionary models based on diploid inheritance with dominance, for instance, can show substantially different dynamics (e.g., Switkes and Moody 2001). The same can be true for multilocus models of coevolution that incorporate epistasis (e.g., Peters and Lively 1999). It is worth noting, however, that the current results may apply more broadly than might be expected from their genetic simplicity. We have run additional simulations that assume interactions are mediated by additive polygenic traits. The results (not shown) are qualitatively similar to those of the single locus model. This is also true for in-

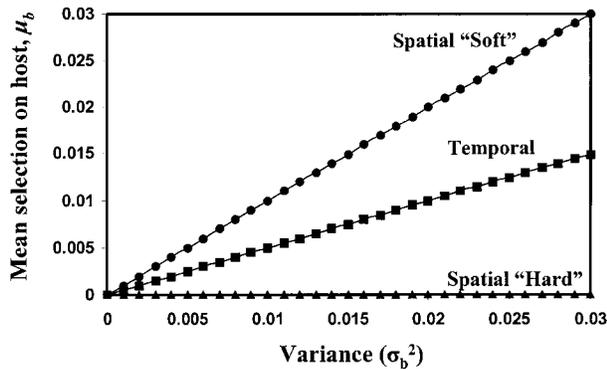


Figure 4: A plot of the critical values of mean selection sensitivity μ_b required for the stability of a fixed match for “soft” spatial variation (circles), “hard” spatial variation (triangles), and temporal variation (squares). These values were calculated from equations (3), (5), and (6) in the text.

interactions mediated by more general multilocus matching alleles models. While we have not attempted to analyze these or other more complicated scenarios in detail, we anticipate that our primary results will apply qualitatively across a range of coevolutionary genetic systems.

The likely ramifications of several other simplifications used in our model are worth addressing. For instance, we have not considered mutation, which is known to promote polymorphism in antagonistic interactions (Seger 1988). The addition of mutation would likely strengthen the current results by accentuating the difference between mutualistic and antagonistic outcomes. In contrast, our assumption of infinite population size precludes genetic drift, which, if incorporated, could blur the distinction between mutualistic and antagonistic outcomes. Other potentially important simplifications include a lack of explicit demography and an absence of community-level coevolution. Models that explicitly include variable population sizes (e.g., Gandon et al. 1996; Thrall and Burdon 1999) or multispecies coevolution (e.g., Christensen et al. 2002; Gomulkiewicz et al. 2003) may lead to different predictions.

More broadly, our results have implications for interpreting two empirical patterns predicted by the geographic mosaic theory of coevolution: trait mismatches and species-level polymorphism for coevolved traits (Thompson 1994; Thompson 1999b). Examples of these patterns are widespread within mutualisms and include, for instance, the interactions between the mimetic butterfly *Heliconius cydno* and its mullerian co-models. In this interaction, *H. cydno* has not converged on the warning coloration of its mullerian co-models in parts of its geographic range (Kapan 2001). Instead, considerable trait

mismatching and color-pattern polymorphism are maintained between these potentially coevolving species. These patterns are not predicted by most models of mutualistic coevolution with constant selection sensitivities and panmixis (e.g., Law 1985; Gavrillets and Hastings 1998) but arise readily in models with spatially variable selection sensitivities and gene flow between populations (Nuismer et al. 1999, 2000; Parker 1999; Gomulkiewicz et al. 2000; Sasaki et al. 2002). This theoretical result suggests that spatially variable selection sensitivities and gene flow may be necessary for mosaic patterns to emerge within mutualistic interactions (Parker 1999; Thompson 1999a; Nuismer et al. 2000; Thompson et al. 2002). Results presented here, however, show that temporally variable selection sensitivities can generate similar patterns even in the absence of gene flow.

Our comparison of spatial and temporal models helps to clarify parameter values that lead to these mosaic patterns in spatially versus temporally variable environments. Assuming that selection sensitivities are independent across both space and time, the predicted patterns of incomplete trait matching and few species-level coevolved traits are favored by spatially variable “soft” selection under the broadest range of parameters ($\mu_b < \sigma_b^2$), followed by temporal variability ($\mu_b < \sigma_b^2/2$), and finally “hard” selection with the most stringent conditions ($\mu_b < 0$). As a consequence, evaluating the significance of spatial versus temporal variation will require quantitative assessment of selection sensitivities over multiple populations and years. The work of Galen and Cuba (2001) and Schemske and Horvitz (1989), for instance, provides excellent examples of methodology that might be profitably applied to studies of conditional mutualisms.

We have used a simple model to illustrate the importance of temporal variability for the outcome of coevolution between conditional mutualists. Despite its simplicity, our model generates unique and testable predictions for the conditions that lead to tight trait matching versus polymorphism and trait mismatching. We hope that our results will stimulate further empirical and theoretical interest in the coevolutionary dynamics of conditional mutualisms.

Acknowledgments

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APPENDIX A

Stability Conditions for Fixed Matching in a Temporally Variable Environment

Here we determine conditions for the stability of the equilibrium corresponding to fixed matching between the species ($\hat{p}_1 = \hat{p}_2 = 0$) in a temporally variable environment. Our derivation extends the analysis of stochastic local stability presented by Karlin and Lieberman (1974) to two coevolving species. Stability conditions for ($\hat{q}_1 = \hat{q}_2 = 0$) can be derived in an identical fashion.

For initial allele frequencies sufficiently close to $\hat{p}_1 = \hat{p}_2 = 0$, equations (2) are approximately

$$p'_1 = p_1 \frac{1}{1 + c}, \tag{A1a}$$

$$p'_2 = p_2 \frac{1}{1 + b_t}. \tag{A1b}$$

Primes denote the next generation, and products and terms of second order or higher in p_1 and p_2 have been ignored. Equations (A1) show that at time T , the allele frequencies p_1 and p_2 are given by

$$p_{1,T} \approx p_{1,0} \left(\frac{1}{1 + c} \right)^T, \tag{A2a}$$

$$p_{2,T} \approx p_{2,0} \prod_{i=0}^T \frac{1}{1 + b_i}, \tag{A2b}$$

where $p_{1,0}$ and $p_{2,0}$ are the initial and sufficiently small allele frequencies at time $t = 0$. By assumption, c is always positive (i.e., the parasite/mutualist always benefits through interacting), so $p_1 \rightarrow 0$ as $T \rightarrow \infty$. However, since b_t varies in sign over time, there may be conditions under which $p_{2,T}$ is bounded away from $\hat{p}_2 = 0$ as $T \rightarrow \infty$, precluding the stability of matching alleles. Therefore, fixed matching will be evolutionarily stable if and only if

$$\prod_{i=0}^T \frac{1}{1 + b_i} < 1, \tag{A3}$$

with sufficiently high probability as $T \rightarrow \infty$. Taking the natural logarithm of both sides of equation (A3) and dividing by $T + 1$ leads to the equivalent condition

$$\frac{1}{T + 1} \sum_{i=0}^T \ln(1 + b_i) > 0. \tag{A4}$$

If we now assume that the b_t are independent and identically distributed random variables, the Strong Law of Large Numbers ensures that the left-hand side converges

to $E[\ln(1 + b_t)]$ with probability 1 as $T \rightarrow \infty$, where E denotes expectation with respect to the distribution of b_t . Thus, $\hat{p}_1 = \hat{p}_2 = 0$ is evolutionarily stable if and only if

$$E[\ln(1 + b_t)] > 0. \tag{A5}$$

This is equivalent to requiring the geometric mean of $1 + b_t$ to exceed 1; that is, the geometric mean interaction must be mutualistic for stability.

We can obtain a useful approximation for equation (A5) by assuming weak selection. Expanding equation (A5) in a Taylor series and using $E(b_t) = \delta\mu_b$, $\text{Var}(b_t) = \delta\sigma_b^2 = E(b_t^2) + o(\delta^2)$ as $\delta \rightarrow 0$ gives

$$\begin{aligned} E[\ln(1 + b_t)] &\approx E\left[b_t - \frac{b_t^2}{2} + o(b_t^2)\right] \\ &= \delta\left(\mu_b - \frac{\sigma_b^2}{2}\right) + o(\delta^2) > 0. \end{aligned} \tag{A6}$$

Thus, the approximate condition for evolutionary stability assuming weak selection is simply

$$E[b_t] > \frac{1}{2} \text{Var}[b_t]. \tag{A7}$$

Condition (A7) can be derived assuming the b_t are weakly autocorrelated by using the Central Limit Theorem (R. Gomulkiewicz, unpublished results).

APPENDIX B

Stability Conditions for Fixed Matching in a Spatially Variable Environment

Here we determine stability conditions for the equilibrium corresponding to a fixed match between species ($\hat{p}_1 = \hat{p}_2 = 0$). Due to the symmetry of the model, the stability conditions derived here are identical to those for the alternative matching equilibrium ($\hat{p}_1 = \hat{p}_2 = 1$). We assume that the environment consists of n equally sized habitat patches connected by free dispersal. At the beginning of each generation, zygotes of both species are distributed from a common mating pool such that all patches have identical allele frequencies. We first consider hard selection, where the mating pool consists of contributions from the different patches in proportion to local mean fitness. The allele frequencies of the two species after one generation are

$$p_1' = \frac{p_1(1 + cp_2)}{p_1(1 + cp_2) + q_1(1 + cq_2)}, \quad (\text{A8a})$$

$$p_2' = \frac{p_2 \sum_{i=1}^n (1 + b_i p_1)}{p_2 \sum_{i=1}^n (1 + b_i p_1) + q_2 \sum_{i=1}^n (1 + b_i q_1)}. \quad (\text{A8b})$$

Linearizing these equations around the equilibrium $\hat{p}_1 = \hat{p}_2 = 0$ gives the following approximate recursions for allele frequencies in the next generation:

$$p_1' = p_1 \frac{1}{1 + c}, \quad (\text{A9a})$$

$$p_2' = p_2 \frac{1}{1 + (1/n) \sum_{i=1}^n b_i}. \quad (\text{A9b})$$

Since $c > 0$, inspection of equations (A9) shows that matching will be stable whenever

$$\frac{1}{n} \sum_{i=1}^n b_i > 0. \quad (\text{A10})$$

Thus, with hard selection the arithmetic mean interaction must be mutualistic for fixed matching to be stable.

We next consider soft selection, where the mating pool consists of fixed contributions from the different patches, independent of mean fitness. The allele frequencies in the two species after one generation are given by

$$p_1' = \frac{p_1(1 + cp_2)}{p_1(1 + cp_2) + q_1(1 + cq_2)}, \quad (\text{A11a})$$

$$p_2' = \frac{1}{n} \sum_{i=1}^n \frac{p_2(1 + b_i p_1)}{p_2(1 + b_i p_1) + q_2(1 + b_i q_1)}. \quad (\text{A11b})$$

Linearizing these equations around the equilibrium $\hat{p}_1 = \hat{p}_2 = 0$ gives the following approximate recursions:

$$p_1' = p_1 \frac{1}{1 + c}, \quad (\text{A12a})$$

$$p_2' = \frac{1}{n} p_2 \sum_{i=1}^n \frac{1}{1 + b_i}. \quad (\text{A12b})$$

Inspection of equations (A12) shows that fixed matching will be stable whenever

$$\frac{1}{n} \sum_{i=1}^n \frac{1}{1 + b_i} < 1. \quad (\text{A13})$$

The left-hand side of equation (A13) is the reciprocal of

the harmonic mean of $1 + b_i$. Thus, equation (A13) is equivalent to requiring that the harmonic mean interaction must be mutualistic. If the mean μ_b and variance σ_b^2 of the b_i are both small, equation (A13) is closely approximated by condition (6).

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