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# Gene flow and geographically structured coevolution

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Many of the dynamic properties of coevolution may occur at the level of interacting populations, with local adaptation acting as a force of diversification, as migration between populations homogenizes these isolated interactions. This interplay between local adaptation and migration may be particularly important in structuring interactions that vary from mutualism to antagonism across the range of an interacting set of species, such as those between some plants and their insect herbivores, mammals and trypanosome parasites, and bacteria and plasmids that confer antibiotic resistance. Here we present a simple geographically structured genetic model of a coevolutionary interaction that varies between mutualism and antagonism among communities linked by migration. Inclusion of geographic structure with gene flow alters the outcomes of local interactions and allows the maintenance of allelic polymorphism across all communities under a range of selection intensities and rates of migration. Furthermore, inclusion of geographic structure with gene flow allows fixed mutualisms to be evolutionarily stable within both communities, even when selection on the interaction is antagonistic within one community. Moreover, the model demonstrates that the inclusion of geographic structure with gene flow may lead to considerable local maladaptation and trait mismatching as predicted by the geographic mosaic theory of coevolution.

**Keywords:** coevolution; antagonism; mutualism; geographic mosaic theory; maladaptation

## 1. INTRODUCTION

Coevolution is widely accepted as one of the major forces driving the creation of biodiversity and maintaining the complex structure of interspecific interactions within biological communities (Ehrlich & Raven 1964; Mitter *et al.* 1988; Thompson 1994). In addition to its contribution to historical patterns of interactions, coevolution plays an integral role in shaping the dynamics of interactions and ongoing ecological processes. Proceeding on time-scales as short as centuries, such rapidly evolving and coevolving interactions have the potential to shape community dynamics, patterns in epidemiology, the efficacy of biological control programmes and conservation efforts (Herre 1993; Bull 1994; Ewald 1994; Thompson 1996, 1998; Holt & Hochberg 1997; Burdon & Thrall 1999). Many of the dynamic properties of coevolution may be occurring at the level of interacting populations, with local adaptation acting as a force of diversification, while migration homogenizes these isolated interactions. This interplay between local adaptation and migration may result in a geographic mosaic of coevolutionary outcomes in which considerable local maladaptation and trait mismatching may occur (Thompson 1994). This type of structuring may be particularly important in interactions that vary from mutualism to antagonism across the range of an interacting set of species.

Interactions that vary between mutualism and antagonism across the geographic range of a species are known for a wide range of taxa and have been hypothesized as a potential origin of many obligate mutualisms and symbioses (Thompson 1994). One of the best known examples of an interaction that may vary between mutualism and antagonism is found between bacteria and those plasmids that produce drug resistance or allow the use of alternative carbon sources (Nguyen *et al.* 1989; Duncan *et al.* 1995). In these interactions, the plasmid is beneficial to its associated bacterium when selection favours the expression of the plasmid-encoded gene, but costly when selection for its function is absent. At the same time, the interaction between plasmid and bacterium is always beneficial for the plasmid, independent of local ecological conditions. A diverse array of other interactions, including those between moths of the genus *Gryea* and their host plants, mammals and their associated trypanosome parasites, and cowbirds and their avian hosts, follow a similar structure (Munger & Holmes 1987; Michalakis *et al.* 1992; Thompson & Pellmyr 1992).

## 2. THE MODEL

We investigated the role of geographic structuring and gene flow on interactions that range from antagonism to mutualism across communities using a spatially explicit matching alleles model. The model builds upon the results of recent ecological models showing that spatial structure

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may significantly modify the dynamics of species interactions (Ferguson *et al.* 1997; Hassell & Wilson 1997). Through migration, our model links a community in which local selection favours the evolution of mutualism and one in which local selection is antagonistic. We assume that each community consists of a pair of interacting haploid species with discrete generations, whose interactions are governed by a single locus with two alleles. Species X has alleles *A* and *a*, with  $x_j$  denoting the frequency of allele *A* in population *j*, whereas species Y has alleles *B* and *b*, with  $y_j$  denoting the frequency of *B* in population *j*. Species X, hereafter referred to as the ‘symbiont’, always receives a fitness increase through matching alleles (e.g. genotype *A* benefits through interacting with genotype *B* but not with genotype *b*). Species Y, the ‘host’, receives a fitness increase for matching alleles with the symbiont in community 1 where the interaction is mutualistic and a fitness penalty for matching in community 2 where the interaction is antagonistic. We model these assumptions as simply as possible, following previous theoretical studies using linear fitness functions:

<p>community 1: mutualistic interaction</p> $W_{A,1} = 1 + Cy_1$ $W_{a,1} = 1 + C(1 - y_1)$ $W_{B,1} = 1 + K_M x_1$ $W_{b,1} = 1 + K_M(1 - x_1)$	<p>community 2: antagonistic interaction</p> $W_{A,2} = 1 + Cy_2$ $W_{a,2} = 1 + C(1 - y_2)$ $W_{B,2} = 1 - K_A x_2$ $W_{b,2} = 1 - K_A(1 - x_2),$
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where  $W_{i,j}$  is the fitness of allele *i* in community *j*, parameter *C* is the sensitivity of symbiont fitness to changes in host allele frequency,  $K_A$  is the sensitivity of host fitness to changes in antagonistic symbiont allele frequencies and  $K_M$  is the sensitivity of host fitness to changes in mutualistic symbiont allele frequencies. Finally, we assume for simplicity that migration is symmetrical between communities, occurs at rate *m* for both interacting species and occurs before selection. These assumptions lead to the following system of four recursion equations for the between-generation change in  $x_j$  and  $y_j$ , where primes denote the next generation:

$$x'_j = \frac{x_j^* W_{A,j}}{x_j^* W_{A,j} + (1 - x_j^*) W_{a,j}} \tag{1}$$

$$y'_j = \frac{y_j^* W_{B,j}}{y_j^* W_{B,j} + (1 - y_j^*) W_{b,j}}, \tag{2}$$

for  $j=1, 2$ , where  $x_1^* = x_1(1 - m) + x_2 m$ ,  $x_2^* = x_2(1 - m) + x_1 m$ ,  $y_1^* = y_1(1 - m) + y_2 m$  and  $y_2^* = y_2(1 - m) + y_1 m$  are the post-migration allele frequencies.

### 3. GENE FREQUENCY DYNAMICS

We iterated recursion equations (1) and (2) for a range of migration rates and types of local coevolutionary selection. The results show that, without migration ( $m=0$ ), local selection produces unstable allelic oscillations within the antagonistic interaction (community 2) and fixation of matching alleles within the mutualistic interaction (community 1) (figure 1*a* and 2*a*). The intensity of local

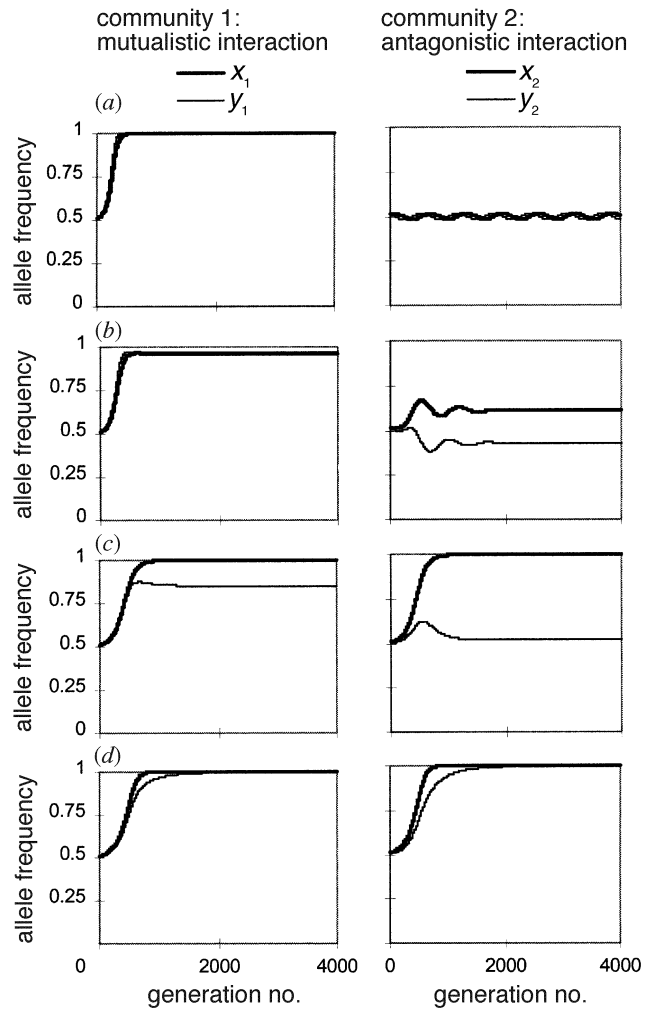


Figure 1. Dynamics of a mutualistic interaction linked through migration to a weaker antagonistic interaction in another community. For this set of simulations, selection for mutualism within one community was two times stronger than antagonistic selection within the other. For all graphs,  $C = 0.02$ ,  $K_M = 0.04$ ,  $K_A = 0.02$  and migration rates between the two communities increase from (a) to (d), with  $m_a = 0$ ,  $m_b = 0.002$ ,  $m_c = 0.015$  and  $m_d = 0.050$ .

selection on hosts, which is reflected in the values of sensitivities  $K_A$  and  $K_M$ , affects the rate at which matching alleles become fixed within the mutualistic interaction and the rate at which oscillations increase in amplitude in the antagonistic interaction. Without migration between communities, stable polymorphic equilibria are absent for both types of interaction and across all parameter values. These results are comparable to those of Gavrillets & Hastings (1998), who analysed a similar one-patch model of coevolutionary chase.

With migration between communities ( $m > 0$ ), coevolutionary dynamics depend upon the relative intensity of selection for matching alleles within the mutualistic interaction and against matching alleles within the antagonistic interaction. This interplay between the intensity of localized selection for mutualism within one interaction and antagonism within the other creates two distinct types of complementary coevolutionary dynamics. Namely, as the migration rate is increased, both sets of selective conditions lead to an initial phase in which the dynamics of each local community resemble their

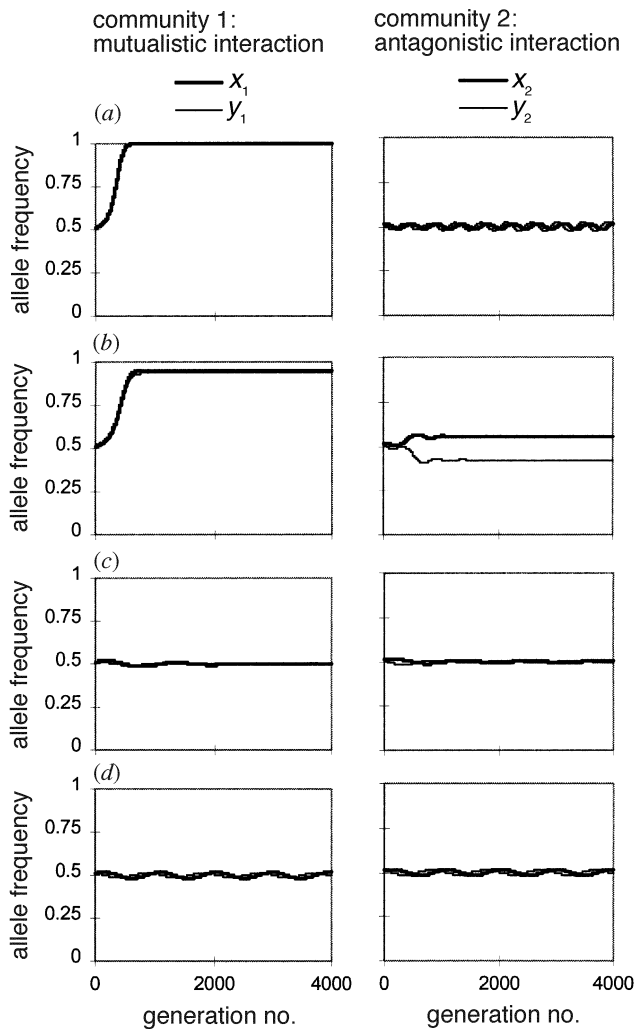


Figure 2. Dynamics of an antagonistic interaction linked through migration to a weaker mutualistic interaction. For this set of simulations, selection for antagonism within one community was twice as strong as selection for mutualism within the other. For all graphs,  $C = 0.02$ ,  $K_M = 0.02$ ,  $K_A = 0.04$  and migration rates between the two communities increase from (a) to (d), with  $m_a = 0$ ,  $m_b = 0.001$ ,  $m_c = 0.015$  and  $m_d = 0.050$ . Although not readily apparent, the amplitude of oscillations in (d) increases with time.

dynamics at  $m = 0$ , followed by a stage in which a novel dynamic occurs within each community (e.g. figures 1b and 2b). In both cases further increases in the migration rate lead to the spread of slightly modified forms of the more strongly selected dynamics across both communities (figures 1d and 2d).

One distinct class of dynamics occurs when selection for mutualism within one interaction outweighs antagonistic selection in the other ( $K_M > K_A$ ; figure 1). Under these conditions, small levels of migration damp allelic oscillations within the antagonistic interaction, relative to  $m = 0$ , while preventing the fixation of matching alleles within the mutualistic interaction (figure 1b). At increased rates of migration, oscillations within the antagonistic interaction disappear, while the expected matching of alleles within the mutualistic interaction is further impaired (figure 1c). These dynamics are associated with the maintenance of limited polymorphism within both interacting species, producing equilibria in which all

alleles are present. Further increases in migration impose essentially mutualistic dynamics upon the antagonistic community, with the matching of alleles occurring despite the nature of local selection (figure 1d). At these high levels of migration, a polymorphism is no longer maintained: equilibria consist of fixed matched alleles within both interacting species.

The second complementary class of coevolutionary dynamics occurs when local selection for antagonism exceeds that for mutualism ( $K_A > K_M$ ; figure 2). As in the case above, low rates of migration damp allelic oscillations within the antagonistic community, relative to  $m = 0$ , while preventing the fixation of matching alleles within the mutualistic community (figure 2b). In this case, however, higher rates of migration lead to damped oscillations within both communities. Allele frequencies converge towards a completely polymorphic equilibrium at which both alleles are present in equal frequencies within both species and communities (figure 2c). If migration is increased further, antagonistic-like dynamics occur in both communities, with increasing allelic oscillations that would ultimately lead to monomorphism in finite populations (figure 2d).

In addition to affecting allele frequency dynamics, the relative strengths of selection for mutualism within one interaction and antagonism within the other create two distinct patterns of equilibria. When the strength of selection for mutualism exceeds that for antagonism ( $K_M > K_A$ ), sufficiently strong migration between communities reduces allelic diversity and leads to the eventual fixation of matching alleles across both communities and species (figure 3a). When selection for antagonism outweighs selection for mutualism ( $K_A > K_M$ ), increased rates of migration between communities produce stable polymorphic equilibria with increased allelic diversity, but, past a critical value of migration, polymorphic equilibria are unstable and allele frequencies oscillate (figure 3b). These patterns suggest that substantial allelic diversity is most likely to be stably maintained at relatively low levels of migration, with higher levels potentially leading to the loss of allelic diversity within finite populations.

We found that qualitatively similar equilibria and patterns of dynamic behaviour occur across a range of selection intensities and rates of migration, with the critical points between dynamic classes being determined by the combination of the relative intensities of local selection and rates of migration. Hence, these general dynamic features may be common to geographically structured interactions where (i) interactions vary from antagonism to mutualism, (ii) relative selection intensities vary among communities, and (iii) migration links communities.

#### 4. STABILITY ANALYSES

We further investigated the effects of population subdivision on the evolution of interactions by performing a local stability analysis of the completely monomorphic equilibria associated with complete allelic matching within both species and across both communities. Our analysis showed that the local stability of this globally fixed mutualism is independent of symbiont sensitivity,

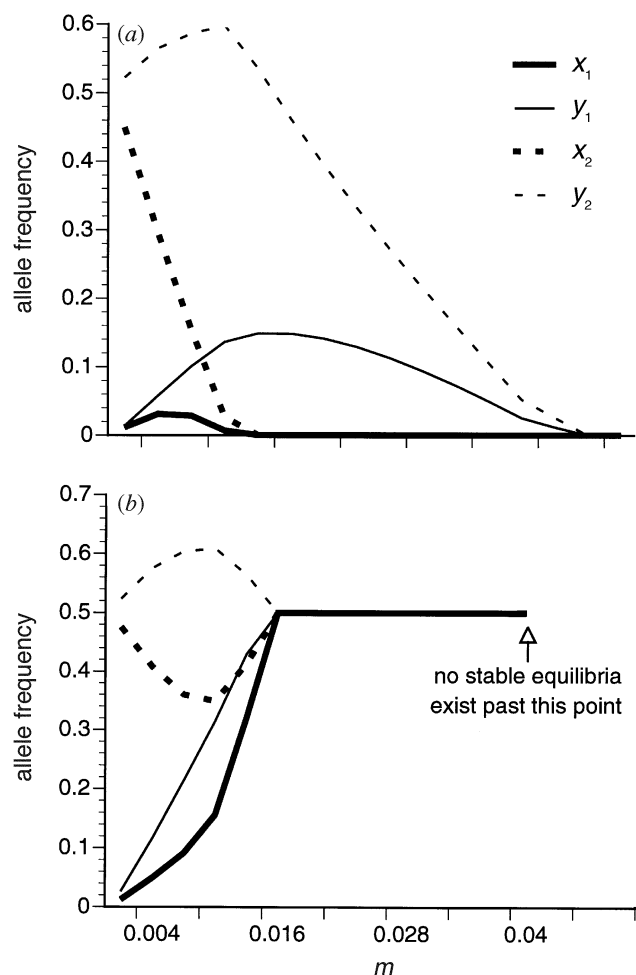


Figure 3. Representative equilibrium allele frequencies of interacting species within both communities graphed as a function of migration. Equilibria were determined through numerical simulations. Regions not plotted are those values of migration for which no equilibria exist. (a) The intensity of selection for mutualism exceeds that for antagonism with  $C = 0.04$ ,  $K_M = 0.04$  and  $K_A = 0.02$ . (b) The intensity of selection for antagonism exceeds that for mutualism with  $C = 0.04$ ,  $K_M = 0.02$  and  $K_A = 0.04$ .

parameter  $C$ , and will persist despite local antagonistic selection within one interaction if  $K_M > K_A$  and

$$m > (K_A \times K_M) / (K_M - K_A). \quad (3)$$

If local selection for antagonism exceeds that for mutualism ( $K_A > K_M$ ), the fixed mutualism is never stable in both communities. This result suggests that a fixed mutualism within both patches can be evolutionarily stable provided the selection intensity for mutualism in one patch exceeds that for antagonism in the other and the rate of migration exceeds the critical level in equation 3 (figure 4).

We also numerically evaluated the local stability of the fully polymorphic equilibrium, in which all alleles are present at equal frequencies. This analysis suggested that the stability of the completely polymorphic equilibrium depends upon all model parameters, including  $C$  and can only be stable if  $|K_A| > K_M$ . Since this holds trivially for values of  $K_M < 0$ , stable polymorphisms are possible even when both communities are antagonistic. Hence, the

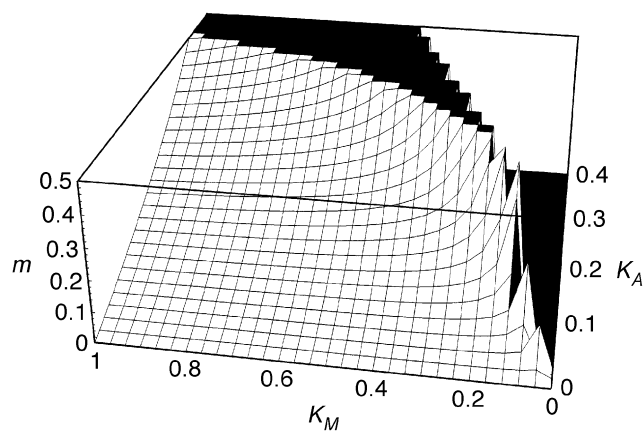


Figure 4. A plot of equation (3) showing the minimum critical level of migration between antagonistic and mutualistic communities consistent with the stability of fixed allelic matching across both communities. The stability of fixed matching was determined analytically by evaluating the local stability of equilibria at which all populations and communities are fixed for the same allele. The graph depicts the rate of migration ( $m$ ) necessary to maintain local stability of the system as a function of the selection constants  $K_M$  and  $K_A$ . Regions of the graph plotted in black cannot result in the stability of the fixed mutualism for any biologically plausible values of migration.

range of conditions in which a stable polymorphism may be maintained within subdivided interactions linked through migration may be enhanced when antagonistic selection within one patch outweighs mutualistic selection within the other. Furthermore, the scope for maintaining a stable polymorphism within subdivided antagonistic interactions may be greatly enhanced through migration between communities.

## 5. CONCLUSION

Overall, our analyses indicate that geographical structuring of interactions with gene flow can have strong effects on the coevolutionary dynamics of interacting species. The results of this model also demonstrate that the addition of geographical structure may play an important role in maintaining allelic polymorphisms within interacting species, particularly at low levels of migration. Moreover, the results show that migration between communities can produce local evolutionary dynamics and equilibria which bear little resemblance to those that would be predicted from patterns of local selection. The result can sometimes be local maladaptation of interacting species as suggested by the geographic mosaic theory of coevolution (Thompson 1994, 1997). These dynamics and equilibria occur for a broad range of values of selection and migration, indicating that such phenomena could be common in natural systems. Furthermore, the results of this study indicate that the evolutionary stability of a fixed mutualism may be strongly influenced by geographical structure and gene flow, with stability possible even in the face of local antagonism.

The diversity of our results is striking given the numerous simplifying assumptions of our model and suggest that further investigation into more complicated

models that incorporate diploidy, multiple populations, and ecological dynamics may prove fruitful. Taken together with recent results from analyses of other more spatially complex models (Gandon *et al.* 1996; Antonovics *et al.* 1997; Hochberg & Van Baalen 1998), our results suggest that empirical studies focusing only on local communities—or, at the other extreme, on entire species—are likely to underestimate or even misinterpret the biological causes of geographically structured coevolutionary dynamics.

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