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Author for correspondence:

Leandro G. Cosmo

e-mail: lvcosmo@usp.br

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Mutualistic coevolution and community diversity favour persistence in metacommunities under environmental changes

Leandro G. Cosmo¹, Lilian P. Sales^{3,4}, Paulo R. Guimarães Jr² and Mathias M. Pires³

¹Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo - USP, São Paulo, SP, Brazil

²Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo - USP, São Paulo, SP, Brazil

³Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas - UNICAMP, Campinas, SP, Brazil

⁴Biology Department, Faculty of Arts and Science, Concordia University, Montreal, Canada

LGC, 0000-0003-2541-2645

Linking local to regional ecological and evolutionary processes is key to understand the response of Earth's biodiversity to environmental changes. Here we integrate evolution and mutualistic coevolution in a model of metacommunity dynamics and use numerical simulations to understand how coevolution can shape species distribution and persistence in landscapes varying in space and time. Our simulations show that coevolution and species richness can synergistically shape distribution patterns by increasing colonization and reducing extinction of populations in metacommunities. Although conflicting selective pressures emerging from mutualisms may increase mismatches with the local environment and the rate of local extinctions, coevolution increases trait matching among mutualists at the landscape scale, counteracting local maladaptation and favouring colonization and range expansions. Our results show that by facilitating colonization, coevolution can also buffer the effects of environmental changes, preventing species extinctions and the collapse of metacommunities. Our findings reveal the mechanisms whereby coevolution can favour persistence under environmental changes and highlight that these positive effects are greater in more diverse systems that retain landscape connectivity.

1. Introduction

Species are subjected to natural spatio-temporal variation in environmental conditions, but to persist in a changing environment a species may need to track suitable environment by colonizing novel sites or quickly adapt to novel local conditions [1–4]. Colonization success and adaptation are not fully determined by the abiotic environment but modulated by the multiple ecological interactions species establish in local ecological communities. Mutualisms, for instance, can increase dispersal potential [5] as well as allow species to expand their realized niches by increasing environmental suitability under unfavourable conditions [6]. Ecological interactions may also give rise to coevolutionary dynamics when species exert reciprocal selective pressures on each other [7–10]. Evolution in response to the physical environment and coevolutionary outcomes emerging from interactions may either converge, accelerating local adaptation, or diverge, generating conflicting dynamics [11–13]. The interplay between evolution and coevolution might, therefore, shape the response of biodiversity to changing environments [14]. How evolution in response to environmental and biotic pressures shape biodiversity patterns is a pressing question in the context of the global anthropogenic changes and the rise of novel biotas [15–20].

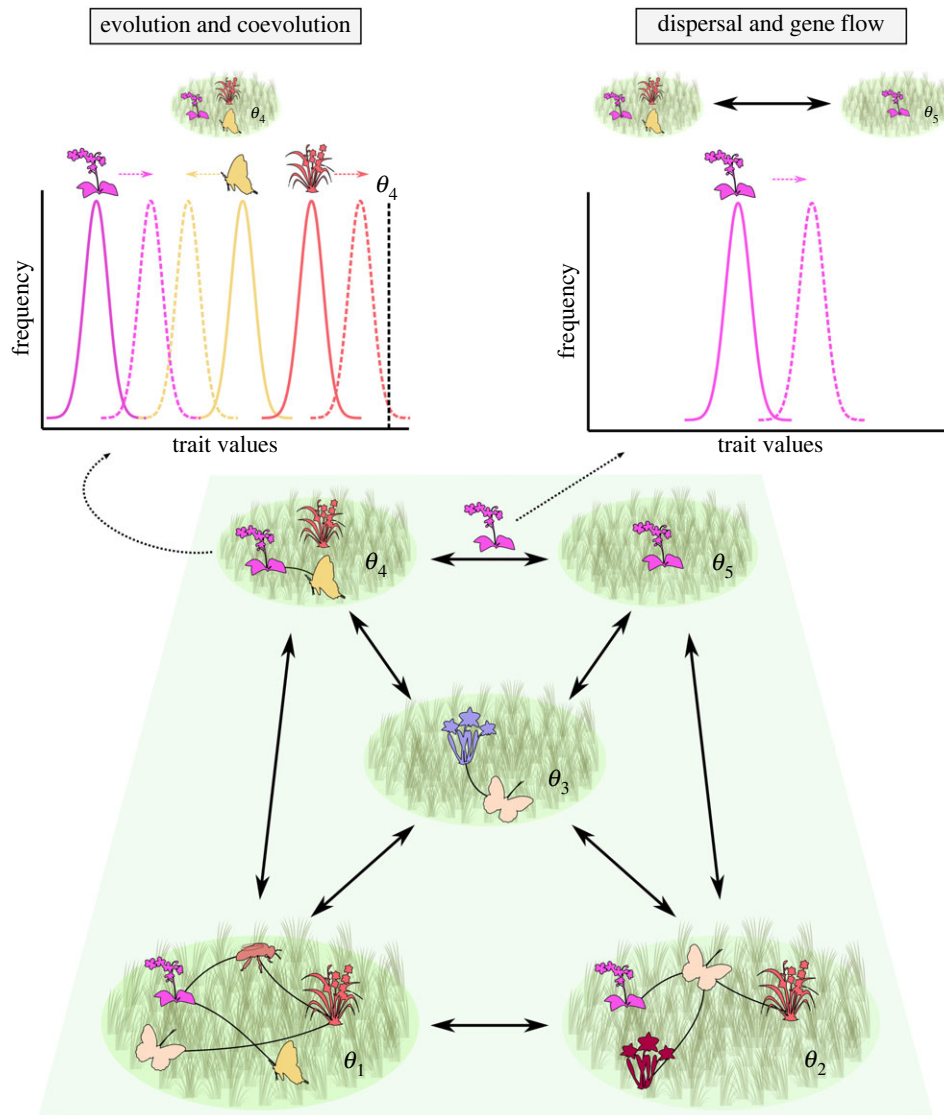


Figure 1. Representation of coevolving mutualists in a metacommunity. Within local patches, populations of different species (here indicated as coloured silhouettes) are subjected to different selective pressures imposed by local the environment (θ). In addition, species within local communities interact forming networks with varying configurations (interactions are depicted as solid lines connecting silhouettes within patches). While species-species interactions promote coevolution, traits also evolve in response to the selective pressures of the local environment (as represented in the upper panels). Trait evolution is depicted in the upper left panels as the change in the mean value of traits from the current generation (solid lines) to the next generation (dashed lines). At the regional scale, local populations can colonize other patches or become locally extinct, reshaping the distribution of genotypes and phenotypes in the metacommunity (from the solid to the dashed lines in the upper right panel). Under this framework, the colonization dynamics connects the local effects of evolution and coevolution to other patches in the metacommunity.

Empirical and theoretical studies have shed light on the consequences of mutualistic coevolution for interacting species [10,21,22]. Coevolution between mutualistic pairs favours the complementarity of traits, for instance, when the mouth parts of a pollinating insect matches the floral tube of a plant [23]. In this context, trait complementarity may increase the overall survival and reproduction of mutualistic partners, but it may also lead to highly specialized and intimate interactions in which the loss of a mutualistic partner highly increases the risk of co-extinctions [24–26]. Progressing to species-rich communities, theory predicts that coevolution can increase the similarity of traits among all mutualists resulting in evolutionary convergence [27–30]. In a changing environment, trait similarity may prevent co-extinctions because convergence increases functional redundancy, allowing mutualists to compensate for the extinction of partners through rewiring [31,32]. Thus, pairwise and multispecies coevolution may lead to different outcomes: from an increased

risk of coextinction to the coevolutionary rescue of ecological functions from environmental changes.

When considering larger spatial scales, however, the outcome of coevolution may further depend on how populations of the same species are distributed and connected through gene flow across space [10]. Spatial heterogeneity may impose different local evolutionary regimes, but colonization dynamics may alter the distribution of genotypes and phenotypes of populations across space, which feeds back and affects local evolutionary and coevolutionary dynamics [33–38] (figure 1). For instance, variation in mutualistic selection across space can create geographical mosaics of adaptation [39–44]. By contrast, when two species-rich, local communities are linked by gene flow, mutualistic coevolution increases the convergence and matching of traits among all species of the two local communities [45]. While the effects of spatial processes on coevolution are starting to be unravelled [39,41,42,45,46], we still know little about how coevolution can affect distribution patterns in a

heterogeneous environment or whether coevolution favours or hinders persistence across space under environmental changes.

Here, we use numerical simulations to investigate how patterns of adaptation and coadaptation in two-species and multispecific scenarios affect patterns of population persistence in heterogeneous and changing environments. To do so, we developed a spatially explicit framework of a coevolving metacommunity by combining a mathematical model of evolution (in response to environmental selection) and coevolution (in response to mutualistic interactions) with colonization and extinction dynamics. Specifically, we explored the following questions: (1) how does coevolution in species-rich communities affects patterns of colonization, extinctions and the persistence of populations at the metacommunity scale? (2) How does coevolution in species-rich communities affect the persistence of local populations and species under environmental changes? The results of our numerical simulations show that mutualistic coevolution and species richness synergistically drive patterns of occupancy, colonization, extinction and trait matching in metacommunities. Furthermore, we show that coevolution can buffer negative effects of environmental changes, preventing the extinction of species and the collapse of metacommunities, especially in species-rich systems.

2. Methods

(a) Model description

We developed a spatially explicit metacommunity modelling framework that combines a coevolutionary model with colonization and extinction dynamics in a cellular automaton representing an ecological metacommunity where populations of S species can occur within any of K patches. Our model builds upon previous models of mutualisms in metacommunities [47–49]. However, instead of assuming fixed colonization and rates, we explicitly link these rates to the mean trait values of populations via a patch suitability function. We motivate our model using plant–insect mutualisms such as those between plants and insect pollinators. However, our overall framework can also be applied to other mutualistic interactions mediated by a trait matching mechanism, for instance, birds that disperse seeds [50]. For simplicity, we assumed that of the total pool of S species there are $S/2$ plants and $S/2$ animals in the metacommunity. The populations of plants and animals are assumed to be sufficiently large so that each one can be described by the mean trait value, z , of its individuals. Furthermore, we assumed that at each patch K there is a different environmental optimum for each species i , which can be summarized by a single value, θ_{ik} . Biologically this value can be interpreted as an average value of all the environmental factors in a patch that significantly affect the fitness of species i , for instance, linear combinations of variables related to temperature and precipitation. We initially assumed that the local environmental optimum of each species i at each patch k , θ_{ik} , did not vary over time (figure 1). By doing so, we simulated a heterogeneous but constant adaptive landscape where each local population is subjected to selective forces from the environment and from the local mutualistic partners. Later, we evaluated the effect of environmental change on emerging patterns of coevolution, colonization and extinction at the metacommunity level by varying the local environmental optima of species over time.

Each of these K patches can be occupied by one population of each species. When populations of plants and animals co-occur, they may interact and exert selective pressures on each other. Because functional mutualistic interactions often depend on the matching of the traits of the interacting individuals [26] (e.g. when the mouth part of an insect pollinator matches the floral

tube of a plant), we modelled the probability of successful interactions as a trait matching rule:

$$p(a_{ijk}^{(t)} = 1) = e^{-\alpha(z_{jk}^{(t)} - z_{ik}^{(t)})^2}, \quad (2.1)$$

in which $p(a_{ijk}^{(t)} = 1)$ is the probability of a successful interaction between individuals of co-occurring populations of species i and j in patch k , and α is a parameter that controls how sensitive $p_{ijk}^{(t)}$ is to differences between the trait values of species i , $z_{ik}^{(t)}$, and species j , $z_{jk}^{(t)}$.

At each time step of our model four events occur. First, at each patch k a local interaction network is formed by the local pairwise interactions according to equation (2.1). Second, the populations of each species evolve (see below) in response to the selective pressures of the environment and, when they interact, coevolve in response to their mutualistic partner's traits. Third, following evolution and coevolution, these populations can colonize adjacent patches. Finally, after all populations had the opportunity to colonize adjacent patches, local populations may become extinct depending on the local species-specific patch suitability.

(b) Evolution and coevolution

In our model, mutualistic interactions are a function of the trait matching between populations of different species and may change as populations evolve. As a consequence, at each time step of the model these interactions can give rise to distinct local interaction networks. To model evolution and coevolution, we adapted a model of coevolution in mutualistic networks [51] to our framework. This coevolutionary model is grounded on quantitative genetics [52] and connects the evolution of species' traits to the mean fitness consequences of mutualistic interactions and other selective pressures in the environment. For a given population of species i , in patch k , the change in the mean trait value z_{ik} from one generation to the next is given by:

$$z_{ik}^{(t+1)} = z_{ik}^{(t)} + \sigma_{Gz_{ik}}^2 \frac{\partial \ln(\bar{w}_{ik})}{\partial z_{ik}^{(t)}}, \quad (2.2)$$

where $\sigma_{Gz_{ik}}^2$ is the additive genetic variance of trait z_i at patch k and the selection gradient, $\partial \ln(\bar{w}_{ik}) / \partial z_{ik}^{(t)}$ describes how a change in the mean value of z_{ik} affects the mean fitness, \bar{w}_{ik} of population i . We assumed that mutualistic interactions contribute with a proportion m_{ik} to the selection gradient, while other selective pressures in the environment contributes with $1 - m_{ik}$. Hence, the higher the value of m_{ik} , the stronger the effects of mutualistic interactions on the mean fitness of populations and therefore, on trait evolution when compared to other selective pressures in the environment. Because of the dependence of some mutualisms on trait complementarity [28,53], we assumed that the selection gradient favours complementarity with the traits of co-occurring mutualistic partners (z_{jk}) and with other selective pressures of the environment in patch k (θ_k):

$$z_{ik}^{(t+1)} = z_{ik}^{(t)} + \sigma_{Gz_{ik}}^2 \left[m_{ik} \sum_{j=1, j \neq i}^S q_{ijk}^{(t)} (z_{jk}^{(t)} - z_{ik}^{(t)}) + (1 - m_{ik})(\theta_k - z_{ik}^{(t)}) \right]. \quad (2.3)$$

The parameter q_{ijk} controls the sensitivity of species fitness to the function that defines the selection gradient, i.e. the terms within the brackets. These terms within brackets correspond to the fitness effects of trait matching with mutualistic partners and the fitness effects of trait matching with the environment, respectively. We defined $q_{ijk}^{(t)}$ as the importance of a given mutualistic partner j for species i at time t and at patch k and assumed that $q_{ijk}^{(t)}$ depends on a trait matching rule relative to all mutualistic partners:

$$q_{ijk}^{(t)} = m_{ik} \frac{a_{ijk}^{(t)} e^{-\alpha(z_{jk}^{(t)} - z_{ik}^{(t)})^2}}{\sum_{j=1, j \neq i}^S a_{ijk}^{(t)} e^{-\alpha(z_{jk}^{(t)} - z_{ik}^{(t)})^2}}. \quad (2.4)$$

Furthermore, we assume that if $\sum_{j=1, j \neq i}^S a_{ijk}^{(t)} = 0$, i.e. at a given time step, species i does not interact with any mutualist at patch k , then $m_{ik} = 0$ and all the evolution of trait $z_{ik}^{(t)}$ occurs only in response to the environment θ_{ik} :

$$z_{ik}^{(t+1)} = z_{ik}^{(t)} + \sigma_{Gz_{ik}}^2 e_{ik} (\theta_{ik} - z_{ik}^{(t)}). \quad (2.5)$$

Because some of the parameters used in the model such as m_{ik} and q_{ik} , are hard to estimate, especially in a multispecific context, we could not parameterize the model based on empirical systems. Thus, we explore a wide range of variation in those parameters in our analyses to understand whether our results are robust to parameter choice (see below).

(c) Patch suitability, colonization and extinction

Following evolution and coevolution, at each time step, species can colonize empty adjacent patches depending on how suitable the patch is to the colonizing species. Thus, similar to what is observed in empirical systems, the abiotic and biotic features filter whether or not colonization of adjacent patches will be successful [54–56]. To simplify species-environment relationships, we assumed that the suitability of patch k for species i , $\gamma_{ik}^{(t)}$, depends exclusively on the mean trait complementarity with mutualistic partners and the trait complementarity with the environment, according to:

$$\gamma_{ik}^{(t)} = e^{-e_{ik} \left[m_{ik} \left(\sum_{j=1, j \neq i}^S a_{ijk}^{(t)} (z_{jk}^{(t)} - z_{ik}^{(t)})^2 / \sum_{j=1, j \neq i}^S a_{ijk}^{(t)} + (1 - m_{ik}) (\theta_{ik} - z_{ik}^{(t)})^2 \right) \right]}. \quad (2.6)$$

Thus, $0 < \gamma_{ik}^{(t)} \leq 1$ and assumes its maximum value ($\gamma_{ik}^{(t)} = 1$) only when traits perfectly match the traits of all mutualistic partners and the environmental optimum. Furthermore, in equation (2.6) suitability increases only if species traits match both mutualistic partners traits and the local environmental optimum. Because we only model facultative mutualisms, if a patch k does not hold any mutualistic partner (i.e. $\sum_{j=1, j \neq i}^S a_{ijk}^{(t)} = 0$), we set $m_{ik} = 0$ and assumed that the suitability of the patch k is solely determined by the trait complementarity with the environment:

$$\gamma_{ik}^{(t)} = e^{-e_{ik} (\theta_{ik} - z_{ik}^{(t)})^2}. \quad (2.7)$$

In the colonization events, each species in each patch can colonize empty patches among any of the other eight adjacent patches with periodic boundary conditions (i.e. the Moore neighbourhood in a cellular automata). We assume that the probability of success of each colonization event is equal to the suitability of each k adjacent patch, $s_{ik}^{(t)}$. When a colonization event is successful, if the patch that receives dispersers is already occupied by another population of the same species, then there is gene flow among the dispersing and resident populations. For simplicity, we assume that following dispersal the new mean trait value of a population of a given species is comprised of a fraction of 0.95 of the resident population trait value and another 0.05 fraction averaged over the trait values of all other successfully dispersing populations of that species. If the patch is not already occupied by a population of the same species, it is then occupied with a trait value composed of the average trait values of all successfully dispersing populations. We also explored situations in which the contribution of gene flow is larger than 0.05 (from 0.1 to 0.5 in 0.1 steps), which yielded similar qualitative results (electronic supplementary material, Information).

Besides affecting colonization, we assume suitability also determines population persistence. We assumed that the extinction of a given population of species i that occurs in patch k depends on the suitability of the occupied patch for that species and occurs with probability $1 - \gamma_{ik}^{(t)}$. Thus, we modelled both the colonization of adjacent patches and extinction of populations as probabilistic events that depend on the suitability of patches. A given population will be more likely to colonize patches with greater suitability and undergo extinction in those patches where suitability is low or has

become lower over time. Although we are specifically interested in colonization/extinction dynamics, we implicitly model demographic effects because fitness vary across time and space and environmental suitability affects local population density [57].

(d) Numerical simulations

We performed numerical simulations of our model using the Julia programming language v. 1.5.3 [58]. In these simulations we explored how different levels of strength of mutualistic interactions ($m_{ik} = 0.0 - 0.9$), species richness (2, 4, 8, 16 and 32 species) and spatial and temporal variation in the environment affected patterns of distribution of traits and populations in the metacommunity. For simplicity, we initially fixed the relative importance of mutualisms, m_{ik} , to be the same for all species in all patches in each simulation.

We ran 100 simulations per combination of value of m_{ik} , species pool and environmental conditions (fixed versus changing environment). At the beginning of each simulation, we sampled the values of the environmental optimum (θ_{ik}) and initial trait values from a uniform distribution $U[0, 10]$. To avoid situations in which all populations of a given species become extinct at the beginning of the simulation, the initial number of populations for all species were fixed as \sqrt{K} . For convenience we fixed the number of patches K to 100 (hence the initial number of populations of each species to 10). All simulations ran for 1200 time steps, which was enough for species traits in all patches to achieve quasi-equilibrium values.

To test how coevolution can modulate the response to environmental changes, we performed simulations while assuming directional changes on the environmental optima of each patch. We simulate environmental change by incrementing the values of the environmental optimum (θ_{ik}) by 0.25 at the end of each time step. In these simulations, all the remaining parameters of the model were held fixed and were the same for all populations/species ($\sigma_{Gz_{ik}}^2 = 1.0$, $q_{ik} = 0.1$, $\alpha = 0.1$). Since the strength of mutualistic interactions can also vary across space [10], we also performed an additional set of simulations in which we allowed m_{ik} to vary among patches (electronic supplementary material, Information). Varying m_{ik} across the space from neutral ($m_{ik} = 0$) to strong ($m_{ik} = 1.0$) allowed us to test how a geographical mosaic of coevolution can affect species response to environmental changes. Furthermore, we also explored the sensitivity of our model to different parameter values (increasing q_{ik} in 10% steps up to a 50% increase, from 0.1 to 0.15) which yielded equivalent results (electronic supplementary material, Information).

At the end of each simulation, we measured six state variables. All variables were averaged across all time steps and species. We measured: (1) the trait matching (calculated via equation (2.1)) of species with mutualistic partners at local patches averaged over all partners; (2) the average trait matching between all possible pairs of species in the entire metacommunity (hereinafter called regional trait matching); (3) patch occupancy, defined as the proportion of patches occupied by populations of a given species; (4) the fraction of successful colonization events, defined as the proportion of successful colonization attempts in subsequent time steps; (5) the fraction of populations' extinctions, defined as the proportion of all populations that went extinct in subsequent time steps; and (6) the fraction of the total regional pool of surviving species at the end of simulations.

3. Results

(a) Coevolution and species richness shapes colonization and extinction dynamics

We first performed simulations of our model in a scenario in which the environment is heterogeneous but static over time.

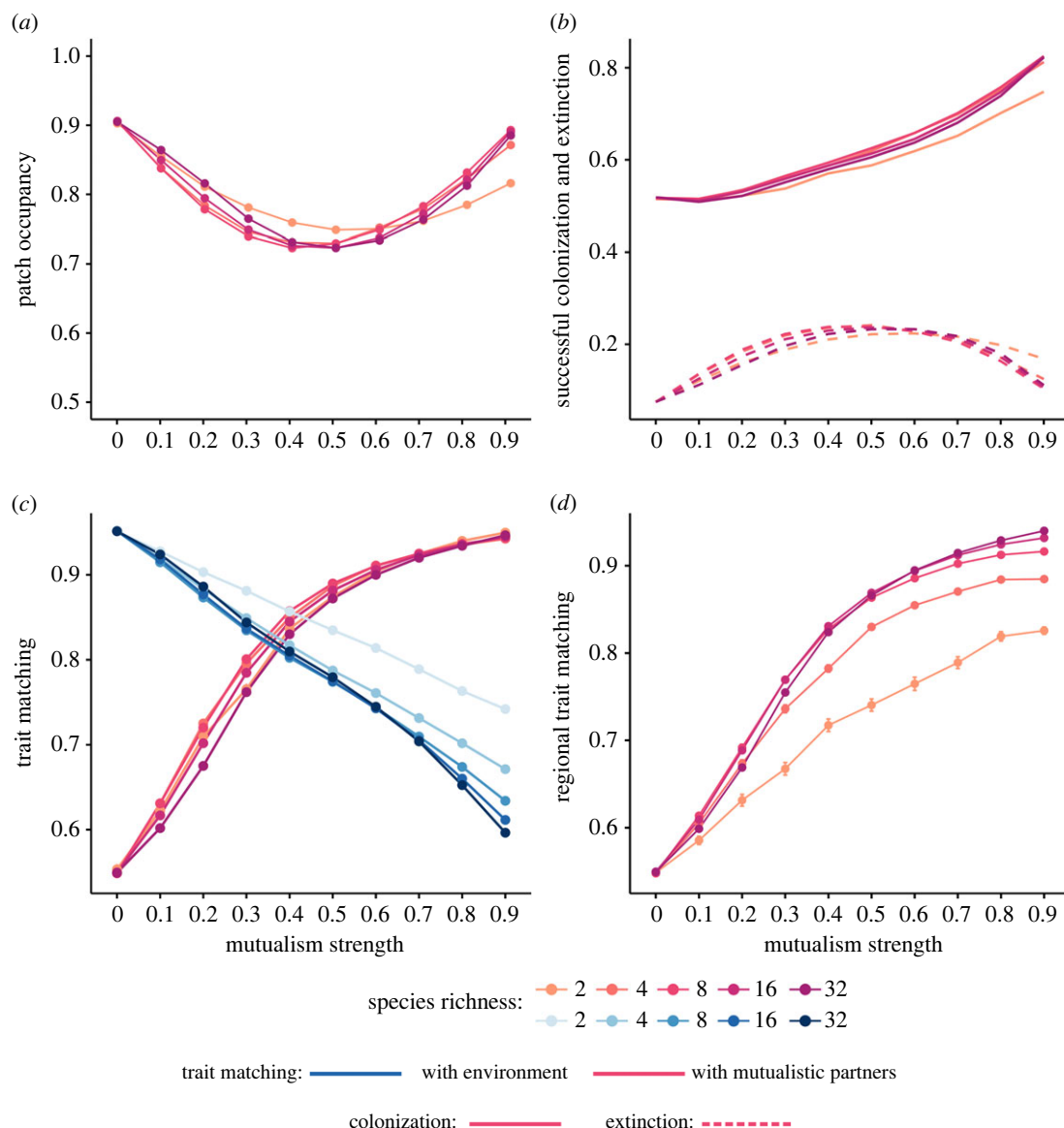


Figure 2. Mutualistic coevolution shapes patterns of (a) occupancy, (b) colonization and extinction and (c,d) trait matching in metacommunities. In (b), solid lines represent the rate of colonization and dashed lines the rate of extinction of populations. On panel (c), green lines and points represent the local trait matching of populations with the environment, while red lines the local trait matching with mutualistic partners. Points represents the mean value for 100 simulations and bars 95% confidence intervals. Parameter values are as follows: $m_{ik} = 0.0 - 0.9$, $\sigma_{\alpha_{ik}}^2 = 1.0$, $Q_{ik} = 0.1$, $\alpha = 0.1$.

Our simulations show that under this scenario, multispecific coevolution has nonlinear effects on metacommunity dynamics. Up to moderate levels of mutualism strength ($m_{ik} = 0.1 - 0.5$), coevolution decreases patch occupancy (figure 2a). However, as m_{ik} increases further, patch occupancy goes back to the same levels as the scenario without coevolution ($m_{ik} = 0$, figure 2a). Such changes in patch occupancy occur because at low levels of m , mutualistic coevolution simultaneously increases the rate of successful colonization and the rate of local extinctions (figure 2b). The rates of colonization and extinction are further modulated by species richness such that for the same levels of m_{ik} higher species richness in the metacommunity increased the rate of colonization relative to the rate of local extinction (figure 2b). The effects of coevolution on colonization and extinction rates result from how coevolution shapes patterns of local and regional trait matching in the metacommunity (figure 2c,d). As m_{ik} increases, the conflicting selective pressure from mutualisms decreases the local trait matching of populations with the environment, increasing local extinctions (figure 2c). However, at high m , trait matching

with mutualistic partners throughout the entire metacommunity, compensates mismatches with the environment, by increasing the likelihood that populations have suitable mutualistic partners at any patch, which increases the rate of successful colonization (figure 2d). Local and regional trait matching also increase with species richness, which explains why increasing richness has a positive effect on occupancy (figure 2c,d).

(b) Coevolution and species richness buffer the effects of environmental changes

We next performed simulations in which the environment changes over time. Our simulations show that when coevolution strength is low, patch occupancy is much lower than expected for static environmental settings (figure 3a). Increasing coevolution strength and species richness raises occupancy sharply by synergistically creating a more positive balance between the rates of population colonization and extinction (figure 3b). Indeed, as coevolution strength increases, mean

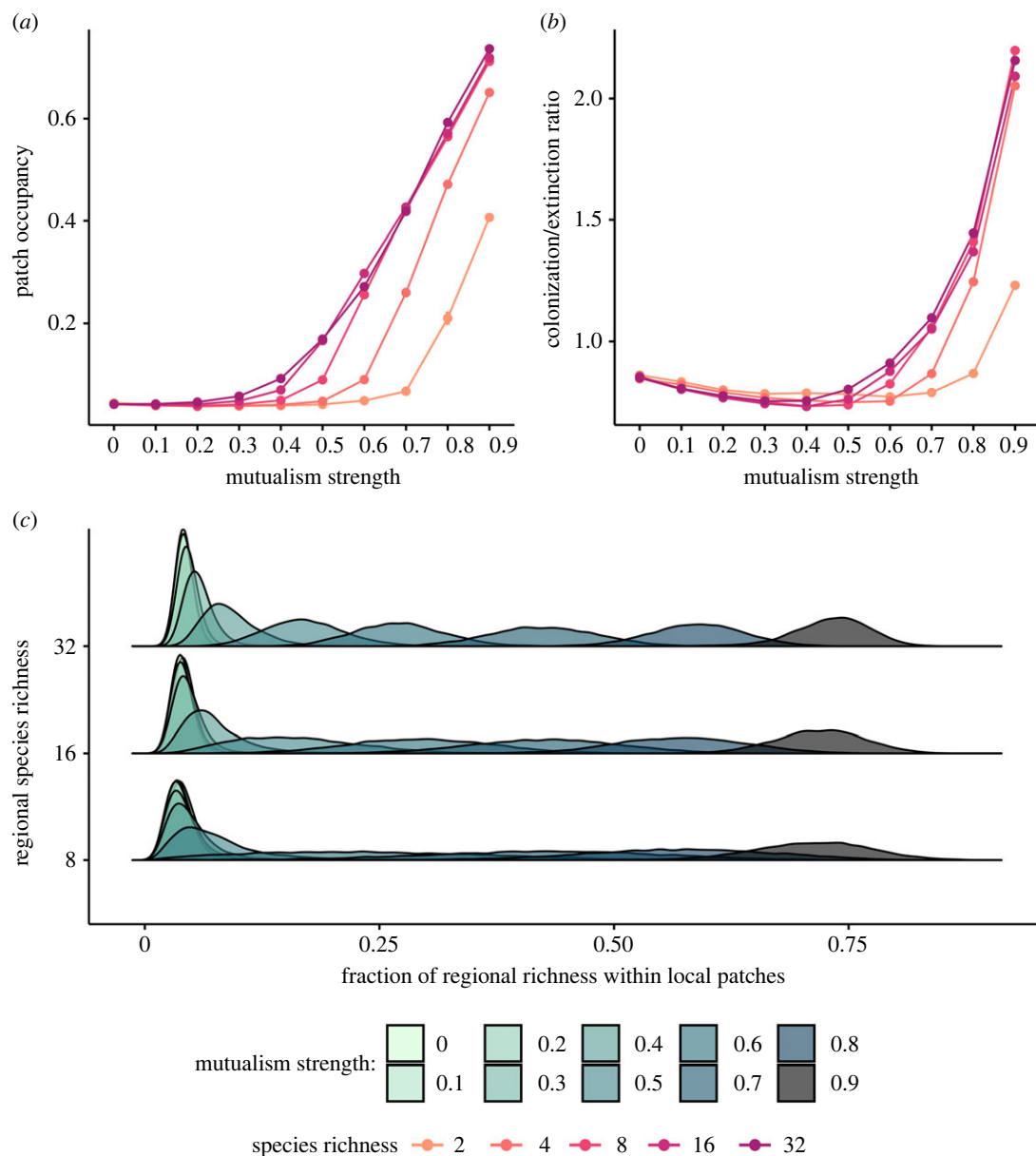


Figure 3. Mutualistic coevolution shapes patterns of (a) occupancy, by altering the (b) balance between colonization and extinction (calculated as the ratio of population colonization/extinction), thus affecting local patterns in species richness (c) in metacommunities under environmental changes ($\theta_{ik} + 0.25$ per generation). In (a, b) points and lines represent the mean value for 100 simulations. In panel (c), curves correspond to the distribution of the fraction of regional richness within local patches (averaged over time) across 100 simulations. Parameter values are as follows: $m_{ik} = 0.0 - 0.9$, $\sigma_{GZk}^2 = 1.0$, $Q_{ik} = 0.1$, $\alpha = 0.1$.

species richness within patches also increases (figure 3c). Thus, under environmental changes coevolution favours the persistence of species across the entire landscape, not only on a few patches.

This buffering effect occurs because, by favouring regional trait matching, coevolution and gene flow make species more likely to find suitable patches even when they are maladapted to the environment. Sensitivity analyses showed that these results hold for multiple combinations of parameter values (electronic supplementary material, Information). Furthermore, our sensitivity analysis showed that even without gene flow, mutualistic coevolution can buffer the negative effects of environmental change, but gene flow amplifies the buffering effect. Simulations under an alternative model assuming species interact but do not coevolve cannot reproduce the observed patterns of occupancy, resulting in very low occupancy and complete extinction of the metacommunity regardless of the value of mutualism strength (electronic supplementary material, Information). Therefore, the observed

patterns in patch occupancy and richness for varying m , cannot be interpreted only as the effect of decreasing the contribution of the environment as a selective pressure (see the electronic supplementary material, Information for a more detailed discussion).

(c) Coevolution prevents the collapse of metacommunities

Simultaneous extinctions of local populations can result in the regional extinction of a species. According to our simulations, species extinctions, and the eventual collapse of metacommunities in a changing environment can be prevented by mutualistic coevolution (figure 4a). Whenever the strength of mutualisms was weak ($m_{ik} = 0.0 - 0.3$) the metacommunity collapsed. However, further increasing the strength of mutualistic interactions prevented the collapse of the metacommunity and increased the fraction of surviving species. Again, the extent of this buffering effect over persistence was modulated by

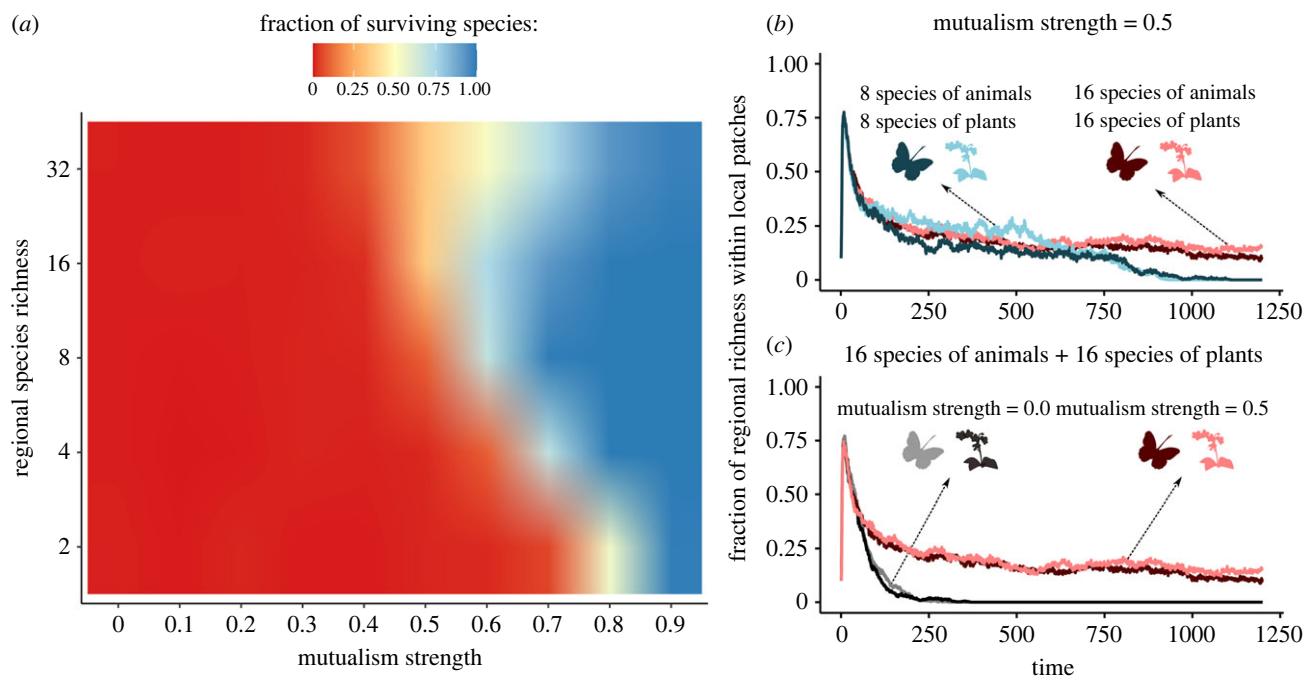


Figure 4. Mutualistic coevolution prevents the collapse of metacommunities under environmental changes ($\theta_{ik} + 0.25$ per generation). (a) Relationship between the strength of mutualisms, species richness and the average fraction of surviving species at the end of simulations. Colours are interpolated to improve visualization. (b) Example of a simulation showing how increasing the regional species richness (from a total of 16 to 32 species) can prevent the collapse of the community for the same value of strength of mutualisms ($m_{ik} = 0.5$). (c) Example of a simulation with 16 animal and 16 plant species, showing how increasing the strength of mutualisms (from 0.0 to 0.5) can prevent the collapse of the metacommunity. On panels (b) and (c) each line represents the average for all plants or animal species. Other parameter values are as follows: $m_{ik} = 0.0 - 0.9$, $\sigma_{G_{ik}}^2 = 1.0$, $Q_{ik} = 0.1$, $\alpha = 0.1$.

diversity, such that extinctions were only prevented in species-poor metacommunities at higher levels of mutualism strength. For instance, in an example of a simulated scenario with $m_{ik} = 0.5$, the metacommunity with 16 species collapsed, while in the one with 32 species nearly 25% of both plant and animal species persisted (figure 4b). However, without any coevolution ($m_{ik} = 0.0$) all 32 species went extinct (figure 4c). This effect of species richness occurred because in species-rich metacommunities, species have potential partners in most patches, which grants a certain baseline suitability even as the environmental conditions deteriorate. Sensitivity analyses showed that the buffering effects of coevolution and species richness against environmental changes held for different parameter values (electronic supplementary material, Information). We also obtained similar results when allowing the strength of coevolution to vary uniformly or in hotspots and coldspots across the landscape, implying that even a few coevolutionary hotspots can prevent the collapse of metacommunities under environmental changes (electronic supplementary material, figure S17).

4. Discussion

In the past decades, evolution has been recognized to occur at timescales that are fast enough to influence contemporary trait distribution patterns and, consequently, the persistence and distribution of ecological populations, thus affecting their response to environmental change [3,59–62]. However, we are only starting to understand how the interplay between local evolution and coevolution scale up and shape ecological patterns across landscapes [10,63]. Here, we integrate coevolution, networks and metacommunity dynamics to show that evolution and mutualistic coevolution acting within local

patches may scale up to an entire metacommunity and affect the spatial distribution of populations, patterns of adaptation, and the response of species to environmental changes [63]. Together, our results suggest three main mechanisms whereby local mutualistic coevolution can affect the trait distribution and persistence of species in metacommunities.

First, mutualistic coevolution can shape patterns of local and regional trait matching of populations, increasing connectivity across the landscape. Because colonization success and persistence are highly determined by species traits, varying patterns of trait matching can affect the rates of colonization and extinction of populations in metacommunities. In our model, the conflicting selective pressures of mutualistic partners decreases the trait matching of local populations with the environment and increases the rate of extinction of populations. By contrast, at the regional scale, coevolution increases the trait matching with mutualistic partners across the entire metacommunity and increases the rate of colonization. Previous theoretical work showed that trait convergence in mutualisms can emerge from coevolution in species-rich communities [7,11,27,28,39,42,45]. This trait convergence is driven by how mutualistic interactions form complex networks whose pathways propagate indirect evolutionary effects [51]. Similarly, in our model, colonization of local patches by coevolving populations forms its own spatial network. This spatial network also creates paths through which indirect effects propagate across the landscape. Taken together with previous work [45], our results further indicate that indirect effects that propagate through dispersal across the landscape may contribute to shape not only patterns of regional trait matching among mutualists, but also rates of local extinctions and colonization. Thus, the disruption of indirect pathways across space because of habitat fragmentation, for instance, besides its impacts on metacommunity

dynamics through dispersal limitation may also affect coevolutionary dynamics at the landscape level, an overlooked question that deserves further attention [47,48,64,65].

Second, coevolution with mutualists facilitates colonization of otherwise unsuitable patches and effectively expand the realized niche of species [6,66,67]. By facilitating colonization, increased trait matching at the regional scale may allow species to expand their spatial distributions, even when certain local populations are maladapted to the local environment. In natural populations, local adaptation may counteract environmental gradients and even out ecological patterns in space, reducing variation in mean fitness and in the local abundance of populations across the landscape [63]. Our simulations show that by favouring trait matching among multiple mutualists across the landscape, coevolution may minimize the negative effects of mismatches with the environment. This mechanism is further amplified by increased metacommunity diversity. Therefore, our results suggest that mutualistic coevolution in species-rich metacommunities can be an important force that allow species to expand and maintain their distribution ranges in a heterogeneous landscape.

Third, metacommunity diversity and coevolution can synergistically counteract the effects of environmental changes. When multiple interacting species exert evolutionary pressures in the same direction, trait matching among mutualists increases across the entire landscape. This increased trait matching sustains higher rates of colonization and allow populations to track environmental changes more efficiently. In species-rich mutualisms, greater complexity overcompensates the strength of mutualism so that populations can track environmental changes and species tolerate greater levels of environmental changes even if the strength of coevolution is relatively weak. The less rich the community, the stronger mutualisms need to be to prevent the extinction of species and the collapse of the metacommunity. Thus, our results highlight that any factor that decreases the strength of mutualistic interactions, hinders coevolution or decreases species richness in mutualistic systems, may reduce the likelihood of biodiversity persistence in a changing environment [68,69]. As the environment rapidly changes globally, understanding the mechanisms that allow populations and species to track and colonize suitable environments is a major concern for biodiversity conservation [17,18,70–73]. Locally, species-rich communities have been shown to buffer the effects of environmental changes, because increased trait convergence allows mutualists to rewire interactions in a way that compensate for the extinctions of their partners [31]. Here, we show that mutualistic coevolution can counteract environmental changes at larger spatial scales by maintaining the connectivity of spatial networks. Multispecific coevolution favours trait convergence at larger scales so that any species may have potential partners in several sites, allowing species to persist and colonize novel sites even as the environment changes. This increases the effective connectivity among sites and may help explain how mutualisms facilitate persistence and range expansions under environmental changes and maintain species richness across landscapes [2,74].

There is plenty of empirical evidence that mutualistic interactions and partner diversity allows populations to persist in a wide range of environments and is associated with range expansion of populations [75]. However, we still do not fully understand the mechanisms through which mutualistic interactions drive these range expansions and how coevolution affects spatial patterns. We present a testable mechanism for how mutualistic interactions can allow species to colonize otherwise unsuitable patches, and increase the distribution range of populations, favouring persistence. Although measuring coevolution in natural systems is challenging, the predictions of our model could be tested by assessing trait matching among interacting species at multiple sites (e.g. [76]) and investigating how variation in trait-matching affects colonization and persistence over time or patterns of patch occupancy (e.g. [77]).

Natural systems are increasingly perturbed by human activities, being subjected to high levels of diversity loss and fragmentation [16,78]. Whereas diversity loss impoverishes and simplifies the structure of communities, fragmentation changes the spatial structure of metacommunities and may reduce the potential of mutualistic coevolution to buffer harmful effects of ongoing environmental changes [79–81]. Our results show that coevolution and high species richness have a favourable impact on colonization success, thus implying that maintaining diversity and landscape connectivity is necessary for species persistence under environmental change. Disrupting connection pathways among natural populations can increase the biodiversity erosion driven by human impacts, threatening essential ecosystem functions related to mutualisms, such as pollination and seed dispersal.

Data accessibility. Code and instructions to perform numerical simulations are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.r2280gbh5> [82] and from GitHub: https://github.com/lgcsmo/Cosmo_et_al_mutualistic_coevolution_metacommunities.

Data are provided in the electronic supplementary material [83].

Authors' contributions. L.G.C.: conceptualization, formal analysis, investigation, methodology, project administration, writing—original draft, writing—review and editing; L.P.S.: conceptualization, methodology, writing—original draft, writing—review and editing; P.R.G.: supervision, writing—original draft, writing—review and editing; M.M.P.: conceptualization, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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