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Gene flow and metacommunity arrangement affects coevolutionary dynamics at the mutualism–antagonism interface

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Interspecific interactions are affected by community context and, as a consequence, show spatial variation in magnitude and sign. The selective forces imposed by interactions at the mutualism–antagonism interface are a consequence of the traits involved and their matching between species. If mutualistic and antagonistic communities are linked by gene flow, coevolution between a pair of interacting species is influenced by how selection varies in space. Here we investigate the effects of metacommunity arrangement, i.e. patterns of connection between communities and the number of communities, on the coevolutionary dynamics between two species for which the sign and magnitude of the interaction varies across the landscape. We quantify coevolutionary outcome as an index that can be decomposed into the contribution of intraspecific genetic diversity and interspecific interaction. We show that polymorphisms and mismatches are an expected outcome, which is influenced by spatial structure, interaction strength and the degree of gene flow. The index describes how variation is distributed within and between species, and provides information on the directionality of the mismatches and polymorphisms. Finally, we argue that depending on metacommunity arrangement, some communities have disproportionate roles in maintaining genetic diversity, with implications for the coevolution of interacting species in a fragmented landscape.

1. Introduction

Species interact in diverse ways [1] and the same interacting species can show spatial or temporal variation in the nature of their interaction [2]. The outcome of interspecies interactions is a consequence of community context, being affected by abiotic and biotic factors, and mutualistic interactions appear to be particularly sensitive to context [3–5]. These factors change the balance between the costs and benefits of interactions resulting in among-community variation in both the sign and magnitude of interaction. In ant–plant symbiosis, myrmecophytic plants (*Cordia nodosa*) provide housing and food for ants (*Allomerus octoarticulatus*) in exchange for protection against herbivores and the density of herbivores determines the costs and benefits of this mutualistic interaction [4]. When herbivore density is low, the costs of housing and feeding the ants exceed the benefits provided by their protection against herbivores and hence the interaction becomes antagonistic for the plant. In a similar fashion, the mutualism between the Caribbean cleaning gobbies (*Elacatinus evelynae*) and their client longfin

damselfish (*Stegastes diencaeus*) is influenced by the amount of ectoparasites [5]. When ectoparasite load is low, Caribbean cleaning gobbies consume longfin demselfish tissues, such as scales and mucus, increasing the costs of the interaction and hence changing its sign to antagonistic for the client species [5]. In both cases, geographical variation in density of herbivores and ectoparasites will result in spatial variation in the outcome of the interaction.

Interacting species often vary in their geographical distribution and degree of overlap [6]. As a consequence, fitness landscapes can vary across the species geographical range, creating selection mosaics [7,8]. The selective forces imposed by species interactions, which is a consequence of the traits involved in the process, lead to reciprocal changes in the species, i.e. coevolution [9]. Coevolution and selection mosaics result in patterns of local adaptation between species [10]. These patterns, however, can be homogenized by the effects of gene flow between communities [11]. As a result, the geographical structure of interacting species along with processes acting in a local scale exert a central role in coevolutionary dynamics [12]. Hence unravelling the effects of evolutionary forces, such as gene flow and local selection, is crucial to understanding how coevolution will proceed.

Metacommunity theory is a useful framework for studying the effects of the geographical distribution of species and gene flow on population dynamics [13–15]. Here, we take advantage of the spatial aspect of metacommunity theory and integrate it with a coevolutionary model to investigate the role of metacommunity arrangement in the coevolution between two species for which the sign of interaction varies in space. We define metacommunity arrangement as the patterns of connections (i.e. gene flow) between communities and the size of the metacommunity (number of patches within the landscape). Our main goal is to determine how coevolution at the interface between mutualism and antagonism is affected by different spatial configurations and magnitudes of gene flow. To this end, we asked the following questions: (i) how does metacommunity arrangement determine the outcome of coevolution between a pair of interacting species? and (ii) how does among-community variation in selective forces affect coevolution? In order to address these questions, we propose a coevolutionary index to quantify the degree of allele matching between species. This index has the convenience of being partitioned into two meaningful components: genetic diversity within species and interaction matching between species. We show that polymorphism and mismatches are a common outcome of coevolutionary dynamics even when mutualism is stronger than antagonism. In star-shaped metacommunities the allele frequency distribution, as measured by the coevolutionary index, is dominated by the central community but is also strongly influenced by antagonistic interactions even if they are peripheral, depending on the intensity of gene flow. Our results highlight the importance of geographical mosaics when making predictions about coevolutionary dynamics in fragmented landscapes.

2. Methods

We used a matching allele model to describe the interaction between two coevolving species [16,17]. Owing to its simplicity, this model allows the analysis of situations that are relevant to the study of coevolution. It has, for example, provided insight into how coevolution is affected by reciprocal selection between

communities [18], the effect of a third species on a pairwise interaction [19], and the location of coevolutionary hotspots and coldspots [14]. In this model, each community is constituted of a pair of haploid species and the interaction between species is governed by a single locus with two alleles in each species. The 'symbiont species' (e.g. ant species, cleaner fish, pollinator) S_1 has alleles A and a, with x_i denoting the frequency of allele A in community i. The 'host species' (e.g. myrmecophytic plant, client fish, pollinated plant) S_2 has alleles B and b, with y_i denoting the frequency of B in community i. Generations are discrete, gene flow between communities involves both species and selection occurs after gene flow. Simulations were run for 4000 generations and, because the model is deterministic, one run for each set of parameter combination provides the resulting dynamics for that particular combination. Species can interact either mutualistically or antagonistically and the type of the interaction is fixed for each community. The effect of the interaction on fitness is modelled as a linear function [18]

$$W_{A,i} = 1 + Cy_i \tag{2.1}$$

$$W_{a,i} = 1 + C(1 - y_i) \tag{2.2}$$

$$W_{B,i} = 1 + \kappa_i x_i \tag{2.3}$$

and

$$W_{b,i} = 1 + \kappa_i(1 - x_i), \tag{2.4}$$

where $W_{\alpha,i}$ is the fitness of an individual carrying the allele $\alpha = (A, a, B, b)$ in community i, C is the effect of the interaction on species S_1 (that always benefits from the interaction) and κ_i is the effect of the interaction on species S_2 (that can be either positively or negatively affected by the interaction) in community i. C is always positive whereas κ_i can vary from positive (when the outcome of the interaction is mutualistic for species S_2) to negative (when the outcome of the interaction is antagonistic for species S_2). Communities are classified as mutualistic ($\kappa_i = \kappa_{\mathrm{mut}}$) when the interaction benefits both species, and antagonistic ($\kappa_i = \kappa_{\mathrm{ant}}$) when one of the species suffers a decrease in its fitness as a consequence of the interaction. As the type of interaction is fixed for each community, individuals are subject to the local pattern of selection. Communities are linked by gene flow and gene flow rates are fixed for the whole metacommunity but the number of migrants sent to neighbouring communities varies as a consequence of community sizes. We recorded changes in allele frequencies through time within each community. The allele frequencies after gene flow (represented by x^* and y^*) are given by

$$x_i^* = \frac{x_i e^{-md_i} + \sum_{j=1}^{d_i} (x_j(1 - e^{-md_j})N_j/N_id_j)}{e^{-md_i} + \sum_{j=1}^{d_i} ((1 - e^{-md_j})N_j/N_id_j)} \tag{2.5}$$

and

$$y_i^* = \frac{y_i e^{-md_i} + \sum_{j=1}^{d_i} (y_j(1 - e^{-md_j})N_j/N_id_j)}{e^{-md_i} + \sum_{j=1}^{d_i} ((1 - e^{-md_j})N_j/N_id_j)}, \tag{2.6}$$

where d_i is the degree of community i, i.e. the number of neighbouring communities with which community i exchanges individuals. When gene flow (m) is zero, communities are isolated and dynamics occur only within each local community. The term $x_i e^{-md_i}$ represents the proportion of individuals that remain in community i. For $d_i = 1$ and small values of m, the exponential form is equivalent to $x_i(1 - m)$ [18]. $x_j(1 - e^{-md_j})$ represents gene flow from the j community and for $d_j = 1$ and small values of m, the exponential form is equivalent to x_jm [18]. N_i and N_j are the size of community i and community j, respectively. The same applies to y_i.

The allele frequency at the subsequent generation is given by the allele frequency within each community after gene flow and selection:
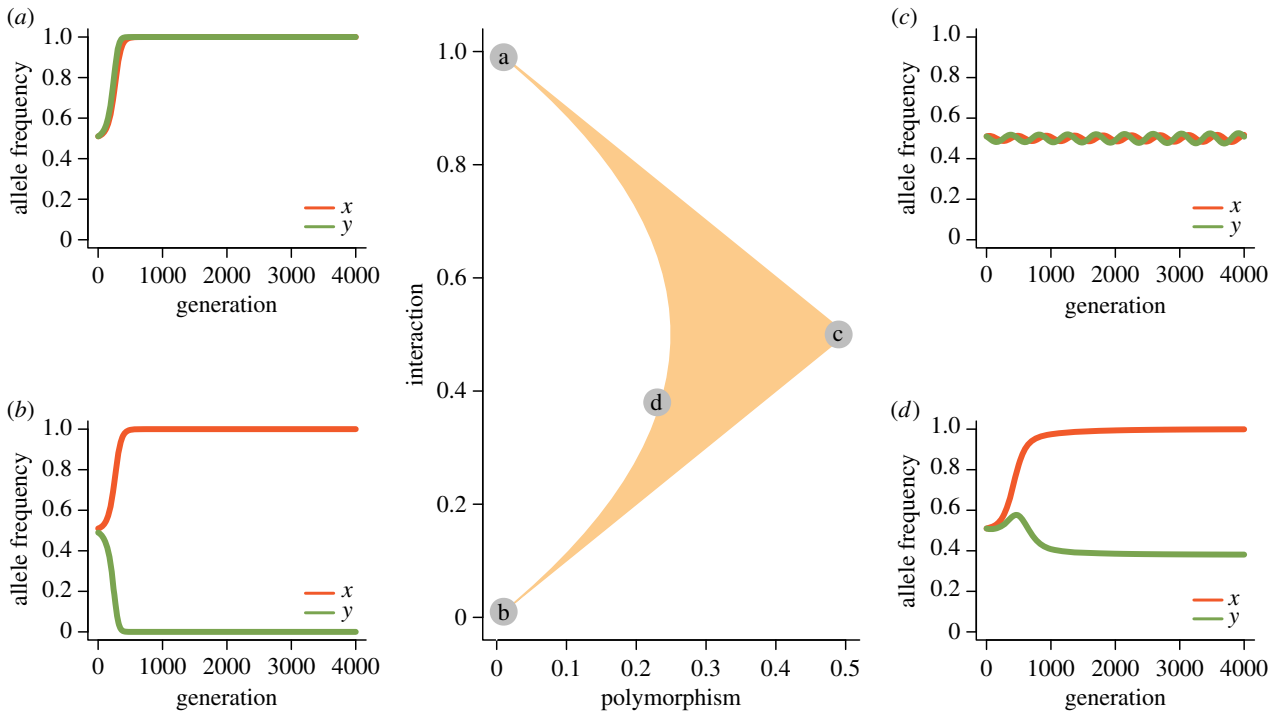
Figure 1. Parametric plot (central panel) showing where different dynamic outputs are located within the parametric space (shaded area in the central graph) as defined by equations (2.9)–(2.11) and corresponds to all possible combinations of allele frequencies x and y (or polymorphism P and interaction I). Each axis represents a component of the coevolutionary index. The upper diagonal boundary connecting points a and c corresponds to $x = y$ whereas the lower diagonal connecting points b and c corresponds to $x = 1 - y$; along the curved line connecting a and b $x = 1$ (see the electronic supplementary material). (*a*) Example of model output showing an isolated mutualistic community ($m = 0$) with fixation of matching alleles for both species. Both species receive a benefit from interaction with $\kappa_{mut} = 0.02$ and $C = 0.02$. In this scenario, interaction between species is maximum and polymorphism is minimum. x is the frequency of allele A from species S_1; y is the frequency of allele B from species S_2. (*b*) Output with fixation of non-matching alleles. For this scenario, both interaction and polymorphism are minimum and species interact competitively $C = -0.02$ and $\kappa_{ant} = -0.02$. (*c*) Output showing an isolated antagonistic community with oscillation of alleles. The interaction benefits one species while decreasing the fitness of the other species ($\kappa_{ant} = -0.02$ and $C = 0.02$). In this scenario, interaction assumes an intermediate value and polymorphism is maximum. (*d*) Output of an antagonistic community connected to a mutualistic community by gene flow of $m = 0.01$ per generation ($C = 0.02$, $\kappa_{mut} = 0.04$ and $\kappa_{ant} = -0.02$). For this scenario, allele A from species S_1 is fixed and species S_2 remains polymorphic.

$$x_i(n + 1) = \frac{x_i^*(W_{A,i})}{x_i^*(W_{A,i}) + (1 - x_i^*)W_{a,i}} \quad (2.7)$$

and

$$y_i(n + 1) = \frac{y_i^*(W_{B,i})}{y_i^*(W_{B,i}) + (1 - y_i^*)W_{b,i}}. \quad (2.8)$$

2.1. Quantifying the coevolutionary outcome

The mismatch between two interacting species can be quantified as the difference between the values of traits involved in the interaction [20]. In a simplistic way, the traits determining the interaction can be described as alleles and interaction is defined as matching alleles [21]. In this case, the mismatch between a pair of interacting species is estimated as the absolute difference between allele frequencies $\delta = |x - y|$ [18]. Here, we propose a metric similar to $(1 - \delta)$, which is the degree of matching, that has the advantage of being decomposable into two simple expressions related to a species's genetic diversity and the probability of individuals finding an interaction partner. We define

$$\phi = 1 - \delta^2 \quad (2.9)$$

$$= 1 - (x - y)^2 \quad (2.10)$$

$$= \underbrace{x(1 - x) + y(1 - y)}_{\text{polymorphism }(P)} + \underbrace{xy + (1 - x)(1 - y)}_{\text{interaction }(I)}. \quad (2.11)$$

The choice of $(1 - \delta^2)$ instead of $(1 - \delta)$ is clear from the relation $\phi = P + I$. The first component, $P = x(1 - x) + y(1 - y)$, refers to the sum of the degree of polymorphism within each

species, where x is the frequency of allele A, and $(1 - x)$ is the frequency of allele a in species S_1; y is the frequency of allele B, and $(1 - y)$ is the frequency of allele b in species S_2. P ranges from 0, when all individuals in the population share the same allele, to 0.5, when half of the population carries one allele while the other half carries the other allele.

The second component of the metric, $I = xy + (1 - x)(1 - y)$, refers to the interaction between species and ranges from 0 to 1. Considering a matching allele model, allele A in species S_1 matches allele B in species S_2, and xy indicates the matching between these two alleles given their frequencies. The same applies to allele a in species S_1 and allele b in species S_2. I is maximum (equal to 1) when both species have the matching alleles fixed, so that all individuals would find a suitable partner to interact with. When polymorphism is maximum in both species ($P = 0.5$), individuals have a 50% chance of finding a suitable partner in a random encounter and $I = 0.5$. If one allele is fixed in one species and the non-complementary allele is fixed in the other species, there is no interaction and $I = 0$.

The coevolutionary index ϕ is calculated for each community, ranges from zero to one, and can be thought of as a matching index that incorporates intraspecific polymorphism and interspecific interaction. The metric is equal to 1 both for 'pure' mutualism (fixation of matching alleles) and for 'pure' antagonism (maximum polymorphism), which is the theoretical expectation of a coevolving pair of interacting species within a mutualistic or antagonistic isolated community (figure 1). However, the relative contribution from each component of the metric (different axes on central panel of figure 1) allows the distinction between these two scenarios.

2.2. Parameters and structure of metacommunity

We investigated metacommunity structure using a star-like network, with a central community connected to peripheral ones. Nodes represent communities and links represent gene flow between communities [13,14]. Both species are assumed to occur in every community and the strength of interaction is assumed to be the same for all peripheral communities. The sign of interaction (mutualistic versus antagonistic) within each community was fixed for each simulation. Therefore, regardless the number of patches, there were only two values of interaction strength in each case: κ_{ant} in antagonistic communities and κ_{mut} in mutualistic communities. Our goal was to unravel the role of increasing the number of peripheral communities on the coevolutionary process. We investigated scenarios where the effects of antagonism and mutualism had equal strength ($C = |\kappa_i| = 0.02$) and scenarios where interactions were asymmetric ($|\kappa_i| = 0.02$ in the central community and $|\kappa_i| = 0.04, 0.06, 0.08$ or 0.1 in the peripheral communities). As we expect the central community to have a larger effect on the dynamics, when interaction strength was asymmetric we always assigned the lower $|\kappa_i|$ to the central community. For instance, when the central community was mutualistic, the strength of mutualism was $\kappa_{mut} = 0.02$, whereas when the central community was antagonistic, $\kappa_{ant} = -0.02$.

The effect of initial allele frequencies was investigated with a set of simulations to evaluate if the outcome depends strongly on initial conditions (see the electronic supplementary material). These simulations indicate that initial allele frequencies can alter the result for isolated communities ($m = 0$), as expected, but small rates of gene flow ($m < 0.006$) are sufficient to synchronize all communities. For this reason, we standardize the initial conditions of allele frequencies as $x_i = 0.51$ and $y_i = 0.51$, which also represents a value close to a fixed point ($x = 0.5$, $y = 0.5$) of isolated antagonistic communities [17,18]. The magnitude of gene flow ranged from $m = 0$ to $m = 0.1$, at steps of 0.002. The following number of neighbouring communities were considered: $n = 1, 2, 4, 8$. The relative size of the central community was fixed (N_c) and the sum of the size of all peripheral communities (N_p) was always equal to N_c. Community size influences the amount of gene flow between communities, but we assume that within communities population sizes are large enough to overcome the effect of genetic drift. As a consequence, the stochastic effects due to community size within the communities can be disregarded, because we are interested in the effects of selection in determining changes in allele frequencies over time. In each simulation, we estimated the P and I components of the coevolutionary index (equations (2.9)–(2.11)), using the final allele frequency of each species at the end of the simulation of the dynamical model. Numerical simulations, estimation of coevolutionary index and figures were carried out using R [22].

3. Results

The interplay between the predominant type of interaction, interaction strength, gene flow and spatial structure determines the outcome of coevolution between two species distributed in a metacommunity. The case with two communities ($n = 2$) corresponds to the model proposed in [18] and the model presented here displays the same qualitative outcomes, despite different community sizes and a different migration form. In isolated mutualistic communities, alleles become fixed in both species (figure 1a) whereas in isolated antagonistic communities allele frequencies oscillate around 0.5 in both species (figure 1c). In figure 1, the positions (a) and (c) characterize the genotypic states expected for mutualistic and antagonistic communities, respectively. Fixation of non-matching alleles in both species (figure 1b) is not mathematically possible in our

simulations, because fitness is always positive for one of the species [23]. This condition would require both C and κ_{ant} to be negative. In an antagonistic community connected to a mutualistic community with parameter values of $\kappa_{mut} = 0.04$ and $\kappa_{ant} = -0.02$ and $m = 0.01$, allele A becomes fixed in species S_1 and species S_2 remains polymorphic (figure 1d).

First, we investigated symmetric interaction strengths with mutualism and antagonism having the same effect on fitness (figure 2). For a metacommunity with two patches, as gene flow increases the mutualistic community exhibits genotypic patterns expected by an antagonistic community, with intermediate values of interspecific interaction ($I = 0.5$) and maximum genetic diversity ($P = 0.5$) (figure 2a). As the number of patches in the metacommunity increases, the central community assumes a preferential role. When the central community is antagonistic (figure 2b,d), it always presents high levels of polymorphisms and intermediate values of interspecific interaction regardless of the degree of gene flow. In the peripheral mutualistic communities, low levels of gene flow lead to high polymorphism and intermediate values of interspecific interaction. The higher the number of peripheral patches in the metacommunity, the less gene flow is needed for the peripheral mutualistic communities to reach an antagonistic-like state (right plots of figure 2b,d). Note that the trajectories within the parametric plot follow the upper diagonal boundary (right plots in figure 2b,d) where the frequency of allele A is equal to frequency of allele B and the coevolutionary index assumes its maximum value ($\phi = 1$; electronic supplementary material).

Assigning mutualistic interactions to the central community (figure 2c,e) allows the maintenance of monomorphism in both species when gene flow is high, even when mutualism and antagonism have the same effect on species fitness. For larger values of m, all communities present high interaction and low polymorphism, which is the theoretical expectation for isolated mutualistic communities. As gene flow increases, antagonistic communities become less polymorphic following the trajectory of least possible polymorphism for a given amount of interaction (curved boundary of the diagram in the right plots of figure 2c,e). The trajectories along the curve correspond to the minimum possible coevolving index ϕ for a given distribution of allele frequencies and also to the fixation of allele A in species S_1 while species S_2 remains polymorphic until m is high and allele B becomes fixed.

Interaction asymmetry has an effect similar to increasing spatial structure when interaction strength is symmetric. This similarity is evident when comparing figure 2b,c (metacommunity with three communities, and symmetric interaction strength) with figure 3a,b (metacommunity with two communities and asymmetric interaction strength). For the case of two communities, large gene flow leads to genotypic patterns dominated by the highest $|\kappa_i|$ (figure 3a,b) as reported in previous work [18]. Metacommunities with three patches and asymmetric interaction strengths present different allele distributions. If we assume that mutualistic interactions are stronger than antagonistic interactions ($|\kappa_{mut}| > |\kappa_{ant}|$) and the central community is antagonistic, then within the central community (left plot in figure 3c), small changes in gene flow lead to small changes in outcome, as can be seen by the continuous dots in the parametric plot. As gene flow increases, the central community moves from an antagonistic-like state to a mutualistic-like state, following the curved boundary in the parametric plot (with allele A fixed for species S_1). In the mutualistic peripheral communities (right plot in figure 3c), as gene flow increases,
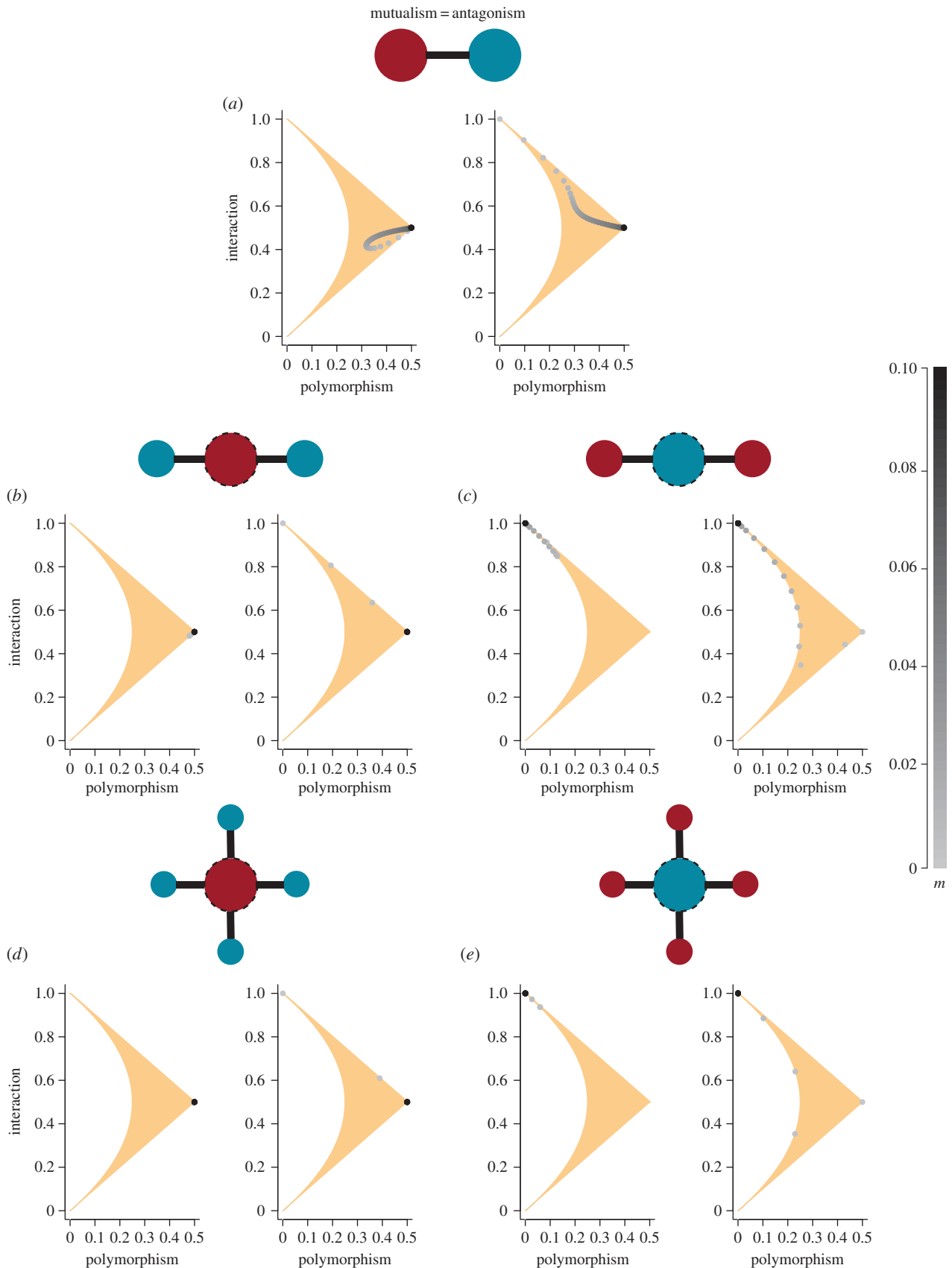
Figure 2. Parametric plots when mutualism and antagonism have the same contribution to species' fitness ($\kappa_{mut} = 0.02$, $\kappa_{ant} = -0.02$ and $C = 0.02$) with increasing gene flow ($m = 0$, light grey to $m = 0.1$ black in the colour scale). Each point represents the value of the coevolutionary index for a given degree of gene flow. (a) Two communities, one antagonistic and one mutualistic connected by gene flow. Parametric plot for the antagonistic community is shown on left side and for the mutualistic community on the right side. (b) Three communities, with a central antagonistic community connected to two peripheral neighbour communities. Left plot represents the central antagonistic community and right plot represents a peripheral mutualistic community. (c) Three communities with a central mutualistic community, connected to two peripheral antagonistic communities. Left plot represents parametric plot in the mutualistic community and right plot in an antagonistic community. (d) Five communities with a central antagonistic community connected to four neighbouring mutualistic communities. Right plot shows parametric plot for the antagonistic community and left plot for a peripheral mutualistic community. (e) Five communities with a central mutualistic community connected to four neighbouring antagonistic communities. Left plot shows parametric plot for the mutualistic community and right plot for an antagonistic community.
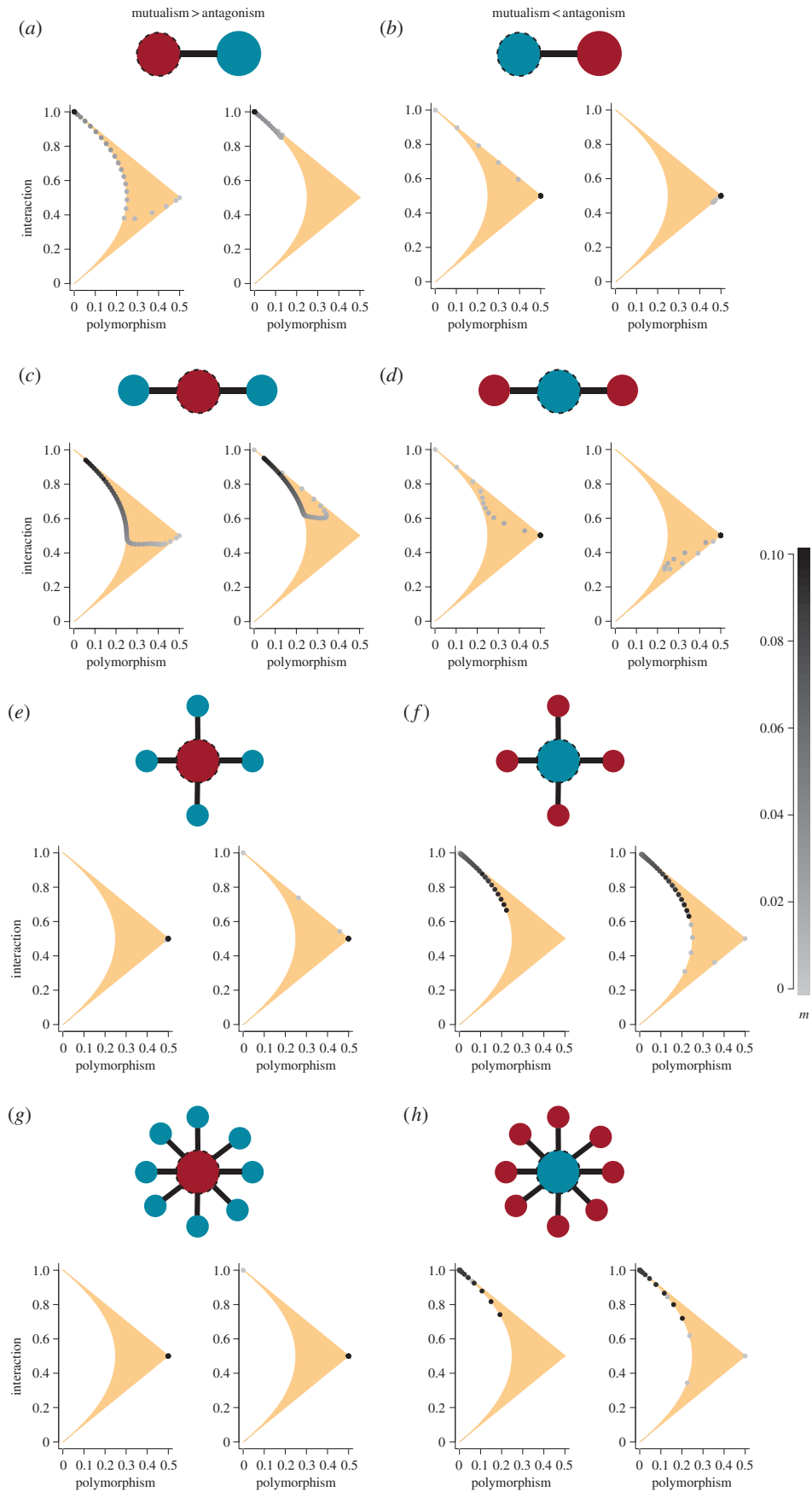
Figure 3. Parametric plots with asymmetric interaction strength and increasing levels of gene flow. In the left column (*a,c,e,g*) mutualism has a higher effect on fitness than antagonism ($\kappa_{mut} = 0.04$ and $\kappa_{ant} = -0.02$) and antagonistic community is in the centre of the metacommunity. Within the left column, the plots in the left are for the antagonistic community and plots in the right are for mutualistic communities. In the right column (*b,d,f,h*) antagonism has a higher effect on species' fitness than mutualism ($\kappa_{mut} = 0.02$ and $\kappa_{ant} = -0.04$) and mutualistic community is in the centre of the metacommunity. Within the right column, the plots in the left are for the mutualistic community and plots in the right are for antagonistic communities. (*a*) Two communities, with mutualism having a higher effect on fitness. (*b*) Two communities, with antagonism having a higher effect on fitness. (*c*) Three communities with a central antagonistic community. (*d*) Three communities with a central mutualistic community. (*e*) Five communities with a central antagonistic community. (*f*) Five communities with a central mutualistic community. (*g*) Nine communities with a central antagonistic community. (*h*) Nine communities with a central mutualistic community.

there is fixation of allele A for species S_1 and the trajectory is the same as the one found in the antagonistic community. For intermediate to high values of gene flow ($m > 0.04$), central antagonistic and peripheral mutualistic communities present the exact same pattern of allele frequencies, and hence share the same values of the coevolutionary index (figure 3c).

When antagonistic interactions are stronger than mutualistic interactions ($|\kappa_{ant}| > |\kappa_{mut}|$) and the central community is mutualistic (left plot in figure 3d), the trajectory from a monomorphic outcome to a polymorphic one in the asymmetric three-patch metacommunity differs from that observed for the two-patch scenario (comparing figure 3b,c). In the peripheral antagonistic community, the trajectory on the lower part of the parametric plot implies a greater difference in allele frequency between species, with the lowest values of the coevolutionary index (right plot in figure 3d). The lower diagonal of the parametric plot corresponds to the greatest mismatch between allele frequencies, and within this region the relation between frequency of allele A and frequency of allele B is given by $x = 1 - y$ (electronic supplementary material). As gene flow increases, the difference between the frequency of alleles A and B decreases, increasing interaction and polymorphism until alleles reach an antagonistic-like state.

Increasing the number of peripheral patches to four or eight enhances the effect of the central community (figure 3e–h). Even with asymmetry in interaction strength, the landscape is dominated by the genotypic patterns found in the central community. When the central community is antagonistic, regardless of the degree of gene flow, within the central community species remain polymorphic and with intermediate values of interspecific interaction. In the mutualistic peripheral communities, very low levels of gene flow are enough to result in an antagonistic-like genotypic pattern (figure 3e,g). When the central community is mutualistic and antagonism has a higher effect on species fitness, low to intermediate levels of gene flow lead the antagonistic communities to the mutualistic-like genotypic state (right plots in figure 3f,h), with fixation of alleles and maximum degree of interespecific interaction. Increasing the number of patches in the metacommunity decreases the amount of gene flow required to cause peripheral communities to display genotypic patterns expected by the interaction sign found in the central community. Nevertheless, when antagonism has a higher effect on fitness, the role of the central mutualistic community is prominent for a narrower range of gene flow. As gene flow increases, polymorphism in species S_2 increases, decreasing interaction and showing a tendency for communities to move to an antagonistic-like state (see video in electronic supplementary material).

Next, we increased interaction asymmetry for metacommunities with four and eight peripheral patches and investigated the critical degree of gene flow for which all communities present genotypic patterns expected by the prevalent interaction strength (figure 4). The higher the interaction asymmetry the less gene flow is needed for the effect of interaction to overcome the disproportionate role of the central patch in determining the outcome (figure 4). This effect is stronger when antagonism has a higher effect on fitness, evidenced by lower values of critical gene flow when the asymmetry favours antagonistic interactions (black points in comparison to grey in figure 4). By contrast, considering the same interaction asymmetry, the bigger the metacommunity, the higher the degree of gene flow needed before the effect of the central metacommunity is overcome (comparing cross and asterisk in figure 4).
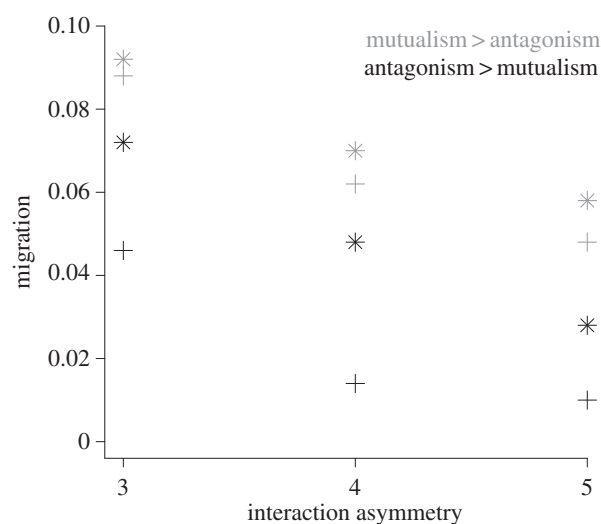

Figure 4. Critical degree of gene flow for which all communities within a metacommunity present genotypical patterns expected by the interaction that influences fitness the most. The x-axis shows the magnitude of interaction asymmetry. Grey colour indicates mutualism having a higher effect on fitness than antagonism ($\kappa_{mut} = 0.06$, $\kappa_{mut} = 0.08$ and $\kappa_{mut} = 0.1$ with $\kappa_{ant} = -0.02$). Black colour indicates antagonism having a higher effect on fitness ($\kappa_{ant} = -0.06$, $\kappa_{ant} = -0.08$ and $\kappa_{ant} = -0.1$ and $\kappa_{mut} = 0.02$). Cross symbol indicates a metacommunity with five communities and asterisk a metacommunity with nine communities.

4. Discussion

We show that the size of the metacommunity, interaction asymmetry and gene flow play a fundamental role in determining coevolutionary dynamics between a pair of interacting species. We describe coevolution in terms of the combined contributions of intraspecific polymorphism and interspecific interaction (figure 1). With respect to how metacommunity arrangement affects coevolution, we found that increasing the number of patches in a metacommunity enhances the influence of the central community in relation to the peripheral ones. As a consequence, the central community swamps the genotypical patterns expected by the process occurring in peripheral communities and the landscape is dominated by the patterns expected by the process found within the central community (figures 2 and 3). However, there is a critical size of the metacommunity for which increasing interaction asymmetry coupled with gene flow reverts the effect of the central community and the final distribution of allele frequencies is given by the predominant pattern of interaction (figure 4). This result indicates how among-community variation in selective forces can play a determining role in coevolutionary dynamics. Taken together our results contribute to the theory of coevolutionary interactions between species in four different ways.

First, the results indicate that mismatches and polymorphisms should be common in most metacommunities, even when the effect of the interaction on fitness is stronger at mutualistic patches than at antagonistic ones. The simplest scenario with a symmetric effect on fitness shows that gene flow within a two-patch metacommunity lead species in both communities to a polymorphic state (figure 2a). Models investigating temporal variable selection found that polymorphisms can persist even when species interaction is predominantly mutualistic over time [24]. Our results point to a similar direction, as the spatial and temporal components have a similar

effect on coevolutionary dynamics [23,25]. Even when mutualism has a higher effect on fitness and a predominant spatial or temporal distribution across the landscape, gene flow between communities with different selection regimes will lead both species to a polymorphic state within mutualistic and antagonistic communities. Complete monomorphism of matching traits should be uncommon in most metacommunities. That does not necessarily mean that mutualisms are uncommon. Rather, it means that there should be a distribution of outcomes even at patches where the interaction is primarily mutualistic. This is commonly seen in nature for multiple reasons. Mutualisms can result in a distribution of outcomes for a few reasons; some individuals are genetically mismatched, some are developmentally mismatched, and some are mismatched for interacting in that particular environment [6,9,26]. Our current model evaluates only genetic effects, mediated through trait mismatching, but it reinforces the view that coevolution of mutualisms or antagonisms is about changes in the proportions of individuals showing weak to strong mutualistic or antagonistic effects in each locality and in the metacommunity [27].

Second, our results suggest that there is an interplay between size of the metacommunity, asymmetry in interaction strength and the rate of gene flow in determining coevolutionary dynamics (figure 3). The spatial structure of a metacommunity is determined by the patterns of connection among communities, and certain topologies favour cascading effects across the landscape, with some communities exerting greater influence on dynamics [13,28]. In metacommunities with a star structure, the central community determines the outcome of coevolutionary dynamics when interaction is symmetric (figure 2*b–e*). For asymmetric interaction strength, we show that spatial structure changes the expectation that the stronger selection will determine the resulting coevolutionary dynamics [14,18,23]. If interaction strength is characterized by a twofold asymmetry, in metacommunities with four or more peripheral communities coevolutionary dynamics will be determined by the central community and not the strongest selective pressure (figure 3*e–h*). However, increasing interaction asymmetry reinforces the role of the strength of selection as well as the spatial predominance of one type of interaction at the metacommunity level, diminishing the effect of the central community, and leading to a coevolutionary outcome predicted by the interaction with stronger effect on fitness (figures 3*a–d* and 4). Asymmetry in interaction strength is a common pattern between partner species [29] and can be a consequence of community context. When scaled up, differences in community context experienced by interacting species lead to spatial variation in the strength of selection [4,30]. Our results highlight the view that there is an optimal spatial scale for the observation of coevolutionary processes that encompasses not only the spatial structure of interacting species but also its interplay with gene flow and the degree of interaction asymmetry [21,30]. We suggest that such asymmetries coupled with the effect of the spatial structure are an important component of the coevolutionary process as predicted in [23].

Third, by describing coevolution between a pair of interacting species as the combined contribution of intraspecific polymorphism and interspecific interaction we gain insights into how different processes can generate trait mismatch within coevolving populations across a landscape and how they change with spatial structure and gene flow. The final distribution of allele frequencies presents predictable patterns within the parametric space with gene flow influencing each component of the metric in a different way depending on the spatial structure of selection. When mutualistic communities are influenced by the effects of antagonism, gene flow increases polymorphism equally in both species, with alleles' frequencies mirrored between matching alleles (trajectories that lie within the upper diagonal). In this scenario, mismatch results from gene flow increasing the degree of polymorphism in both species but maintaining the same distribution of allele frequencies. Gene flow often prevents phenotypic matching between interacting species by two mechanisms: introduction of maladaptive phenotypes or prevention of local adaptation [12,31]. When antagonistic communities are influenced by the effects of mutualism, one species remains polymorphic while the other becomes monomorphic (trajectories that lie within the curved boundary of the parametric plot). In this second scenario, mismatch is caused by fixation of allele in one species ('symbiont') while the other remains polymorphic ('host'), generating asymmetry in trait matching between species. Asymmetric trait matching is a recurring pattern within interacting species [20] and an expected outcome of theoretical coevolutionary models [16,17]. Whether antagonistic communities exert an influence on mutualistic communities or the inverse, increased mismatch is caused by changes in different components of the coevolutionary index. In this sense, describing coevolutionary outcomes using the proposed axis provides predictions regarding the directionality of the mismatches found between coevolving species [20].

Fourth, our results reinforce the role of geographical mosaics for coevolutionary dynamics and the importance of considering these mosaics in making predictions about coevolutionary outcomes in fragmented landscapes. There is an increasing emphasis in conserving functional diversity as well as species diversity, and ecosystem function is often mediated by species interactions [32–34]. Our study shows that some communities have disproportionate roles in maintaining or eliminating genetic and potentially phenotypic diversity. In neutral metacommunities, in which species interact competitively, diversity, in terms of number of species, is maintained by increasing protected area rather than biodiversity representation [35]. If we adapt the concept of protected area to the size of the metacommunity, our results suggest that increasing metacommunity size (protected area) may decrease the diversity of coevolutionary outcomes but retain genetic diversity and therefore future coevolutionary potential amid environmental change. In this sense, contrasting predictions achieved by different modelling approaches improve our understanding of the consequences of habitat fragmentation for the conservation of coevolving species [35]. Depending on the structure of the geographical mosaics, increasing connectivity within a landscape by connecting smaller patches to large patches impacts the conservation of functional diversity, as local patterns of interactions can be swamped by the effect of a larger central reserve. The interplay between connectivity of a landscape and conservation of functional diversity is especially important for mutualistic interactions, as mutualisms inherently present a wide distribution of ecological outcomes and also appear to be more sensitive to the effects of forest fragmentation [34,36]. The challenge is how to maintain coevolving interactions across different scales (locally, regionally and globally) considering geographical mosaics, the homogenizing effects of gene flow and its consequences in maintaining (or eliminating) future coevolutionary potential across a metacommunity.

Finally, our work can serve as a baseline for investigating other community arrangements, alternative migration schemes and initial conditions. For instance, in all our simulations we used the same initial conditions for allele frequencies ($x_i = 0.51$, $y_i = 0.51$), because our goal was to investigate the role of metacommunity arrangement on the simplest scenario. This choice represents a value close to the polymorphic unstable fixed point of $x_i = 0.5$, $y_i = 0.5$ and also leads to the smallest amplitude oscillations in the antagonistic isolated community (see electronic supplementary material, figures S2 and S3). Initial conditions can influence the dynamical behaviour of isolated coevolutionary systems and increase oscillation amplitude [17], thus using different initial conditions for different communities can lead to oscillations of larger amplitudes. Our results suggest that gene flow and metacommunity arrangement have the potential to influence the amplitude of allelic cycles and/or the synchronization of allele frequencies between sites. Such larger amplitudes and synchronization can give rise to richer dynamics when combined with variation in spatial structure.

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