Coevolução em redes mutualistas: fluxo gênico e mosaicos de seleção

Coevolution in mutualistic networks: gene flow and selection mosaics

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Prof. Dr. Paulo Roberto Guimarães Junior
(Orientador)
Ao meu avô Geraldo,
por me inspirar a ser cientista
"Hence, between the vast, macroscopic systems for which universal laws hold sway and the simple systems that can be analyzed using the fundamental laws of nature, there is a substantial middle ground of systems that are too complex for fundamental analysis but too simple to be universal — plenty of room, in short, for all the complexities of life as we know it."

Terence Tao
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Interações ecológicas como predação, competição e mutualismo são importantes forças que influenciam a evolução de espécies. Chamamos de coevolução a mudança evolutiva recíproca em espécies que interagem. A Teoria do Mosaico Geográfico da Coevolução (TMGC) fornece um arcabouço teórico para entender como conjuntos de populações coevoluem ao longo do espaço. Dois aspectos fundamentais da TMGC são o fluxo gênico entre populações e a presença de mosaicos de seleção, isto é, conjuntos de locais com regimes de seleção particulares. Diversos estudos exploraram como o acoplamento entre fenótipos de diferentes espécies evolui em pares ou pequenos grupos de espécies. Entretanto, interações ecológicas frequentemente formam grandes redes que conectam dezenas de espécies presentes em uma comunidade. Em redes de mutualismos, por exemplo, a organização das interações pode influenciar processos ecológicos e evolutivos. Um próximo passo para a compreensão do processo coevolutivo consiste em investigar como aspectos da TMGC influenciam a evolução de espécies em redes de interações. Nesta dissertação, tentamos preencher esta lacuna usando um modelo matemático de coevolução, ferramentas de redes complexas e informação sobre redes mutualistas empíricas. Nossas simulações numéricas do modelo coevolutivo apontam para três principais conclusões. Primeiro, o fluxo gênico influencia os padrões fenotípicos gerados por coevolução e pode favorecer a emergência de acoplamento fenotípico entre espécies dependendo do mosaico de seleção. Segundo, a organização de redes mutualistas influi na coevolução, mas este efeito pode desaparecer quando o fluxo gênico favorece acoplamento fenotipico. Mutualismos íntimos, como proteção de plantas hospedeiras por formigas, formam redes pequenas e compartimentalizadas que geram um maior acoplamento fenotípico do que as redes grandes e aninhadas típicas de mutualismos entre espécies de vida livre, como polinização. Por fim, a fragmentação de habitat, ao extinguir o fluxo gênico, pode reduzir as adaptações recíprocas entre espécies e ao mesmo tempo tornar cada espécie mais adaptada ao seu ambiente abiótico local. Em suma, mostramos que interações complexas entre fluxo gênico, estrutura geográfica da seleção e organização de redes ecológicas moldam a evolução de grandes grupos de espécies. Dessa forma, podemos traçar previsões sobre como impactos ambientais como a fragmentação de habitat irão alterar a evolução de interações ecológicas.
Abstract

Ecological interactions such as predation, competition, and mutualism are important forces that influence species evolution. Coevolution is defined as reciprocal evolutionary change in interacting species. The Geographic Mosaic Theory of Coevolution (GMTC) provides a theoretical framework to explain how collections of populations should coevolve across space. Two fundamental aspects of the GMTC are gene flow among populations and the presence of selection mosaics, which are collections of localities with particular selection regimes. Several studies have explored how phenotypic trait matching between species evolves in pairs or small groups of species. However, ecological interactions frequently form large networks that connect dozens of species present in a given community. In networks of mutualisms, for instance, the organization of interactions may affect ecological and evolutionary processes. A next step in understanding the coevolutionary process is to investigate how aspects of the GMTC affect the evolution of species embedded in interaction networks. In this dissertation, we tried to fill this gap using a mathematical model of coevolution, complex networks tools, and information on empirical mutualistic networks. Our numerical simulations of the coevolutionary model allow us to draw three main conclusions. First, gene flow affects trait patterns generated by coevolution and may favor the emergence of trait matching depending on the selection mosaic. Second, the organization of mutualistic networks influences coevolution, but this effect may vanish when gene flow favors trait matching. Intimate mutualisms, such as protection of host plants by ants, form small and compartmentalized networks that generate higher trait matching than large and nested networks typical of mutualisms among free-living species, such as pollination. Third, habitat fragmentation resulting in the disruption of gene flow should reduce the reciprocal adaptations between interacting species and at the same time promote adaptations to the local abiotic environment. In conclusion, we show that a complex interplay between gene flow, the geographic structure of selection, and the organization of ecological networks shapes the evolution of large groups of species. Our results therefore allow predictions of how environmental impacts such as habitat fragmentation will modify the evolution of species interactions.
Gene flow and selection mosaics shape coevolution in mutualistic networks

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Statement of authorship: LPM and PRG conceived and designed the study. LPM and PRG developed the mathematical model. LPM conducted the numerical simulations and analyses. LPM wrote the manuscript with substantial input from PRG.
Abstract

Coevolution is considered a major force shaping the traits of interacting species. Processes of the geographic mosaic of coevolution such as gene flow and selection mosaics have been shown to be of central importance for coevolution. Furthermore, work on multispecies coevolution show that additional interacting species may dramatically alter pairwise coevolution. However, the specific roles of the geographic mosaic of coevolution in species-rich systems are largely unexplored. Here, we fill this gap for mutualisms by combining a mathematical model of coevolution, network tools, and information on empirical mutualistic networks to investigate how gene flow and selection mosaics affect trait patterns generated by coevolution. Our simulation results allow us to draw three main conclusions. First, gene flow affects trait patterns generated by coevolution and may favor the emergence of trait matching depending on the selection mosaic. Second, the network structure of different mutualisms affects coevolution in distinct ways, but the effect of network structure may vanish when gene flow favors trait matching. Third, habitat fragmentation resulting in the disruption of gene flow should reduce the coadaptations between mutualistic partners and promote adaptations to the local abiotic environment. This set of results provides clear predictions of how the geographic mosaic shapes species-rich interactions often considered diffuse and how the widespread fragmentation of natural landscapes may modify the coevolutionary process.
Introduction

Ecological interactions among species constitute one of major forces organizing the Earth’s biodiversity (Thompson 2005). Interacting species may influence each other’s population dynamics (Krebs et al. 1995; Frederickson & Gordon 2009), phenotypic trait evolution (Grant & Grant 2006; Gervasi & Schiestl 2017), and diversification dynamics (Ramírez et al. 2011; Silvestro et al. 2015). When two interacting species exert selection upon each other such reciprocal selection may lead to coevolution, the reciprocal evolutionary change between interacting species. An extensive amount of research has shown that coevolution is capable of producing adaptation and coadaptation in interacting pairs of species via a variety of dynamics (Thompson 2005). In the last few decades, coevolutionary research has broaden its scope to embrace the notion that the majority of interacting pairs of species co-occur at several distinct localities and are often embedded in even larger interacting assemblages (Iwao & Rausher 1997; Thompson & Cunningham 2002; Strauss & Irwin 2004; Benkman et al. 2013; Newman et al. 2014). Unraveling this geographical and ecological complexity of the coevolutionary process constitutes a major challenge at the interface of ecology and evolution (Thompson 2009).

Spatial processes such as gene flow and metapopulation dynamics connect populations from the same species that are subject to distinct local evolutionary forces and may alter evolutionary dynamics in profound ways (Gandon 2002; Lenormand 2002). Gene flow, for instance, may either preclude phenotypic differentiation between different populations or promote adaptive evolution by increasing local genetic variation (Hendry & Taylor 2004; Fitzpatrick et al. 2015). The processes and patterns involved in the coevolution of connected populations across landscapes has been organized by the Geographic Mosaic Theory of Coevolution (GMTC; Thompson 2005). Central to the GMTC is the concept of a selection mosaic, which is a collection of localities exhibiting particular selection regimes for interacting species. In particular, two kinds of regimes constitute the core of selection mosaics: (i) hotspots, in which selection is reciprocal between interacting species and (ii) coldspots, in which at least one of the species is not under selection imposed by the other species. Selection mosaics are usually associated with variation in community context as has been estimated for a wide range of interactions including pollinating seed parasites and plants (Thompson & Cunningham 2002), seed-eating birds and
conifers (Benkman et al. 2003), protective ants and plants with extrafloral nectaries (Rudgers & Strauss 2004), and plants with both herbivores and pollinators (Gómez et al. 2009).

The combination of selection mosaics, hotspots and coldspots, and processes that remix species traits across space such as gene flow may lead to differentiation among populations in the traits mediating the interaction and to trait mismatching in some localities (Thompson 2005). We now know that geographical variation in traits and trait mismatching in pairwise interactions emerge as a result of one or more processes of the GMTC (Anderson & Johnson 2008; Hanifin et al. 2008). A next step to further understand the coevolutionary process is to investigate how trait matching and mismatching are distributed across a landscape for species-rich assemblages. In this sense, quantitative tools that deal with multiple selection pressures acting on species embedded in large ecological assemblages are needed to improve our understanding of coevolution in a spatial context.

Network theory provides tools to investigate the organization of interactions and the ecological and evolutionary dynamics of species-rich assemblages (Jordano 1987; Thompson 2005; Ings et al. 2009). Particular interest has been devoted to mutualisms, which frequently form small to large networks that connect the species present at a given community (Bascompte & Jordano 2014). Such mutualistic networks greatly vary in the organization of interactions depending on the degree of physiological integration as well as physical and trophic dependence between interacting partners (i.e. the interaction intimacy; Ollerton 2006; Guimarães et al. 2007a; Fontaine et al. 2011). Mutualisms with low interaction intimacy (hereafter low-intimacy mutualisms) such as seed dispersal by fruiting-eating vertebrates generate large networks with high heterogeneity in the number of partners of different species (Jordano 1987; Bascompte et al. 2003; Guimarães et al. 2007b). On the other hand, mutualisms with high interaction intimacy (hereafter high-intimacy mutualisms) such as the protection of host plants (myrmecophytes) by defensive ants are characterized by small networks with semi-isolated groups of interacting species (Fonseca & Ganade 1996; Ricciardi et al. 2010; Dáttilo et al. 2013b). Such differences in network architecture indicate that different ecological and evolutionary processes shape patterns of interaction at the community level in different mutualisms (Blüthgen et al. 2007; Guimarães et al. 2007a; Raimundo et al. 2014).
The evolution of species traits in mutualistic networks has only been explicitly investigated in a handful of theoretical studies (Santamaría & Rodríguez-Gironés 2007; Loeuille 2010; Guimarães et al. 2011; Nuismer et al. 2013). When coevolutionary selection is based on trait complementarity such as the match between a plant’s corolla and a pollinating hummingbird’s bill, trait complementarity and trait convergence (i.e. trait similarity in unrelated species) increase in mutualistic networks (Guimarães et al. 2011). Furthermore, super-generalist species that interact with a disproportionate number of other species modify the network structure and fuel the emergence of trait complementarity and trait convergence (Guimarães et al. 2011). Nevertheless, the emergence of these trait patterns may depend on the strength and type of mutualistic selection (Nuismer et al. 2013). Because Guimarães et al. (2011) and Nuismer et al. (2013) only explored pollination and seed-dispersal networks, one question that remains unanswered is whether networks formed by high-intimacy mutualisms would promote similar coevolutionary dynamics. It is unclear, for example, whether the reciprocal specialization between species within semi-isolated groups in high-intimacy mutualisms should favor higher levels of trait matching than the centralization promoted by generalist species in low-intimacy mutualisms.

Given that ecological networks often show spatial variation in species composition and structural aspects (Dáttilo et al. 2013a; Carstensen et al. 2014; Gilarranz et al. 2015; Trojelsgaard et al. 2015), it is expected that selection should greatly vary at different localities. It is also expected that spatial processes will be even more crucial for the ecology and evolution of multispecies systems with the widespread habitat fragmentation driven by human action (Hagen et al. 2012; Cheptou et al. 2017). Across a given landscape with several mutualistic networks, coevolution should generate higher levels of trait matching at localities where mutualism is an important selection pressure (i.e. hotspots) than at localities where other biotic or abiotic factors exert greater selection (i.e. coldspots; Fig. 1a). Additionally, it is reasonable to expect that gene flow should homogenize species traits across the landscape (Fig. 1b). However, understanding how the interplay between gene flow, selection mosaics, and multiple selection pressures shapes trait matching patterns at different localities is a current major challenge for coevolutionary research.
In this study, we bridge the conceptual framework of the GMTC with ecological network theory to understand how species coevolve in multispecies ecological assemblages across landscapes. We combined a mathematical model of single-trait evolution, network tools, and a comprehensive dataset of empirical networks to investigate the effects of gene flow and selection mosaics on network- and species-level trait patterns generated by coevolution. We concentrated on three central questions: (i) How does gene flow and geographical variation in the selection imposed by mutualism affect the trait matching between interacting species generated by coevolution? (ii) How does the network structure of different kinds of mutualisms mediate the coevolutionary effects of gene flow and geographical variation in the selection imposed by mutualism? (iii) What are the coevolutionary consequences of habitat fragmentation that results in the disruption of gene flow to the adaptation of species to their mutualistic partners and to their local environment?

Material and methods

Dataset

Our dataset consisted of 72 empirical mutualistic networks, which represent the recorded interactions between species at a given locality through extensive fieldwork (Table S1). Our dataset had a broad geographic and taxonomic span and included eight types of mutualisms. These types of mutualisms can be divided in two broad categories according to their degree of interaction intimacy (Ollerton 2006; Guimarães et al. 2007a; Fontaine et al. 2011; Raimundo et al. 2014). First, high-intimacy mutualisms: (i) anemones that protect anemonefishes (n = 11 networks) and (ii) ants that protect their host plants, the myrmecophytes (n = 8). Second, low-intimacy mutualisms: (iii) ants that protect plants with extrafloral nectaries (EFN; n = 5), (iv) insects and vertebrates that pollinate flowering plants (n = 28), (v) fruit-eating vertebrates that disperse the seeds of plants with fleshy fruits (n = 17), and (vi) fishes and shrimps that clean client fishes (n = 3). The majority of networks is published and available online as described in Table S1. Some of the networks are from unpublished datasets and were used by us with the kind permission of Victor Rico-Gray, Cristina Sazima, Ivan Sazima, and Thiago Izzo (Table S1).
Network structure

We quantified five widely used metrics of network structure to characterize the arrangement of interactions in our networks: (i) species richness \( (R) \), (ii) degree variance \( (\sigma_k^2) \), (iii) connectance \( (C) \), (iv) nestedness \( (NODF) \), and (v) modularity \( (Q; \text{Supporting Information}) \). For these analyses we represented each network as a bipartite adjacency matrix that defines the interactions between two distinct sets of species (e.g. pollinators and plants; Supporting Information). Although some of our networks have information on interaction strength, we decided to use only the information on presence and absence of interactions (i.e. 1 and 0) in order to use the same type of data for all our networks and because the interaction strengths evolve in our coevolution model (see below). Degree variance is defined as the variance of all degree values (i.e. the number of interaction partners of a species) and measures the heterogeneity in the number of partners in the network. Connectance is the proportion of all possible interactions that are in fact realized and represents how well connected species are to each other in the network (Jordano 1987). Nestedness measures how much the interactions of species with low degree values are proper subsets of the interactions of species from the same set that have higher degree values (Bascompte et al. 2003). We quantified nestedness using the metric \( NODF \), which varies from 0 (no nestedness) to 1 (perfect nestedness; Almeida-Neto et al. 2008). Finally, modularity measures how much the network is partitioned in groups of species (i.e. modules) with many interactions within groups and few interactions among different groups (Olesen et al. 2007). We computed modularity using a simulated annealing algorithm to optimize the value of a bipartite version of the metric \( Q \), which varies from 0 (no modularity) to 1 (perfect modularity; Barber 2007; Marquitti et al. 2013). Nestedness and modularity are known to be affected by other network properties (Bascompte et al. 2003; Fortuna et al. 2010). To control the effects of network richness, degree variance, and connectance on nestedness and modularity, we standardized the \( NODF \) and \( Q \) values using null models (Supporting Information).

Because network structural metrics are often highly correlated among each other (Jordano 1987; Bascompte et al. 2003; Fortuna et al. 2010), we used principal component analysis (PCA) to describe how the values of our five metrics covary across networks. We used the correlation matrix among our five metrics in the PCA because of large differences in the scale of our metrics (Table S1). By using PCA, we
were able to obtain two axes of structural variation — the first two principal components (PC1 and PC2) — that describe the variation in network structure of our dataset. We used our values of PC1 and PC2 to explore how network structure affects the outcome of coevolution. Modularity was calculated using the program MODULAR (Marquitti et al. 2014) and the other metrics were calculated in R 3.3.2 (Dormann et al. 2008; R Core Team 2016).

Coevolution model for one locality

We developed a mathematical model of coevolution based on previous theory on evolution in ecological networks (Guimarães et al. 2011; Nuismer et al. 2013; Andreazzi et al. 2017). In our model, we represented each of the $R_A$ species that engage in a given mutualism at locality $A$ as a single population. We modeled the evolution by natural selection of the mean value ($z_{i,A}$) of a single trait $z_i$ of each species $i$ (Fig. 1). We assumed that population sizes are large enough for genetic drift to be negligible. We also assumed that the phenotypic variance of trait $z_i$, $\sigma^2_{z_i,A}$, is fixed through time, which is a reasonable approximation if population sizes are large and selection does not erode genetic variance. We considered that trait $z_i$ mediates mutualistic interactions between individuals (e.g. hummingbird bill length, flower corolla length) and affects the fitness benefits of mutualism. In addition to mutualism, $z_i$ also determines fitness components related to abiotic factors and other ecological interactions (Nuismer et al. 2010, 2013; Andreazzi et al. 2017). Thus, $z_i$ is under selection imposed by mutualism (hereafter mutualistic selection) and selection imposed by abiotic factors and other ecological interactions (hereafter environmental selection; Fig. 1).

In our model, the change in the mean trait value of species $i$ at locality $A$ between generation $t + 1$ and generation $t$ was derived using the classical equation by Lande (1976): $\Delta z_{i,A}(t) = h^2_{z_{i,A}} \frac{\sigma^2_{z_i,A}}{\sigma^2_{z_{i,A}(t)}} \frac{\partial \ln \bar{W}_{i,A}}{\partial z_{i,A}(t)}$. Here, $h^2_{z_{i,A}} (0 \leq h^2_{z_{i,A}} \leq 1)$ is the trait heritability that we assumed to be constant over time and $\frac{\partial \ln \bar{W}_{i,A}}{\partial z_{i,A}(t)}$ is the selection gradient. To describe an adaptive landscape related to mutualistic and environmental selection we defined a linear selection gradient as follows: $\frac{\partial \ln \bar{W}_{i,A}}{\partial z_{i,A}(t)} = \rho_{i,A} [z'_{i,A}(t) - z_{i,A}(t)]$, where $\rho_{i,A}$ is a scaling constant that relates changes in mean fitness to
changes in mean trait values and \(z'_{i,A}(t)\) is the trait value that defines the adaptive peak of the population at generation \(t\). We decomposed \(z'_{i,A}(t)\) into two components, one related to mutualism and one related to the environment:

\[z'_{i,A}(t) = m_{i,A} \sum_{j \neq i}^{R_A} q_{ij,A}(t)x_{ij,A}(t) + (1 - m_{i,A})\theta_{i,A}(t)\]

Here, \(m_{i,A}\) measures the relative importance of mutualism as a selection pressure (0 \(\leq m_{i,A} \leq 1\)), \(q_{ij,A}(t)\) represents the evolutionary importance of species \(j\) to species \(i\), \(x_{ij,A}(t)\) is the mean trait value of species \(i\) favored by selection imposed by species \(j\), and \(\theta_{i,A}(t)\) is the mean trait value favored by environmental selection (Fig. 1).

We used two additional assumptions to obtain a final equation describing the dynamics of trait \(z\) at a single locality. First, we supposed that the trait value selected by the environment is fixed over time (\(\theta_{i,A}(t) = \theta_{i,A}\)). Second, we assumed that mutualistic selection favors the complementarity of traits (i.e. phenotype matching, Nuismer et al. 2010, 2013). Thus, the selected trait value with respect to partner \(j\) at generation \(t\) is \(Z_{j,A}(t) = x_{ij,A}(t)\), which corresponds to the value that maximizes the trait matching between \(z_{i,A}\) and \(Z_{j,A}\). Using our equations for the adaptive landscape and the fact that \(h_{z_{i,A}}^2 = \frac{\sigma_{G_{z_{i,A}}}}{\sigma_{Z_{i,A}}}\sigma_{Z_{i,A}}^2\) in which \(\sigma_{G_{z_{i,A}}}^2\) is the additive genetic variance of trait \(z_o\), the dynamics of trait \(z\) may be described as follows:

\[\Delta z_{i,A}(t) = \phi_{i,A} \left\{ m_{i,A} \sum_{j \neq i}^{R_A} q_{ij,A}(t) \left[ Z_{j,A}(t) - Z_{i,A}(t) \right] + (1 - m_{i,A})[\theta_{i,A} - z_{i,A}(t)] \right\} \]

(1),

in which \(\phi_{i,A}\) is a compound parameter (\(\phi_{i,A} = \sigma_{G_{z_{i,A}}^2}\rho_{i,A}\)).

We now describe how \(q_{ij,A}(t)\) changes through time. The term \(q_{ij,A}(t)\) represents the evolutionary importance of species \(j\) to species \(i\) in relation to all other mutualistic partners of \(i\) \((0 \leq q_{ij,A}(t) \leq 1\) and \(\sum_{j \neq i}^{R_A} q_{ij,A}(t) = 1\)). The term \(q_{ij,A}(t)\) has two components that represent how different traits mediate the fitness consequences of the mutualism. First, the component \(e^{-\alpha(z_{j,A}(t) - \bar{z}_{i,A}(t))^2}\) is associated with trait \(z\) and represents the magnitude of trait matching between species \(i\) and \(j\). This component is 1 when there is maximum matching \((\bar{z}_{i,A} = \bar{z}_{j,A})\) and approximates 0 if there is poor matching. The parameter \(\alpha\) represents the sensitivity of mutualistic selection to trait matching and was assumed to be the same for every species and to be fixed over time. Second, the component \(a_{ij}(t)\) encapsulates the effects of a suite of other traits not
explicitly modeled by us and defines if an interaction is allowed to occur (i.e. $a_{ij}(t) = 1$) or represents a forbidden link (i.e. $a_{ij}(t) = 0$) between $i$ and $j$. We assumed that $z_i$ evolves a faster rate than all other traits related to the mutualism and, therefore, $a_{ij}(t)$ may be considered fixed in our model ($a_{ij}(t) = a_{ij}$). In our simulations, we parameterized $a_{ij}$ using our empirical mutualistic networks. Therefore, $a_{ij}$ imposes a fixed structure of potential interactions, while $e^{-a\left(\hat{z}_{jA}(t) - \hat{z}_{LA}(t)\right)^2}$ defines a dynamic structure of the evolutionary strength of interactions. Thus, $q_{ij,A}(t)$ is given by:

$$q_{ij,A}(t) = \frac{a_{ij}e^{-a\left(\hat{z}_{jA}(t) - \hat{z}_{LA}(t)\right)^2}}{\sum_{k,k \neq i} a_{ik}e^{-a\left(\hat{z}_{kA}(t) - \hat{z}_{LA}(t)\right)^2}}$$

(2).

**Coevolution model for two localities**

We now extend our model to a scenario in which there are two localities and there may be gene flow between the populations of the same species that occur at both localities (Fig. 1b). We considered that, at generation $t$, a fraction $g_i(t)$ of the population of species $i$ migrates from locality $A$ to locality $B$ and from locality $B$ to locality $A$ and a fraction $(1 - g_i(t))$ remains at its own locality. Therefore, we supposed that migration is symmetric between localities, which would not alter the population sizes through time. We also assumed that local individuals and migrants mate randomly, which allowed us to use $g_i(t)$ as a measure of gene flow. Although $g_i(t)$ may depend on species traits and therefore vary over time, we assumed that migration ability is a fixed property of each species, which allowed us to use $g_i(t) = g_i$. Using a final assumption that $\varphi_i$ is the same for both populations of the same species, we defined a new equation for the evolutionary change in $\hat{z}_{i,A}$:

$$\Delta \hat{z}_{i,A}(t) = (1 - g_i)\varphi_i \left\{ m_{i,A} \sum_{j \neq i}^{R_A} q_{ij,A}(t)\left[\hat{z}_{j,A}(t) - \hat{z}_{LA}(t)\right] + (1 - m_{i,A})[\theta_{i,A} - \hat{z}_{LA}(t)] \right\}$$

$$+ g_i \varphi_i \left\{ m_{i,B} \sum_{j \neq i}^{R_B} q_{ij,B}(t)\left[\hat{z}_{j,B}(t) - \hat{z}_{LB}(t)\right] + (1 - m_{i,B})[\theta_{i,B} - \hat{z}_{LB}(t)] \right\}$$

(3).

The equation for $\hat{z}_{i,B}$ is obtained by exchanging the subscript $A$ for $B$ and vice versa in equation (3). In our simulations, we used equation (3) to explore the effects of gene flow ($g_i$) and geographical variation in mutualistic selection ($m_{i,A}$ and $m_{i,B}$) on coevolution.
Our model is general enough to allow for differences in species composition and network structure between localities A and B. However, we restrict our analyses to the case in which both localities have the same species composition (i.e. $R_A = R_B$) and the same adjacency matrix describing mutualistic interactions. Although $a_{ij}$ is the same at both localities, the parameters $m_i$ and $\theta_i$ may vary between the two populations of each species $i$, generating distinct adaptive landscapes for each population.

**Characterization of trait patterns**

We used three metrics to describe network- and species-level trait patterns that could be affected by coevolution. The first metric measures the degree of adaptation of each species to its mutualistic partners and was termed trait matching. Trait matching was calculated for each pair of interacting species $i$ and $j$ at locality $A$ in generation $t$ as $\tau_{ij,A}(t) = e^{-a(x_{j,A}(t)-x_{i,A}(t))^2}$. Because this metric is based on the difference between the traits of $i$ and $j$, it is highly correlated with the metric of trait complementarity used by Guimarães et al. (2011; results not shown). The second metric quantifies the degree of adaptation of each species to its local environment and was called environmental matching. Environmental matching was calculated for species $i$ at locality $A$ in generation $t$ as $\varepsilon_{i,A}(t) = e^{-a(\theta_{i,A}-\varepsilon_{i,A}(t))^2}$. Trait matching and environmental matching at locality $B$ have an equivalent definition. Finally, the third metric measures the degree of trait divergence between two populations of the same species and was termed geographical divergence. Geographical divergence was calculated for species $i$ in generation $t$ as $\delta_i(t) = e^{-a(x_{i,B}(t)-x_{i,A}(t))^2}$. Using the pairwise values for $\tau_{ij,A}(t)$ and the values of $\varepsilon_{i,A}(t)$ and $\delta_i(t)$ for each species, we also calculated the network-level mean values ($\tau_A(t), \varepsilon_A(t),$ and $\delta(t)$) and the standard deviation ($\sigma_{\tau_A}(t), \sigma_{\varepsilon_A}(t),$ and $\sigma_{\delta}(t)$) of these metrics in each generation $t$.

**Numerical simulations and statistical analyses**

We performed numerical simulations of our coevolution model to investigate how gene flow ($g_i$), geographic variation in mutualistic selection ($m_{i,A}$ and $m_{i,B}$), and network structure ($PC1$ and $PC2$) affect the emergence of trait patterns. We performed
three sets of simulations that are described in the following paragraphs. In the beginning of all simulations, we sampled parameter values for each species \( i \) according to the following distributions: (i) \( g_i \): truncated normal distribution between 0 and 1 with mean = \( \bar{g} \) and sd = 0.001, (ii) \( m_{i,A} (m_{i,B}) \): truncated normal distribution between 0 and 1 with mean = \( \bar{m}_A (\bar{m}_B) \) and sd = 0.01, (iii) \( \varphi_i \): truncated normal distribution between 0 and 1 with mean = 0.2 and sd = 0.01, and (iv) \( \theta_{i,A} (\theta_{i,B}) \): uniform distribution with range [0, 20] ([20, 40] for locality \( B \)). We set \( g_i = \bar{g} \), \( m_{i,A} = \bar{m}_A \), or \( m_{i,B} = \bar{m}_B \) for every species \( i \) whenever the mean value (\( \bar{g}, \bar{m}_A, \) or \( \bar{m}_B \)) was either 0 or 1 to avoid sampling problems. In addition, we used \( \alpha = 0.2 \) for all simulations. We decided to use a fixed value for \( \alpha \) and for the mean value of \( \varphi_i \) in all our simulations because previous work shows that analogous parameters have a weak effect on coevolutionary dynamics (Guimarães et al. 2011; Andreazzi et al. 2017). Our distributions for \( \theta_{i,A} \) and \( \theta_{i,B} \) were chosen to explore a scenario in which different communities present contrasting environments as is observed for many kinds of interacting species (Thompson 2005; Anderson & Johnson 2008; Piculell et al. 2008; Gómez et al. 2009). In all simulations, species started at the selected trait value in relation to the environment (\( \bar{z}_{i,A}(0) = \theta_{i,A} \) and \( \bar{z}_{i,B}(0) = \theta_{i,B} \)). Simulations ran until the average difference \( |\bar{z}_{i,A}(t) - \bar{z}_{i,A}(t+1)| \) for all species \( i \) at both localities was less than \( 10^{-6} \) or until \( 10^4 \) generations were reached. This condition was sufficient to reach equilibrium in trait values (Fig. S1, S2). We recorded the values of trait matching (\( \tau_{ij} \)), environmental matching (\( \epsilon_i \)), and geographical divergence (\( \delta_i \)) at both localities in the beginning and end of each simulation.

We now describe our three sets of simulations. In our first set of simulations we explored five scenarios of selection mosaics: (i) \( \bar{m}_A = \bar{m}_B = 0.9 \); (ii) \( \bar{m}_A = 0.9 \) and \( \bar{m}_B = 0.7 \); (iii) \( \bar{m}_A = 0.9 \) and \( \bar{m}_B = 0.5 \); (iv) \( \bar{m}_A = 0.9 \) and \( \bar{m}_B = 0.3 \); (v) \( \bar{m}_A = 0.9 \) and \( \bar{m}_B = 0.1 \). We focused our analyses on scenario (i), which represents two hotspots, and scenario (v), which represents one hotspot (locality \( A \)) and one coldspot (locality \( B \)). For each scenario, we used 21 different values of mean gene flow (\( \bar{g} \)) between 0 and 0.1 in increments of 0.005. We performed 100 simulations for each of our 72 empirical networks per combination of selection mosaic and gene flow (\( n = 756,000 \) simulations). We performed statistical tests to investigate the effects of mutualism type, degree of interaction intimacy, mean value of gene flow (\( \bar{g} \)), and network structure (\( PC1 \) and \( PC2 \)) on the network-level trait matching (\( \tau \)) at the end of
simulations. We are aware of the issues regarding statistical testing using simulation data (White et al. 2014). Here, we performed statistical tests to have a measure of the effect size of each parameter or factor of interest to us and we do not ground our conclusions on significance (i.e. p-values). We used one-way ANOVA to test for differences among different mutualisms in the mean value for 100 simulations per network of the network-level trait matching ($\tau_{n=100}$). We used t-tests to test if $\tau_{n=100}$ differed between high-intimacy and low-intimacy mutualisms. We used linear mixed models to test for the effects of gene flow and mutualism type on $\tau_{n=100}$. In our models, $\tau_{n=100}$ was our response variable and gene flow, mutualism type, and the interaction between gene flow and mutualism type were our three predictor variables. In this analysis we used only two values of $\bar{g}$ (0 and 0.1) in order to obtain a simple effect size of gene flow on coevolution. We defined the network identity as a random effect in our linear mixed model. Finally, we used linear regression to test for the effects of network structure (either PC1 or PC2) on $\tau_{n=100}$. We fitted separate regressions for three different values of gene flow ($\bar{g} = 0, \bar{g} = 0.01, \bar{g} = 0.1$). Because our previous statistical analyses showed that high- and low-intimacy mutualisms generate disparate degrees of trait matching, we also fitted separate regressions for high- and low-intimacy mutualisms.

In our second set of simulations we explored a larger region of the parameter space for two networks with contrasting structures (networks 29 and 65 in Table S1). To do so we defined 882 combinations of $\bar{m}_A$, $\bar{m}_B$, and $\bar{g}$. Combinations of $\bar{m}_A$ and $\bar{m}_B$ were either symmetric ($\bar{m}_A = \bar{m}_B$ for $\bar{m}_A$ between 0 and 1 in increments of 0.05) or asymmetric ($\bar{m}_A = 1 - \bar{m}_B$ for $\bar{m}_A$ between 0 and 1 in increments of 0.05). For each combination of $\bar{m}_A$ and $\bar{m}_B$, we explored 21 different values of mean gene flow ($\bar{g}$) between 0 and 0.1 in increments of 0.005. We performed 100 simulations per network for each combination of $\bar{m}_A$, $\bar{m}_B$, and $\bar{g}$ $\text{(n = 176,400 simulations)}$.

Finally, our third set of simulations aimed to verify the coevolutionary effects of habitat fragmentation by removing the gene flow between two connected hotspots ($\bar{m}_A = \bar{m}_B = 0.9$). In these simulations traits evolved to equilibrium with high gene flow ($\bar{g} = 0.1$) and then gene flow was removed ($\bar{g} = 0$) and coevolution proceeded to a new equilibrium. We performed 100 simulations for each of our 72 empirical networks $\text{(n = 7,200 simulations)}$. We used linear mixed models to test for the effects of gene flow and mutualism type on the emergence of trait matching ($\tau_{n=100}$) and environmental
matching ($\epsilon_{n=100}$). The structure of these models was identical to the linear mixed models used for our first set of simulations (see above). All simulations and statistical analyses were done in R 3.3.2 (Bates et al. 2015; R Core Team 2016).

**Results**

**Effects of gene flow and selection mosaics on coevolution**

Coevolution in our numerical simulations always proceeded to an equilibrium in which trait values remain fixed over time (Fig. S1, S2). When the selection mosaic consisted of two isolated hotspots ($m_A = m_B = 0.9, g = 0$), the network-level trait matching ($\bar{\epsilon}$) at equilibrium at a given locality was higher for high-intimacy than for low-intimacy mutualisms (high-intimacy: $\bar{\epsilon}_{A,n=100} = 0.85 \pm 0.05$ vs. low-intimacy: $\bar{\epsilon}_{A,n=100} = 0.66 \pm 0.09$, mean $\pm$ sd; Welch two sample t-test: $t_{56.95} = 11.09$, p < 0.0001; $\bar{\epsilon}_{A,n=100}$: mean value for 100 simulations per network of the network-level trait matching at locality $A$; Fig. 2a). In addition, trait matching greatly differed between different mutualisms in isolated hotspots (ANOVA: $F_{5,66} = 17.43$, p < 0.0001; Fig. 2a). In particular, ant-myrmecophyte networks generated the highest levels of trait matching ($\bar{\epsilon}_{A,n=100} = 0.88 \pm 0.06, g = 0$) and frugivore-plant networks generated the lowest levels of trait matching ($\bar{\epsilon}_{A,n=100} = 0.62 \pm 0.09, g = 0$).

Gene flow between two hotspots affected how coevolution leads to trait matching in two main ways. First, gene flow had an unexpected effect of increasing trait matching (Likelihood ratio test for linear mixed model: $\chi^2(1) = 111.64$, p < 0.0001; Table S2). Furthermore, trait matching was higher for high-intimacy mutualisms ($\chi^2(5) = 59.92$, p < 0.0001), but the effect of gene flow was stronger for low-intimacy mutualisms ($\chi^2(5) = 58.24$, p < 0.0001; Fig 2a; Table S2). Second, gene flow decreased the variation in the network-level trait matching across different networks, especially for low-intimacy mutualisms (Fig. 2a). The change in the network-level trait matching ($\bar{\epsilon}$) in a given simulation is the outcome of changes in the trait matching of pairwise interactions ($\tau_{ij}$). We observed that gene flow increases the network-level trait matching in two hotspots by increasing the trait matching of poorly matched pairs of species, spreading coadaptation throughout the network (Fig. S3). Thus, gene flow increases mean pairwise matching and reduces the standard
deviation in pairwise matching ($\sigma_r$) and this effect is stronger for low-intimacy mutualisms (Fig. S4).

We also explored the coevolutionary dynamics when a network in which mutualism is a strong selective pressure (hotspot: $\bar{m}_A = 0.9$) is connected to a network in which mutualism is a weak selective pressure (coldspot: $\bar{m}_B = 0.1$). We observed that, in the absence of gene flow, trait matching at equilibrium was more than three-fold higher at the hotspot than at the coldspot (hotspot: $\bar{\tau}_{A,n=100} = 0.71 \pm 0.12$ vs. coldspot: $\bar{\tau}_{B,n=100} = 0.21 \pm 0.007$, $\bar{g} = 0$, Welch two sample t-test: $t_{71.5} = 36.33$, $p < 0.0001$; Fig. 2b, c). Interestingly, the effect of gene flow varied with the local selection regime (Fig. 2b, c). At the hotspot, low values of gene flow slightly increased trait matching, but higher values of gene flow ($\bar{g}$ higher than 0.025) decreased trait matching (Likelihood ratio test for linear mixed model: $\chi^2(1) = 247.86$, $p < 0.0001$; Fig. 2b; Table S2). In addition, trait matching at the hotspot was higher for high-intimacy mutualisms ($\chi^2(5) = 68.98$, $p < 0.0001$) and the loss of trait matching due to gene flow was slightly stronger for high-intimacy mutualisms ($\chi^2(5) = 17.22$, $p = 0.004$; Fig. 2b; Table S2). In contrast, gene flow promoted a modest increase in trait matching at the coldspot ($\chi^2(1) = 285.02$, $p < 0.0001$; Fig. 2c). Moreover, trait matching at the coldspot was higher for high-intimacy mutualisms ($\chi^2(5) = 63.43$, $p < 0.0001$) and the increase in trait matching due to gene flow was slightly stronger for high-intimacy mutualisms ($\chi^2(5) = 52.441$, $p < 0.0001$; Fig. 2c; Table S2). Our simulations for other combinations of $\bar{m}_A$ and $\bar{m}_B$ showed that the way gene flow affects trait matching changes gradually as the importance of mutualistic selection increases at the coldspot ($\bar{m}_B$ varying from 0.1 to 0.9; Fig. S5, S6).

In addition to trait matching, we also explored how gene flow and selection mosaics influence the emergence of environmental matching and geographical divergence in traits. We observed that, in the absence of gene flow, the network-level environmental matching ($\bar{\varepsilon}$) at equilibrium was more than two-fold higher in coldspots than in hotspots (coldspot: $\bar{\varepsilon}_{B,n=100} = 0.94 \pm 0.02$ vs. hotspot: $\bar{\varepsilon}_{A,n=100} = 0.37 \pm 0.04$, $\bar{g} = 0$, $\bar{m}_B = 0.1$, $\bar{m}_A = 0.9$; Welch two sample t-test: $t_{92.8} = 99.26$, $p < 0.0001$). In addition, the environmental matching always decreased with gene flow, irrespective of the selection mosaic (Fig. S7, S8). In agreement with our expectations (Fig. 1), our simulations also indicated that the network-level geographical divergence ($\bar{\delta}$) strongly decreases with gene flow, irrespective of the selection mosaic (Fig. S9).
Effects of network structure on the geographic mosaic of coevolution

Network structure greatly varied among different mutualistic networks (Table S1). Pollinator-plant interactions formed the largest and less connected networks \((R = 73 \pm 43.8, C = 0.16 \pm 0.09, \text{mean} \pm \text{sd})\), whereas anemone-fish interactions formed the smallest and more connected networks \((R = 8.6 \pm 1.1, C = 0.4 \pm 0.06)\). Ant-EFN bearing plants interactions formed the most nested networks (standardized \(NODF = 7.3 \pm 7.8\)), while ant-myrmecophyte interactions formed the most modular networks (standardized \(Q = 2.3 \pm 0.4\)). Our PCA identified that 83.1% of the variation in network structure is organized in two structural axes, \(PC1\) and \(PC2\) (Fig. 3a; Table S1). \(PC1\) accounted for 58.5% of all variation in our structural metrics and was strongly correlated with species richness (0.54), degree variance (0.48), and nestedness (0.56; Fig. 3a; Table S3). On the other hand, \(PC2\) accounted for 24.6% of all variation in our structural metrics and was strongly correlated with connectance (0.68) and modularity (-0.64; Fig. 3a; Table S3).

We explored how network structure, estimated by \(PC1\) and \(PC2\) scores, affects the emergence of trait matching in distinct types of selection mosaics. We first focused on how network structure affects trait matching in a selection mosaic composed of two hotspots \((\bar{m}_A = \bar{m}_B = 0.9)\). With no or small gene flow, the \(PC1\) scores of low-intimacy mutualisms negatively affected the network-level trait matching \((g = 0: b = -0.022, F_{1,51} = 8.64, p = 0.005; g = 0.01: b = -0.019, F_{1,51} = 9.98, p = 0.003; \text{Fig. 3b; Table S4})\). Thus, large, heterogeneous, and nested low-intimacy networks have a low potential of generating trait matching. In contrast, the \(PC1\) scores of high-intimacy mutualisms did not affect trait matching \((g = 0: b = 0.016, F_{1,17} = 0.14, p = 0.71; g = 0.01: b = 0.013, F_{1,17} = 0.13, p = 0.72; \text{Fig. 3b; Table S4})\). When gene flow was high \((g = 0.1)\), \(PC1\) had no effect on trait matching for both types of mutualisms (low-intimacy: \(b = -0.003, F_{1,51} = 1.04, p = 0.31\); high-intimacy: \(b = 0.004, F_{1,17} = 0.02, p = 0.88; \text{Fig. 3b; Table S4})\). The \(PC2\) scores, however, affected the emergence of trait matching in both types of mutualisms and for all three values of gene flow (low-intimacy: \(g = 0: b = -0.033, F_{1,51} = 10.5, p = 0.002; g = 0.01: b = -0.027, F_{1,51} = 11.24, p = 0.001; g = 0.1: b = -0.015, F_{1,51} = 15.2, p = 0.0002; \text{high-intimacy: } g = 0: b = -0.022, F_{1,17} = 5.17, p = 0.04; g = 0.01: b = -0.018, F_{1,17} = 5.6, p = 0.03; g = 0.1: b = -0.014, F_{1,17} = 5.8, p = 0.03; \text{Fig. 3c; Table S4})\). Therefore, weakly connected and modular networks have a strong potential of generating trait matching.
When the selection mosaic consisted of a hotspot and a coldspot, network structure affected the emergence of trait matching mainly at the hotspot (Fig. S10; Table S4). At the hotspot, PC1 negatively affected trait matching only in low-intimacy mutualisms and this effect was observed for all values of gene flow (Fig. S10; Table S4). On the other hand, PC2 negatively affected trait matching in both types of mutualisms with no gene flow, but only in low-intimacy mutualisms with high gene flow (Fig. S10, Table S4). To sum up, our results indicate that network structure affects coevolution when mutualism is an important selective pressure at both localities (i.e. two hotspots), but this effect vanishes with gene flow. In contrast, network structure affects coevolution for variable degrees of gene flow when mutualism is an important selective pressure at one locality but is unimportant at the other locality (i.e. one hotspot and one coldspot; Fig. S10).

In order to have a detailed picture of the effects of network structure for the whole parameter space, we performed an additional set of simulations in which we used many combinations of $g$, $m_A$, and $m_B$ for one ant-myrmecophyte and one pollinator-plant network with contrasting structures (networks 29 and 65 in Table S1; Fig. 3a). These results confirmed that high-intimacy mutualisms promote the emergence of higher values of trait matching and are weakly affected by gene flow (Fig. S11, S12). On the other hand, low-intimacy mutualisms generate lower values of trait matching in general, but are more affected by gene flow (Fig. S11, S12).

**Coevolutionary effects of habitat fragmentation**

In our last set of simulations, we used our coevolution model to simulate habitat fragmentation that would result in the disruption of gene flow between two hotspots ($m_A = m_B = 0.9$). As expected from our previous analyses, species lost their trait matching with mutualistic partners when gene flow between the two hotspots was removed ($\bar{g} = 0.1$, $\bar{r}_{A,R=100} = 0.85 \pm 0.05$; $\bar{g} = 0$, $\bar{r}_{A,R=100} = 0.79 \pm 0.06$; Fig. 4a). Our linear mixed models confirmed that trait matching decreases with the loss of gene flow (Likelihood ratio test: $\chi^2(1) = 141.8$, $p < 0.0001$), that trait matching is always higher for high-intimacy mutualisms ($\chi^2(5) = 69.89$, $p < 0.0001$), and that the effect of losing gene flow is stronger for low-intimacy mutualisms ($\chi^2(5) = 37.64$, $p < 0.0001$; Fig. 4b). Interestingly, however, the final values of trait matching in these simulations
were higher than the values observed in our previous simulations, especially for low-intimacy mutualisms (Fig. 2a, 4b; $g = 0$). This result indicates that species in fragmented landscapes may attain higher values of trait matching if their initial trait values are highly matched (e.g. traits at equilibrium for $g = 0.1$) than if their initial trait values are poorly matched (e.g. trait values start at the environmental optimum: $z_{iA}(0) = \theta_{iA}$ and $z_{iB}(0) = \theta_{iB}$; Fig. S13).

In parallel with the loss of coadaptations between mutualistic partners following habitat fragmentation, species greatly improved their environmental matching ($\chi^2(1) = 467.7, p < 0.0001$), that environmental matching is lower for low-intimacy mutualisms ($\chi^2(1) = 32, p < 0.0001$), and that the effect of losing gene flow is more pronounced in high-intimacy mutualisms ($\chi^2(1) = 124.4, p < 0.0001$; Fig. 4c).

**Discussion**

The geographical and ecological complexity of coevolution poses a challenge to our understanding of the evolution of interacting species. By simulating coevolution with information on the structure of empirical mutualistic networks we were able to identify three fundamental aspects of how species evolve when embedded in ecological assemblages across simple landscapes. First, gene flow affects the evolutionary outcomes of selection between mutualistic partners and may favor the emergence of trait matching depending on the geographic selection mosaic. Second, the network structure of different mutualisms affects coevolution in distinct ways, but the effect of network structure may vanish when gene flow fuels the emergence of trait matching. Third, habitat fragmentation resulting in the disruption of gene flow should reduce the coadaptations between mutualistic partners while promoting adaptations of species to their local environment.

The influence of gene flow on the evolution of populations is a key aspect of evolutionary theory (Slatkin 1987; Lenormand 2002). In the context of the GMTC, gene flow is a central process affecting patterns of trait matching in pairs of interacting populations (Anderson & Johnson 2008; Yoder et al. 2013). Mathematical models show that some of the phenotypic patterns predicted by the GMTC result from
complex interplays between gene flow and selection mosaics (Nuismer et al. 1999; Gomulkiewicz et al. 2000; Gibert et al. 2013). In networks of interacting species, our simulations indicate that gene flow may either increase or decrease trait matching between interacting populations depending on the selection mosaic. When gene flow connects two networks under strong mutualistic selection (i.e. two hotspots), gene flow has a counterintuitive effect of favoring trait matching between mutualistic partners. We suggest that such an effect is a consequence of how gene flow affects the outcome of selection exerted by mutualistic partners and selection exerted by the environment (i.e. abiotic factors and other ecological interactions). When gene flow connects two hotspots with different environmental adaptive peaks (i.e. $\theta_{i,A} < \theta_{i,B}$ for every species $i$) the effects of environmental selection are cancelled out, leading to a loss of adaptation to the local environment (Fig. S7, S8) and to a geographical homogenization in species traits (Fig. S9). The mismatch with the local environment in turn favors selection for tight coadaptations between mutualistic partners at the landscape level. It is known that traits adapted to certain ecological interactions may reduce survival, reproduction, or performance with respect to other selective pressures (Fine et al. 2006; Ågren et al. 2013). In these circumstances, gene flow could act to fuel coadaptations between interacting populations, providing a mechanism for how traits that mediate ecological interactions become fixed at the species level (Thompson 2005). Our results indicate that such an effect could be amplified when networks of interacting species are connected by gene flow and form a single multilayer network. In fact, recent studies on multilayer networks indicate that linking two or more networks together may substantially alter the ecological dynamics (Kéfi et al. 2016) or other kinds of dynamics such as disease spreading (Boccaletti et al. 2014).

In contrast to two linked hotspots, we observed that gene flow has an opposite effect on trait matching if a network at a hotspot is connected to a network under weak mutualistic selection (i.e. a coldspot). Because populations at the coldspot are locked to their local environmental adaptive peaks, populations at the hotspot receive a constant input of maladapted phenotypes from the coldspot, which leads to trait mismatching at the hotspot. In this sense, our study provides additional evidence that maladaptation may emerge through the combination of gene flow and selection mosaics (Gomulkiewicz et al. 2000; Thompson 2005; Hanifin et al. 2008).
Experimental coevolution between bacteria and phage shows that migration between a hotspot and a coldspot promotes coevolution at the coldspot, but inhibits coevolution at the hotspot (Vogwill et al. 2009). Our results indicate that this phenomenon also occurs in mutualistic networks, suggesting that contrasting selective pressures across localities may also be important for the evolutionary dynamics of whole communities (Urban et al. 2008).

Multispecies mutualistic systems are not randomly organized, but instead show typical architectures that may affect ecological and evolutionary processes (Bascompte & Jordano 2014). Our results show that the network structure of high-intimacy mutualisms promote the emergence of higher levels of trait matching between mutualistic partners than the network structure of low-intimacy mutualisms. Networks of intimate mutualisms are typically characterized by a small number of species grouped in semi-isolated modules (Ricciardi et al. 2010; Dáttilo et al. 2013b; this study). Previous theoretical studies suggest that the compartmentalized nature of these networks may promote reciprocal evolution (Guimarães et al. 2007a) and may emerge as a consequence of trait matching (Andreazzi et al. 2017). These results are in agreement with the impressive degree of specificity observed in interactions such as ants that protect myrmecophytes, in which interacting individuals show very tight morphological, behavioral, and biochemical matches (Brouat et al. 2001; Orona-Tamayo et al. 2013). In fact, we found that the least connected structure of networks of protective ants and their host plants (Fonseca & Ganade 1996; Blüthgen et al. 2007; Guimarães et al. 2007a) favors the coevolutionary emergence of trait matching through reciprocal specialization in our numerical simulations.

In contrast to high-intimacy mutualisms, the emergence of elevated trait matching in low-intimacy mutualisms is contingent upon gene flow between hotspots. Our model suggests that the network structure of low-intimacy mutualisms amplifies the effect of gene flow of cancelling out opposing environmental selective pressures, allowing the emergence of strong trait matching. A collateral effect of this mechanism, however, is that gene flow blurs the effect of the network structure of low-intimacy mutualisms (Fig. 3b, c). Low-intimacy mutualisms between free-living species are characterized by species-rich networks with a core of generalist species (Bascompte et al. 2003; Guimarães et al. 2006, 2007b; this study). Theoretical work on evolution in mutualistic and antagonistic networks indicates that these generalist species may
fuel coevolution and promote trait convergence and trait matching in the network (Guimarães et al. 2011; Andreazzi et al. 2017). Here, we report a similar effect of the network structure of mutualisms among free-living species, which is mediated by gene flow between two hotspots. On the other hand, when a hotspot is connected to a coldspot, gene flow does not promote trait matching at the hotspot and, as a consequence, does not blur the effect of the network structure on trait matching (Fig. S10). These results suggest that network structure plays a prominent role in coevolution whenever there are pairs of species with poorly matched traits, which fuel coevolutionary change through their structural role in the network (Guimarães et al. 2011; Andreazzi et al. 2017). Because hotspots are often surrounded by multiple coldspots (Thompson & Cunningham 2002; Hanifin et al. 2008), we predict that network structure will usually be a central component of the coevolutionary dynamics of species-rich mutualisms.

If gene flow influences the outcome of coevolution in mutualistic networks, habitat fragmentation may affect coevolution through the disruption of gene flow. Indeed, our simulations of habitat fragmentation in two hotspots show that the disruption of gene flow would lead to the reduction of trait matching between mutualistic partners, especially in mutualisms with low interaction intimacy. There is empirical evidence that human impact may fuel evolutionary changes in mutualisms by changing the species composition of interacting partners (Toby Kiers et al. 2010; Galetti et al. 2013). Here, we suggest that habitat fragmentation may have an insidious effect on the organization of mutualistic interactions by changing patterns of coadaptation in species-rich networks. Interestingly, however, we found that the emergence of trait matching in the absence of gene flow depended on the initial trait values (Fig. S13). Biologically, this effect of the initial condition means that species in fragmented areas would still show signs of their coevolved traits when gene flow was present long after the fragmentation event. Therefore, we provide evidence that past coevolutionary events may constrain subsequent evolution in species-rich mutualisms. Although species lose their adaptations to mutualistic partners, we found that species increase their adaptations to the local environment with the loss of gene flow. This effect was stronger for intimate mutualisms, meaning that habitat fragmentation has a stronger potential for population differentiation in mutualisms that are organized as small networks with semi-isolated groups of interacting species.
Thus, the divergence in traits of isolated populations may be an additional consequence of fragmentation for the structure and dynamics of high-intimacy mutualistic networks (Emer, 2013).

In this study, we investigated how fundamental processes of the GMTC affect coevolution in different kinds of mutualistic networks. Although we explored simple simulation scenarios of a mathematical model with many underlying assumptions, we think that our analyses represent a first step to unravel the complexity of the coevolutionary process in multispecies systems across space. Because the species composition of communities and network structure often vary across space (Dâttilo et al. 2013a; Carstensen et al. 2014; Gilarranz et al. 2015; Trojelsgaard et al. 2015), a next step is to use datasets with spatial variation and tools from multilayer networks to explore coevolutionary dynamics. Ultimately, our approach allowed us to strengthen the connections between two research topics in coevolution that are inseparable: multispecies coevolution and the geographic mosaic of coevolution (Thompson 2005; Bascompte & Jordano 2014; Carmona et al. 2015). In particular, we provide a theoretical basis to understand how coadaptations should evolve when communities contain dozens of interacting species. We show that a complex interplay between gene flow, the geographic structure of selection, and the network organization of mutualisms shapes trait matching in mutualistic assemblages. Our results therefore provide clear predictions of how the geographic mosaic of coevolution shapes species-rich interactions often considered diffuse. Such predictions of the evolutionary trajectory of whole communities are key to our understanding of the impacts of widespread modification and fragmentation of natural landscapes driven by human action.

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Figures

**Figure 1.** Hypothesized effects of selection mosaics and gene flow on the coevolution of species embedded in a mutualistic network. Each population \( i \) at a given locality (\( A \) or \( B \)) is associated with a distribution of a trait that mediates the mutualism (\( z_{i,A}, z_{i,B} \)) and a trait value favored by the local environment (\( \theta_{i,A}, \theta_{i,B} \)). At the hotspot (locality \( A \), left), there is strong selection imposed by the mutualism between two pollinators (yellow and red) and one plant species (green) and the environment selects for small trait values (\( \theta_{i,A} \)). At the coldspot (locality \( B \), right), the environment exerts a stronger selection than mutualism and selects for large trait values (\( \theta_{i,B} \)). When both localities are isolated (a), we expect that coevolution should generate a higher trait matching between interacting populations at the hotspot than at the coldspot. At the coldspot,
each population should become well adapted to its local environment. When both localities are connected by gene flow (b), we expect a reduction in the geographical divergence of traits. However, the effects of gene flow on the emergence of trait matching at each locality are hard to predict and define a current major challenge for coevolutionary research.

**Figure 2.** The effects of gene flow and selection mosaics on coevolution in mutualistic networks. For a hotspot connected to another hotspot (a), gene flow increased the network-level trait matching ($\bar{\tau}_A$) generated by coevolution. High-intimacy mutualisms (orange and red points) attained higher values of trait matching and were less affected by gene flow than low-intimacy mutualisms (blue, purple, and green points). For a hotspot connected to a coldspot (b), low values of gene flow slightly increased trait matching, but high values of gene flow ($\bar{g} > 0.025$) decreased trait matching. For a coldspot connected to a hotspot (c), gene flow promoted a modest increase in trait matching. In all plots, each point corresponds to the mean of the network-level trait matching for 100 simulations for a given network ($\bar{\tau}_{A,R=100}$ or $\bar{\tau}_{B,R=100}$). The mean importance of mutualistic selection was $\bar{m}_A = 0.9$ at the hotspot and $\bar{m}_B = 0.1$ at the coldspot.
Figure 3. Mutualistic network structure mediates the effects of gene flow on coevolution in two connected hotspots. Our two principal components (PC1 and PC2) explained 83.1% of the variation of network structure in our dataset (a). PC1 was positively correlated with species richness and nestedness and PC2 was positively correlated with connectance and negatively correlated with modularity. In one extreme we had large and nested networks, such as a network with 25 pollinators (black nodes) and 51 plants (grey nodes) from a semi-arid region in Brazil (PC1 = 2.31, PC2 = 1.16; network 29 in Table S1). In the other extreme we had small and modular networks, such as a network with 6 protective ants (black nodes) and 5 host plants (grey nodes) from the Brazilian Amazon (PC1 = -1.68, PC2 = -0.72; network 65 in Table S1). (b) PC1 only affected the emergence of trait matching in two isolated (\( \bar{g} = 0 \)) or weakly connected (\( \bar{g} = 0.01 \)) hotspots and for low-intimacy mutualisms (blue, purple, and green points; lines show significant regressions). On the other hand (c), PC2 affected the emergence of trait matching for all values of gene flow and for both types of mutualisms (blue lines: low-intimacy mutualisms; red lines and orange and red points: high-intimacy mutualisms). However, the importance of network structure greatly reduced when gene flow favored trait matching (b-c; \( \bar{g} = 0.1 \)). In (b-c) each point corresponds to the mean of the network-level trait matching for 100 simulations for a given network (\( \bar{t}_{A,n=100} \)). The mean importance of mutualistic selection was \( m_A = m_B = 0.9 \).
**Figure 4.** Habitat fragmentation and disruption of gene flow may profoundly impact coevolution in mutualistic networks. In a given simulation in which gene flow between two hotspots was removed (a), species lost their coadaptations with mutualistic partners (i.e. trait matching), but increased their adaptations to the local environment (i.e. environmental matching). In (a) each point represents the network-level trait matching ($\tau_A$) and environmental matching ($\varepsilon_A$) in a given time step and arrows point in the direction of time evolution (red: ant-myrmecophyte network 65 in Table S1; green: pollinator-plant network 29 in Table S1). (b) High-intimacy mutualisms (orange and red points) generated higher values of trait matching, but the reduction in trait matching following the disruption of gene flow was more pronounced in low-intimacy mutualisms (blue, purple, and green points). However (c), the increase in environmental matching following the disruption of gene flow was stronger for high-intimacy mutualisms. Each point in (b-c) corresponds to the mean of the network-level metric for 100 simulations for a given network ($\overline{\tau}_{A,n=100}$ or $\overline{\varepsilon}_{A,n=100}$) and lines connect the same network. The mean importance of mutualistic selection in these simulations was $m_A = m_B = 0.9$. 
Supporting Information

Gene flow and selection mosaics shape coevolution in mutualistic networks

Lucas P. Medeiros & Paulo R. Guimarães Jr.

Network structure metrics

Here we describe how we calculated each of our five metrics of network structure: (i) species richness (R), (ii) degree variance (σ²), (iii) connectance (C), (iv) nestedness (NODF), and (v) modularity (Q). We used these metrics to quantify the organization of interactions of our 72 empirical mutualistic networks, which were represented as binary bipartite adjacency matrices. Each network is composed of two distinct sets of species (e.g. pollinators and plants) and interactions only occur between species of different sets. In matrix A, one set is positioned in the rows and the other in the columns and an element aᵢⱼ = 1 if species i and j are mutualistic partners or aᵢⱼ = 0 if they are not. We used this information to parameterize the simulations of our coevolution model with the additional restriction that aᵢⱼ = 0 if species i and j belong to different sets.

If the first set has R₁ species (i.e. number of rows in A) and the second set has R₂ species (i.e. number of columns in A), then species richness is calculated as R = R₁ + R₂. The number of interactions or degree of species i present in the first set is quantified as kᵢ = Σᵢᵢᵢ aᵢⱼ and the degree of species j present in the second group as kⱼ = Σᵢ₁ aᵢⱼ. The degree variance is simply the variance of the degree values (kᵢ) of all species in the network. Defining the total number of interactions in the network as I = Σᵢ₁ Σⱼᵢajuₐ, network connectance may be calculated as C = I / R₁R₂ and represents the proportion of all possible interactions that are in fact realized (Jordano 1987). Nestedness measures how much the interactions of species with low degree values are proper subsets of the interactions of species from the same set that have higher degree values (Bascompte et al. 2003). We quantified nestedness using a metric based on overlap and decreasing fill (NODF), which varies from 0 (no nestedness) to 1.
(perfect nestedness; Almeida-Neto et al. 2008; Bascompte & Jordano 2014). NODF was computed using the following equation:

\[
\text{NODF} = \frac{\sum_{i<j} R_1 N_{ij}}{[R_1(R_1-1)/2]} + \frac{\sum_{i<j} R_2 N_{ij}}{[R_2(R_2-1)/2]} \tag{S1}
\]

in which the sum on the left is over all pairs of species in the first set and the sum on the right is over all pairs of species in the second set. For each pair of species \(i\) and \(j\), \(N_{ij}\) is defined in the following way:

\[
N_{ij} = \begin{cases} n_{ij} / \min(k_i, k_j), & \text{if } k_i \neq k_j \\ 0, & \text{if } k_i = k_j \end{cases} \tag{S2}
\]

in which \(n_{ij}\) is the number of common interactions between \(i\) and \(j\). Finally, modularity measures how much the network is partitioned in groups of species (i.e. modules) with many interactions within groups and few interactions among different groups (Olesen et al. 2007). We quantified modularity using the metric \(Q\), which varies from 0 (no modularity) to 1 (perfect modularity; Barber 2007; Marquitti et al. 2014). The metric \(Q\) has the following equation:

\[
Q = \sum_{i=1}^{M} \left[ \frac{l_i}{I} - \left( \frac{k_{1,i} k_{2,i}}{I^2} \right) \right] \tag{S3}
\]

in which \(M\) is the number of modules in the network, \(l_i\) is the number of interactions within module \(i\), \(I\) is the total number of interactions in the network, and \(k_{1,i}\) is the sum of the degrees of species in the first set (\(k_{2,i}\) for species in the second set). Each partition of a network in modules renders a different value of \(Q\). Thus, we used an optimization algorithm based on simulated annealing that numerically maximizes \(Q\) and finds the partition that best reflects the organization of the network in modules (Marquitti et al. 2014).

Nestedness and modularity are known to be affected by other network properties such as species richness, degree variance, and connectance (Bascompte et al. 2003; Fortuna et al. 2010). We used a null model approach to calculate standardized values for NODF and \(Q\) and control for the effects of other metrics. We first generated 100 matrices according to the null model 2 of Bascompte et al. (2003) for each of our 72 empirical mutualistic networks. The matrices generated by this null
model maintain the species richness and the total number of interactions of the original empirical matrix. This null model also maintains the heterogeneity in species degrees by using the following probability of assigning 1 to the interaction between species \( k \) and \( l \):

\[
p_{kl} = \frac{1}{2} \left( \frac{\sum_{i} R_{i}^{k} a_{il}}{R_{1}} + \frac{\sum_{j} R_{j}^{l} a_{kj}}{R_{2}} \right)
\]

(S4).

Using our 100 generated matrices, we calculated standardized NODF values as \((NODF_{emp} - \bar{NODF}_{null})/\sigma_{NODF_{null}}\), in which \(NODF_{emp}\) is the NODF value of the empirical matrix, \(\bar{NODF}_{null}\) is the mean NODF value for the set of 100 matrices and \(\sigma_{NODF_{null}}\) is the standard deviation of the NODF values of these 100 matrices. We calculated standardized \(Q\) values in an analogous manner.

Tables and figures

Table S1. Our dataset of 72 empirical mutualistic networks and their structural aspects. Each network is composed of two sets of species (e.g. pollinators and plants) that are placed in the rows or columns of a bipartite adjacency matrix. We calculated each structural metric using these bipartite adjacency matrices. The calculation of each metric is described below (see Network metrics). Intimacy = degree of interaction intimacy (see main text); Mutualism = mutualism type (see main text); \(R\) = species richness; \(C\) = connectance; \(\sigma_{R}^2\) = degree variance; \(NODF\) = standardized nestedness; \(Q\) = standardized modularity; \(PC1\) and \(PC2\) = scores of first two principal components obtained via a principal components analysis. Availability: IWDB = dataset available for download at [https://www.nceas.ucsb.edu/interactionweb/]; Web of life = dataset available for download at [http://www.web-of-life.es/]; Rico-Gray = dataset kindly provided by Victor Rico-Gray; Izzo = dataset kindly provided by Thiago Izzo; Sazima = dataset kindly provided by Cristina and Ivan Sazima.

| Network | Intimacy | Mutualism | Location   | Rows | Columns | \(R\) | \(C\) | \(\sigma_{R}^2\) | \(NODF\) | \(Q\) | \(PC1\) | \(PC2\) | Reference                              | Availability       |
|---------|----------|-----------|------------|------|---------|------|------|-----------|--------|------|--------|--------|----------------------------------------|-------------------|
| 1       | Low      | Ant-EFN   | Mexico     | 10   | 38      | 48   | 0.25 | 18.3      | 3.5    | -0.19| -0.01  | 0.4    | Guimarães et al. 2007a                 | Rico-Gray         |
| 2       | Low      | Ant-EFN   | Mexico     | 28   | 99      | 127  | 0.1  | 58.37     | 13.58  | 3.11 | 2.93   | -1.63  | Guimarães et al. 2007a                 | Rico-Gray         |
| 3       | Low      | Ant-EFN   | Mexico     | 5    | 12      | 17   | 0.22 | 0.89      | -1.9   | 2.56 | -1.93  | -1.17  | Guimarães et al. 2007a                 | Rico-Gray         |
| 4       | Low      | Ant-EFN   | Australia  | 41   | 51      | 92   | 0.14 | 39.5      | 17.13  | -2.48| 3.34   | 1.09    | Bütthgen et al. 2004                   | IWDB              |
| 5       | Low      | Ant-EFN   | Mexico     | 13   | 46      | 59   | 0.21 | 20.43     | 4.32   | 3.51 | -0.33  | -1.53  | Guimarães et al. 2007a                 | Rico-Gray         |
| 6       | Low      | Cleaner-client | Virgin Islands | 4   | 32      | 36   | 0.41 | 20.85     | 1.53   | 0.78 | -0.88  | 0.07    | Johnson & Ruben 1988                   | IWDB              |
| 7       | Low      | Cleaner-client | Brazil     | 5    | 35      | 40   | 0.42 | 35.05     | 5.31   | -1.39| 0.37   | 2.1     | Guimarães et al. 2007b                 | Sazima            |
| Network | Intimacy | Mutualism | Location                    | Rows | Columns | $R$  | $C$  | $\sigma_k^2$ | NODF | $Q$  | PC1 | PC2 | Reference                  | Availability |
|---------|---------|-----------|-----------------------------|------|---------|------|------|-------------|------|------|-----|-----|---------------------------|--------------|
| 8       | Low     | Cleaner-client | Netherlands Antilles        | 6    | 50      | 56   | 0.35 | 46.59       | 6.26 | -0.87| 1.05| 1.61| Wicksten 1998              | IWDB         |
| 9       | Low     | Pollinator-plant | Chile                      | 101  | 87      | 188  | 0.04 | 23.38       | 14.6 | 0.93 | 3.49| -1.76| Arroyo et al. 1982         | IWDB         |
| 10      | Low     | Pollinator-plant | Chile                      | 64   | 42      | 106  | 0.07 | 12.22       | 8.61 | 0.87 | 1.38| -1.35| Arroyo et al. 1982         | IWDB         |
| 11      | Low     | Pollinator-plant | Chile                      | 28   | 41      | 69   | 0.08 | 8.38        | 5.42 | 1.41 | 0.31| -1.44| Arroyo et al. 1982         | IWDB         |
| 12      | Low     | Pollinator-plant | Canada                     | 102  | 12      | 114  | 0.14 | 47.87       | 9.24 | -0.22| 2.55| -0.06| Barrett & Helmersen 1987   | Web of Life  |
| 13      | Low     | Pollinator-plant | Brazil                     | 13   | 13      | 26   | 0.42 | 14.1        | 6.48 | -0.78| 0.36| 1.64 | Bezerra et al. 2009        | Web of Life  |
| 14      | Low     | Pollinator-plant | United Kingdom             | 61   | 17      | 78   | 0.14 | 40.61       | 11.26| -0.98| 2.24| 0.45 | Dicks et al. 2002          | IWDB         |
| 15      | Low     | Pollinator-plant | United Kingdom             | 36   | 16      | 52   | 0.15 | 14.16       | 5.45 | -0.53| 0.45| -0.03| Dicks et al. 2002          | IWDB         |
| 16      | Low     | Pollinator-plant | Spain                      | 38   | 11      | 49   | 0.26 | 16          | 2.45 | 0.31 | -0.29| 0.16 | Dupont et al. 2003         | IWDB         |
| 17      | Low     | Pollinator-plant | Sweden                     | 118  | 23      | 141  | 0.09 | 22.54       | 7.23 | 0.88 | 1.93| -1.34| Elberling & Olesen 1999    | Web of Life  |
| 18      | Low     | Pollinator-plant | Canada                     | 86   | 29      | 115  | 0.07 | 28.07       | 10.8 | -0.95| 2.5 | -0.31| Hocking 1968               | IWDB         |
| 19      | Low     | Pollinator-plant | Australia                  | 91   | 42      | 133  | 0.07 | 21.33       | 12.38| -0.8 | 0.71| -0.55| Inouye & Pyke 1988         | Web of Life  |
| 20      | Low     | Pollinator-plant | Mauritius                  | 100  | 58      | 158  | 0.09 | 66.81       | 24.08| -3.33| 5.98| 1.35 | Kaiser-Bunbury et al. 2010 | IWDB         |
| 21      | Low     | Pollinator-plant | Argentina                  | 45   | 21      | 66   | 0.09 | 9.05        | 4.32 | 1.52 | 0.12| -1.44| Medan et al. 2002          | Web of Life  |
| 22      | Low     | Pollinator-plant | Argentina                  | 72   | 23      | 95   | 0.08 | 20.51       | 8.67 | 0.37 | 1.54| -0.92| Medan et al. 2002          | Web of Life  |
| 23      | Low     | Pollinator-plant | Canada                     | 19   | 11      | 30   | 0.23 | 7.44        | 3.24 | -0.23| -0.52| 0.29 | Mosquin & Martin 1967      | Web of Life  |
| 24      | Low     | Pollinator-plant | Mauritius                  | 13   | 14      | 27   | 0.29 | 7.13        | 3.16 | -0.26| -0.69| 0.57 | Olesen et al. 2002         | Web of Life  |
| 25      | Low     | Pollinator-plant | Portugal                   | 12   | 10      | 22   | 0.25 | 3.06        | 0.99 | 0.47 | -1.16| -0.01| Olesen et al. 2002         | Web of Life  |
| 26      | Low     | Pollinator-plant | South Africa               | 56   | 9       | 65   | 0.2  | 24.96       | 4.77 | 0.27 | 0.55| -0.04| Ollerton et al. 2003       | Web of Life  |
| 27      | Low     | Pollinator-plant | New Zealand                | 60   | 18      | 78   | 0.11 | 8.2         | 1.51 | 1.87 | -0.17| -1.6 | Primack 1983               | Web of Life  |
| 28      | Low     | Pollinator-plant | Venezuela                  | 53   | 28      | 81   | 0.07 | 5.34        | 2.43 | 0.22 | 0.3 | -1.07| Ramírez & Brito 1992       | IWDB         |
| 29      | Low     | Pollinator-plant | Brazil                     | 25   | 51      | 76   | 0.15 | 32.61       | 11.35| -2.66| 2.31| 1.16 | Santos et al. 2010         | IWDB         |
| 30      | Low     | Pollinator-plant | United States              | 32   | 7       | 39   | 0.26 | 20.03       | 5.92 | -0.88| 0.28| 0.89 | Schemske et al. 1978       | Web of Life  |
| 31      | Low     | Pollinator-plant | Canada                     | 34   | 13      | 47   | 0.32 | 20.09       | 1.09 | -1.11| -0.23| 1.17 | Small 1976                 | Web of Life  |
| 32      | Low     | Pollinator-plant | Argentina                  | 29   | 10      | 39   | 0.15 | 9.69        | 4.56 | 0.16 | -0.07| -0.34| Vázquez & Simberloff 2003  | Web of Life  |
| 33      | Low     | Pollinator-plant | Argentina                  | 33   | 9       | 42   | 0.15 | 7.05        | 2.88 | 1.38 | -0.53| -0.96| Vázquez & Simberloff 2003  | Web of Life  |
| 34      | Low     | Pollinator-plant | Argentina                  | 29   | 10      | 39   | 0.14 | 9.82        | 3.56 | 0.89 | -0.31| -0.7 | Vázquez & Simberloff 2003  | Web of Life  |
| 35      | Low     | Pollinator-plant | Argentina                  | 26   | 8       | 34   | 0.17 | 6.77        | 3.06 | 0.48 | -0.5 | -0.39| Vázquez & Simberloff 2003  | Web of Life  |
| 36      | Low     | Pollinator-plant | Argentina                  | 27   | 8       | 35   | 0.22 | 8.16        | 2.46 | 1.02 | 0.72| -0.64| Vázquez & Simberloff 2003  | Web of Life  |
| 37      | Low     | Frugivore-plant | United States              | 21   | 7       | 28   | 0.34 | 9.74        | 2.65 | -0.3 | -0.78| 0.89 | Baird 1980                 | Web of Life  |
| 38      | Low     | Frugivore-plant | Papua New Guinea           | 9    | 31      | 40   | 0.43 | 28.56       | 5.75 | -0.79| 0.11| 1.79 | Beehler 1983               | Web of Life  |
| 39      | Low     | Frugivore-plant | Puerto Rico                | 16   | 25      | 41   | 0.17 | 10.82       | 7.46 | -0.99| 0.47| 0.34 | Carlo et al. 2003          | IWDB         |
| Network | Intimacy | Mutualism      | Location       | Rows | Columns | R   | C   | $\sigma^2_k$ | NODF | Q   | PC1 | PC2 | Reference               | Availability |
|---------|----------|----------------|----------------|------|---------|-----|-----|-------------|------|-----|-----|-----|-------------------------|--------------|
| 40      | Low      | Frugivore-plant| Puerto Rico    | 20   | 34      | 54  | 0.14| 17.58       | 8.43 | -1.51| 1.1 | 0.46| Carlo et al. 2003       | IWDB         |
| 41      | Low      | Frugivore-plant| Puerto Rico    | 13   | 25      | 38  | 0.15| 6.36        | 4.23 | 0.71 | -0.32| -0.62| Carlo et al. 2003       | IWDB         |
| 42      | Low      | Frugivore-plant| Puerto Rico    | 15   | 21      | 36  | 0.16| 6.6         | 4.68 | 0.03 | -0.19| -0.23| Carlo et al. 2003       | IWDB         |
| 43      | Low      | Frugivore-plant| Australia      | 7    | 72      | 79  | 0.28| 59.52       | 7.55 | -1.16| 2.05 | 1.47| Crome 1975               | Web of Life   |
| 44      | Low      | Frugivore-plant| Brazil         | 46   | 45      | 91  | 0.13| 23.76       | 9.63 | 4.12 | 0.84 | -2.27| Donatti et al. 2011     | Web of Life   |
| 45      | Low      | Frugivore-plant| Brazil         | 29   | 35      | 64  | 0.14| 15.93       | 8.29 | -0.61| 0.99 | -0.01| Galetti and Pizo 1996   | Web of Life   |
| 46      | Low      | Frugivore-plant| Spain          | 17   | 16      | 33  | 0.44| 17.85       | 8.44 | 1.3  | -0.4 | 0.05| Jordano 1985             |              |
| 47      | Low      | Frugivore-plant| Mexico         | 27   | 5       | 32  | 0.64| 32.63       | 0.98 | 0.51 | -1.14| 2.3  | Kantak 1979              | Web of Life   |
| 48      | Low      | Frugivore-plant| Malaysia       | 61   | 25      | 86  | 0.34| 83.68       | 11.72| 1.61 | 2.59 | 0.81| Lambert 1987            | Web of Life   |
| 49      | Low      | Frugivore-plant| Papua New Guinea| 32  | 29      | 61  | 0.07| 3.47        | 3.22 | 0.52 | 0.02 | -1.12| Mack & Wright 1996      | Web of Life   |
| 50      | Low      | Frugivore-plant| Panama         | 19   | 4       | 23  | 0.43| 9.12        | 0.98 | 0.67 | -1.45| 0.92| Poulin et al. 1999      | IWDB         |
| 51      | Low      | Frugivore-plant| Panama         | 11   | 13      | 24  | 0.37| 9.12        | 4.62 | -1.07| -0.56| 1.44| Poulin et al. 1999      | IWDB         |
| 52      | Low      | Frugivore-plant| Kenya          | 88   | 33      | 121 | 0.14| 58.97       | 12.91| -0.77| 3.43 | 0.4  | Schleuning et al. 2011  |              |
| 53      | Low      | Frugivore-plant| United Kingdom | 14   | 11      | 25  | 0.3 | 5.73        | 1.57 | -0.27| -0.96| 0.61| Sorensen 1981           | IWDB         |
| 54      | High     | Anemone-fish   | Indonesia      | 4    | 4       | 8   | 0.44| 1.36        | 1.18 | 0.82 | -1.87| 0.05| Ricciardi et al. 2010   | IWDB         |
| 55      | High     | Anemone-fish   | Indonesia      | 5    | 4       | 9   | 0.3 | 0.25        | 0.12 | 1   | -1.72| 0.03| Ricciardi et al. 2010   | IWDB         |
| 56      | High     | Anemone-fish   | Indonesia      | 4    | 4       | 8   | 0.44| 0.5         | -0.97| 0.61 | -2.09| 0.9 | Ricciardi et al. 2010   | IWDB         |
| 57      | High     | Anemone-fish   | Indonesia      | 4    | 4       | 8   | 0.38| 0.29        | -0.85| 0.74 | -1.96| 0.52| Ricciardi et al. 2010   | IWDB         |
| 58      | High     | Anemone-fish   | Indonesia      | 5    | 5       | 10  | 0.32| 0.49        | -0.53| 0.56 | -1.74| 0.33| Ricciardi et al. 2010   | IWDB         |
| 59      | High     | Anemone-fish   | Indonesia      | 5    | 4       | 9   | 0.35| 0.28        | -1.4 | 0.6  | -1.93| 0.45| Ricciardi et al. 2010   | IWDB         |
| 60      | High     | Anemone-fish   | Indonesia      | 5    | 6       | 11  | 0.33| 1.36        | 0.57 | 0.33 | -1.57| 0.52| Ricciardi et al. 2010   | IWDB         |
| 61      | High     | Anemone-fish   | Indonesia      | 5    | 4       | 9   | 0.4 | 0.69        | -0.16| 0.79 | -1.93| 0.64| Ricciardi et al. 2010   | IWDB         |
| 62      | High     | Anemone-fish   | Indonesia      | 4    | 3       | 7   | 0.5 | 0.24        | -1.65| 0.12 | -2.23| 1.44| Ricciardi et al. 2010   | IWDB         |
| 63      | High     | Anemone-fish   | Indonesia      | 4    | 4       | 8   | 0.44| 0.5         | -0.22| 0.24 | -1.94| 1.08| Ricciardi et al. 2010   | IWDB         |
| 64      | High     | Anemone-fish   | Indonesia      | 3    | 5       | 8   | 0.47| 0.5         | -0.07| 0.66 | -2.06| 1.04| Ricciardi et al. 2010   | IWDB         |
| 65      | High     | Ant-myrmecophyte| Brazil         | 6    | 5       | 11  | 0.23| 0.22        | 0.37 | 1.88 | -1.68| -0.72| Guimarães et al. 2007a  | Izzo         |
| 66      | High     | Ant-myrmecophyte| Brazil         | 9    | 7       | 16  | 0.17| 0.25        | 0.02 | 2.19 | -1.58| -1.19| Guimarães et al. 2007a  | Izzo         |
| 67      | High     | Ant-myrmecophyte| Brazil         | 13   | 8       | 21  | 0.16| 0.85        | 0.45 | 1.4  | -1.28| -0.9 | Guimarães et al. 2007a  | Izzo         |
| 68      | High     | Ant-myrmecophyte| Brazil         | 8    | 7       | 15  | 0.16| 0.31        | -1.06| 2.39 | -1.72| -1.36| Guimarães et al. 2007a  | Izzo         |
| 69      | High     | Ant-myrmecophyte| Brazil         | 12   | 9       | 21  | 0.15| 0.46        | -1.95| 2.63 | -1.75| -1.58| Guimarães et al. 2007a  | Izzo         |
| 70      | High     | Ant-myrmecophyte| Peru           | 10   | 8       | 18  | 0.15| 0.47        | -0.48| 2.26 | -1.56| -1.36| Guimarães et al. 2007a  | Izzo         |
| 71      | High     | Ant-myrmecophyte| Brazil         | 16   | 8       | 24  | 0.15| 0.86        | -1.45| 2.77 | -1.67| -1.65| Davidson et al. 1989    | IWDB         |
| 72      | High     | Ant-myrmecophyte| Brazil         | 25   | 16      | 41  | 0.12| 2.38        | 0.28 | 2.59 | -1.11| -1.76| Fonseca & Ganade 1996   | IWDB         |
Table S2. Results of the linear mixed models with the network-level trait matching as the response variable, gene flow ($g = 0$ and $g = 0.1$) and mutualism type as predictor variables, and the network identity as a random effect. For these analyses we used the following selection mosaic scenarios: two hotspots ($\bar{m}_A = \bar{m}_B = 0.9$) and one hotspot and one coldspot ($\bar{m}_A = 0.9, \bar{m}_B = 0.1$). Model: the formula for the linear mixed model as used in the R function lmer (Bates et al. 2015; R Core Team 2016); $\bar{m}_{hot,n=100} =$ mean value for 100 simulations per network of the network-level trait matching at the hotspot (locality A); $\bar{m}_{cold,n=100} =$ mean value for 100 simulations per network of the network-level trait matching at the coldspot (locality B). AIC: Akaike information criterion; Log lik: log likelihood; $\chi^2$: chi-squared value, which is equal to two times the difference between the log likelihood of two nested models; Df: degrees of freedom for the chi-squared test, which corresponds to the difference in the number of factors of two nested models.

| Model | Selection mosaic | AIC   | Log lik | $\chi^2$ | Df   | p     |
|-------|------------------|-------|---------|----------|------|-------|
| $\bar{m}_{hot,n=100} \sim (1|network)$ | hotspot/hotspot | -210.66 | 108.33  |          |      |       |
| $\bar{m}_{hot,n=100} \sim g$ + (1|network) | hotspot/hotspot | -320.3 | 164.15  | 111.64  | 1    | < 0.0001 |
| $\bar{m}_{hot,n=100} \sim g$ + mutualism + (1|network) | hotspot/hotspot | -370.21 | 194.11  | 59.92   | 5    | < 0.0001 |
| $\bar{m}_{hot,n=100} \sim g$ + mutualism + g; mutualism + (1|network) | hotspot/hotspot | -418.46 | 223.23  | 58.24   | 5    | < 0.0001 |
| $\bar{m}_{hot,n=100} \sim (1|network)$ | hotspot/coldspot | -147.84 | 76.92   |          |      |       |
| $\bar{m}_{hot,n=100} \sim g$ + (1|network) | hotspot/coldspot | -393.71 | 200.85  | 247.86  | 1    | < 0.0001 |
| $\bar{m}_{hot,n=100} \sim g$ + mutualism + (1|network) | hotspot/coldspot | -452.68 | 235.34  | 68.98   | 5    | < 0.0001 |
| $\bar{m}_{hot,n=100} \sim g$ + mutualism + g; mutualism + (1|network) | hotspot/coldspot | -459.9 | 243.95  | 17.22   | 5    | 0.0041 |
| $\bar{m}_{cold,n=100} \sim (1|network)$ | hotspot/coldspot | -580.72 | 293.36  |          |      |       |
| $\bar{m}_{cold,n=100} \sim g$ + (1|network) | hotspot/coldspot | -863.74 | 435.87  | 285.02  | 1    | < 0.0001 |
| $\bar{m}_{cold,n=100} \sim g$ + mutualism + (1|network) | hotspot/coldspot | -917.17 | 467.58  | 63.43   | 5    | < 0.0001 |
| $\bar{m}_{cold,n=100} \sim g$ + mutualism + g; mutualism + (1|network) | hotspot/coldspot | -959.61 | 493.81  | 52.44   | 5    | < 0.0001 |
Table S3. Correlations between the first two principal components (PC1 and PC2) obtained via a principal components analysis and our five metrics of network structure.

| Network metric                          | PC1   | PC2   |
|-----------------------------------------|-------|-------|
| Richness (R)                            | 0.538 | -0.232|
| Connectance (C)                         | -0.305| 0.68  |
| Degree variance ($\sigma_k^2$)          | 0.48  | 0.257 |
| Standardized nestedness (NODF)          | 0.562 | 0.066 |
| Standardized modularity (Q)             | -0.266| -0.643|

Table S4. Results of the linear regressions with the network-level trait matching as the response variable and the first or second principal component of a PCA of network structural metrics (PC1 or PC2) as the predictor variable. For these analyses we used the following selection mosaic scenarios: two hotspots ($m_A = m_B = 0.9$) and one hotspot and one coldspot ($m_A = 0.9, m_B = 0.1$). We performed regressions separately for three values of mean gene flow ($\bar{g} = 0, \bar{g} = 0.01$, and $\bar{g} = 0.1$) and for each degree of interaction intimacy (high- and low-intimacy mutualisms). We only used $\bar{g} = 0$ and $g = 0.1$ for the scenario with one hotspot and one coldspot because results for $\bar{g} = 0$ and $g = 0.01$ were similar. $\bar{r}_{\text{hot},n=100}$ = mean value for 100 simulations per network of the network-level trait matching at the hotspot (locality A); $\bar{r}_{\text{cold},n=100}$ = mean value for 100 simulations per network of the network-level trait matching at the coldspot (locality B). Df: factor and error degrees of freedom. P-values smaller than 0.05 are in bold.

| Variables | Selection mosaic | Gene flow | Intimacy | Slope   | R²   | F    | Df  | p     |
|-----------|------------------|-----------|----------|---------|------|------|-----|-------|
| $\bar{r}_{\text{hot},n=100} \sim PC1$ | hotspot/hotspot | 0         | low      | -0.022  | 0.145| 8.641| 1.51| **0.005** |
| $\bar{r}_{\text{hot},n=100} \sim PC1$ | hotspot/hotspot | 0         | high     | 0.017   | 0.008| 0.142| 1.17| 0.711  |
| $\bar{r}_{\text{hot},n=100} \sim PC1$ | hotspot/hotspot | 0.01      | low      | -0.019  | 0.164| 9.979| 1.51| **0.003** |
| $\bar{r}_{\text{hot},n=100} \sim PC1$ | hotspot/hotspot | 0.01      | high     | 0.013   | 0.008| 0.135| 1.17| 0.718  |
| $\bar{r}_{\text{hot},n=100} \sim PC1$ | hotspot/hotspot | 0.1       | low      | -0.003  | 0.02 | 1.044| 1.51| 0.312  |
| $\bar{r}_{\text{hot},n=100} \sim PC1$ | hotspot/hotspot | 0.1       | high     | 0.004   | 0.001| 0.023| 1.17| 0.882  |
| $\bar{r}_{\text{hot},n=100} \sim PC2$ | hotspot/hotspot | 0         | low      | -0.034  | 0.17 | 10.46| 1.51| **0.002** |
| $\bar{r}_{\text{hot},n=100} \sim PC2$ | hotspot/hotspot | 0         | high     | -0.022  | 0.233| 5.168| 1.17| **0.036** |
| $\bar{r}_{\text{hot},n=100} \sim PC2$ | hotspot/hotspot | 0.01      | low      | -0.027  | 0.18 | 11.24| 1.51| **0.001** |
| $\bar{r}_{\text{hot},n=100} \sim PC2$ | hotspot/hotspot | 0.01      | high     | -0.019  | 0.248| 5.598| 1.17| 0.03   |
| $\bar{r}_{\text{hot},n=100} \sim PC2$ | hotspot/hotspot | 0.1       | low      | -0.016  | 0.23 | 15.2 | 1.51| **0.0003** |
| $\bar{r}_{\text{hot},n=100} \sim PC2$ | hotspot/hotspot | 0.1       | high     | -0.015  | 0.254| 5.798| 1.17| **0.028** |
| Variables       | Selection mosaic | Gene flow | Intimacy | Slope | $R^2$ | F    | Df | p    |
|----------------|------------------|-----------|----------|-------|-------|------|----|------|
| $\tau_{hot,n=100} \sim PC1$ | hotspot/coldspot | 0         | low      | -0.024 | 0.162 | 9.871 | 1, 51 | 0.003 |
| $\tau_{hot,n=100} \sim PC1$ | hotspot/coldspot | 0         | high     | 0.011  | 0.003 | 0.054 | 1, 17 | 0.818 |
| $\tau_{hot,n=100} \sim PC1$ | hotspot/coldspot | 0.1       | low      | -0.016 | 0.206 | 13.22 | 1, 51 | 0.0006 |
| $\tau_{hot,n=100} \sim PC1$ | hotspot/coldspot | 0.1       | high     | 0.00001 | 0 | 0 | 1, 17 | 0.999 |
| $\tau_{hot,n=100} \sim PC2$ | hotspot/coldspot | 0         | low      | -0.033 | 0.162 | 9.877 | 1, 51 | 0.003 |
| $\tau_{hot,n=100} \sim PC2$ | hotspot/coldspot | 0         | high     | -0.022 | 0.226 | 4.955 | 1, 17 | 0.04 |
| $\tau_{hot,n=100} \sim PC2$ | hotspot/coldspot | 0.1       | low      | -0.022 | 0.189 | 11.89 | 1, 51 | 0.001 |
| $\tau_{hot,n=100} \sim PC2$ | hotspot/coldspot | 0.1       | high     | -0.015 | 0.138 | 2.717 | 1, 17 | 0.118 |
| $\tau_{cold,n=100} \sim PC1$ | hotspot/coldspot | 0         | low      | -0.001 | 0.147 | 8.78 | 1, 51 | 0.005 |
| $\tau_{cold,n=100} \sim PC1$ | hotspot/coldspot | 0         | high     | 0.009  | 0.114 | 2.193 | 1, 17 | 0.157 |
| $\tau_{cold,n=100} \sim PC1$ | hotspot/coldspot | 0.1       | low      | -0.003 | 0.169 | 10.41 | 1, 51 | 0.002 |
| $\tau_{cold,n=100} \sim PC1$ | hotspot/coldspot | 0.1       | high     | 0.008  | 0.029 | 0.505 | 1, 17 | 0.487 |
| $\tau_{cold,n=100} \sim PC2$ | hotspot/coldspot | 0         | low      | -0.001 | 0.115 | 6.611 | 1, 51 | 0.013 |
| $\tau_{cold,n=100} \sim PC2$ | hotspot/coldspot | 0         | high     | -0.002 | 0.069 | 1.258 | 1, 17 | 0.278 |
| $\tau_{cold,n=100} \sim PC2$ | hotspot/coldspot | 0.1       | low      | -0.004 | 0.184 | 11.5 | 1, 51 | 0.001 |
| $\tau_{cold,n=100} \sim PC2$ | hotspot/coldspot | 0.1       | high     | -0.0003 | 0.0007 | 0.012 | 1, 17 | 0.915 |
Figure S1. Examples of coevolutionary dynamics in a pollinator-plant network (network 25 in Table S1) in two isolated (top; \( g = 0 \)) or connected (bottom; \( g = 0.1 \)) hotspots. The trajectory of the mean trait value \((z_i)\) of all 12 pollinators (black) and 10 plants species (grey) present in the network is shown for both localities. Closer trait values indicate higher trait matching. The coevolutionary dynamics reached equilibrium when trait values stayed fixed over time. In both simulations, the mean importance of mutualistic selection was the same at both localities \((\bar{m}_A = \bar{m}_B = 0.9)\). Trait values started at the selected value in relation to the local environment \((z_{i,A}(0) = \theta_{i,A} \text{ and } z_{i,B}(0) = \theta_{i,B})\). Except for gene flow \((g)\), species parameter values were the same in both simulations.
**Figure S2.** Examples of coevolutionary dynamics in a pollinator-plant network (network 25 in Table S1) in isolated (top; $g = 0$) or connected (bottom; $g = 0.1$) hotspot and coldspot. The trajectory of the mean trait value ($z_i$) of all 12 pollinators (black) and 10 plants species (grey) present in the network is shown for both localities. Closer trait values indicate higher trait matching. The coevolutionary dynamics reached equilibrium when trait values stayed fixed over time. In both simulations, the mean importance of mutualistic selection was $\overline{m}_A = 0.9$ at the hotspot and $\overline{m}_B = 0.1$ at the coldspot. Trait values started at the selected value in relation to the local environment ($z_{iA}(0) = \theta_{iA}$ and $z_{iB}(0) = \theta_{iB}$). Except for gene flow ($g_i$), species parameter values were the same in both simulations.
Figure S3. Changes in the distribution of pairwise trait matching ($\tau_{ij}$) and in the network-level trait matching ($\bar{f}$) through coevolution in a pollinator-plant network (network 25 in Table S1) in two isolated (top; $\bar{g} = 0$) or connected (bottom; $\bar{g} = 0.1$) hotspots. The initial (light grey) and final (black) distribution of pairwise trait matching and value of network-level trait matching (dashed vertical line) are depicted for the two simulations. The change in the network-level trait matching occurred through a change in the distribution of pairwise trait matching. While a fraction of species pairs showed a poor final trait matching in the absence of gene flow (top; $\bar{g} = 0$),
0; black distribution), almost all species pairs showed an elevated final trait matching when gene flow was high (top; $g = 0.1$; black distribution). In both simulations, the mean importance of mutualistic selection was the same at both localities ($\bar{m}_A = \bar{m}_B = 0.9$). Except for gene flow ($g$), species parameter values were the same in both simulations.

Figure S4. The effects of gene flow on the variation in pairwise trait matching ($\tau_{ij}$) in two connected hotspots. Gene flow reduced the standard deviation of the final pairwise trait matching ($\sigma_{\tau_A}$). Low-intimacy mutualisms (blue, purple, and green points) showed greater values of $\sigma_{\tau_A}$. However, the decrease in $\sigma_{\tau_A}$ with gene flow was more pronounced in low-intimacy mutualisms as compared to high-intimacy mutualisms (orange and red points). Each point corresponds to the mean of the standard deviation of pairwise trait matching for 100 simulations for a given network ($\bar{\sigma}_{\tau_A,n=100}$). The mean importance of mutualistic selection was $\bar{m}_A = \bar{m}_B = 0.9$. 

- anemone–fish
- ant–myrmecophyte
- ant–EFN
- cleaner–client
- frugivore–plant
- pollinator–plant
Figure S5. The effects of gene flow on the emergence of trait matching at a hotspot for different selection mosaics. Gene flow decreased the network-level trait matching ($\bar{\tau}_A$) generated by coevolution at a hotspot (locality $A$: $\bar{m}_A = 0.9$) when it was connected to a coldspot (locality $B$: $\bar{m}_B = 0.1$; far left; same as Fig. 2b). This effect of gene flow changes gradually as the importance of mutualistic selection increases at the coldspot ($\bar{m}_A = 0.9, \bar{m}_B = 0.3, \bar{m}_B = 0.5, \bar{m}_B = 0.7, \bar{m}_B = 0.9$). When both localities are hotspots ($\bar{m}_A = 0.9, \bar{m}_B = 0.9$; far right; same as Fig. 2a), gene flow increased the network-level trait matching generated by coevolution. In all plots, each point corresponds to the mean of the network-level trait matching for 100 simulations for a given network ($\bar{\tau}_{A,n=100}$).

Figure S6. The effects of gene flow on the emergence of trait matching for different selection mosaics. Gene flow promoted a slight increase in the network-level trait matching ($\bar{\tau}_B$) generated by coevolution at a coldspot (locality $B$: $\bar{m}_B = 0.1$) when it was connected to a hotspot (locality $A$: $\bar{m}_A = 0.9$; far left; same as Fig. 2c). This effect of gene flow is gradually enhanced as the importance of mutualistic selection at locality $B$ increases ($\bar{m}_A = 0.9, \bar{m}_B = 0.3, \bar{m}_B = 0.5, \bar{m}_B = 0.7, \bar{m}_B = 0.9$). When both localities are hotspots ($\bar{m}_A = 0.9, \bar{m}_B = 0.9$; far right; same as Fig. 2a), gene flow increased the network-level trait matching generated by coevolution. In all plots, each point
corresponds to the mean of the network-level trait matching for 100 simulations for a given network ($\bar{m}_{B,n=100}$).
plots, each point corresponds to the mean of the network-level environmental matching for 100 simulations for a given network ($\varepsilon_{B,n=100}$).

**Figure S9.** The effects of gene flow on the geographical divergence in species traits for different selection mosaics. Gene flow greatly decreased the network-level geographical divergence ($\delta$) irrespective of the selection mosaic ($\bar{m}_A = 0.9, \bar{m}_B = 0.1, \bar{m}_A = 0.3, \bar{m}_B = 0.5, \bar{m}_B = 0.7, \bar{m}_B = 0.9$). This means that gene flow has an effect of homogenizing species traits across space. The decrease in geographical divergence with gene flow was stronger when both localities were hotspots ($\bar{m}_A = 0.9, \bar{m}_B = 0.9$; far right). In all plots, each point corresponds to the mean of the network-level geographical divergence for 100 simulations for a given network ($\delta_{n=100}$).
**Figure S10.** Mutualistic network structure mediates the effects of gene flow on coevolution when a hotspot is connected to a coldspot. Our PCA with network structure metrics showed that PC1 was positively correlated with species richness and nestedness and PC2 was positively correlated with connectance and negatively correlated with modularity. At the hotspot (top row), PC1 and PC2 affected the emergence of trait matching for $\bar{g} = 0$ and $\bar{g} = 0.1$ in low-intimacy mutualisms (blue, purple, and green points; Table S4). For high-intimacy mutualisms (orange and red points), only PC2 affected the emergence of trait matching with no gene flow ($\bar{g} = 0$; Table S4). At the coldspot (bottom row), PC1 and PC2 had a small effect on the emergence of trait matching for $\bar{g} = 0$ and $\bar{g} = 0.1$, but only for low-intimacy mutualisms (Table S4). This effect, however, was stronger with high gene flow ($\bar{g} = 0.1$; Table S4). In all plots, each point corresponds to the mean of the network-level trait matching for 100 simulations for a given network ($\bar{r}_{A,n=100}$ or $\bar{r}_{B,n=100}$). The mean importance of mutualistic selection was $\bar{m}_A = 0.9$ at the hotspot and $\bar{m}_B = 0.1$ at the coldspot.
Figure S11. The combined effects of gene flow and symmetric selection mosaics on the emergence of trait matching for two networks with contrasting structures. Overall, the network-level trait matching ($\bar{r}_A$) was higher for the ant-myrmeccophyte network (top; network 65 in Table S1) than for the pollinator-plant network (bottom; network 29 in Table S1). For the ant-myrmeccophyte network (top) the network-level trait matching was mainly affected by the importance of mutualistic selection ($\bar{m}_A$ and $\bar{m}_B$) and gene flow ($\bar{g}$) had a weak effect. In contrast, for the pollinator-plant network (bottom) the network-level trait matching was affected by both the importance of
mutualistic selection and gene flow. However, the effect of gene flow was only important for high values of $m_A$ and $m_B$ (i.e. two connected hotspots). In these simulations, the importance of mutualistic selection was the same at both localities (symmetric selection mosaic: $m_A = m_B$). In both plots, the color of each square corresponds to the mean of the network-level trait matching at locality $A$ for 100 simulations ($f_{A,n=100}$). Networks depict the interactions between animal (black) and plant species (grey).
**Figure S12.** The combined effects of gene flow and asymmetric selection mosaics on the emergence of trait matching for two networks with contrasting structures. Overall, the network-level trait matching ($\bar{\tau}_A$) was higher for the ant-myrmecophyte network (top; network 65 in Table S1) than for the pollinator-plant network (bottom; network 29 in Table S1). However, the combination of gene flow ($\bar{g}$) and importance of mutualistic selection ($\bar{m}_A$ and $\bar{m}_B$) had a similar effect in both networks. Specifically, gene flow reduced the network-level trait matching, but only when $\bar{m}_A$ was high and $\bar{m}_B$ was low (i.e. a hotspot connected to a coldspot; top part of both plots). In these
simulations, the importance of mutualistic selection was asymmetric between localities ($\tilde{m}_A = 1 - m_B$). In both plots, the color of each square corresponds to the mean of the network-level trait matching at locality $A$ for 100 simulations ($\bar{\tilde{r}}_{A,n=100}$). Networks depict the interactions between animal (black) and plant species (grey).

**Figure S13.** Influence of the initial trait values on the final value of trait matching in one isolated hotspot (i.e. $\tilde{g} = 0$). Each point represents the network-level trait matching ($\tilde{r}_A$) of a pair of simulations with the same parameter values, but with different initial conditions (10 pairs of simulations per network: total = 1440 simulations). The y axis represents the network-level trait matching of simulations in which traits started at the environmental optimum values (i.e. $\bar{z}_{i,A}(0) = \bar{\theta}_{i,A}$ and $\bar{z}_{i,B}(0) = \bar{\theta}_{i,B}$). The x axis represents the network-level trait matching of simulations in which traits started at the equilibrium for the coevolutionary dynamics with high gene flow ($\tilde{g} = 0.1$). Points that fall on the black line ($y = x$) have the same final value of the network-level trait matching for both simulations. Points that do not fall on the black line indicate that different initial conditions generated different values of the network-level trait matching. The mean importance of mutualistic selection in these simulations was $\bar{m}_A = \bar{m}_B = 0.9$. 


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