

# Bitrophic interactions shape biodiversity in space

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**Ecologists and conservation biologists often study particular trophic groups in isolation, which precludes an explicit assessment of the impact of multitrophic interactions on community structure and dynamics. Network ecology helps to fill this gap by focusing on species interactions, but it often ignores spatial processes. Here, we are taking a step forward in the integration of metacommunity and network approaches by studying a model of bitrophic interactions in a spatial context. We quantify the effect of bitrophic interactions on the diversity of plants and their animal interactors, and we show their complex dependence on the structure of the interaction network, the strength of interactions, and the dispersal rate. We then develop a method to parameterize our model with real-world networks and apply it to 54 datasets describing three types of interactions: pollination, fungal association, and insect herbivory. In all three network types, bitrophic interactions generally lead to an increase of plant and animal spatial heterogeneity by decreasing local species richness while increasing  $\beta$ -diversity.**

ecological networks | spatial ecology

Two major frameworks in biodiversity research are network and metacommunity theories. The metacommunity theory highlights the role of spatial processes in community dynamics (1), while the theory of ecological networks highlights the role of multitrophic interactions (2, 3). Metacommunity studies focus generally on one particular trophic group like plants (4–7), whereas network studies consider larger communities across several trophic groups but are generally local (7). From the metacommunity perspective, accumulating evidence suggests that ecological interactions impact community composition (8–10). From the network perspective, it is unclear whether the reported effects of network architecture on species richness (7) stand in spatially extended systems coupled through dispersal. In short, we need to add a spatial component to network studies or a network component to metacommunity studies (11–14).

In recent years, a number of studies have begun the integration of spatial processes and multispecies interactions by exploring community modules of two or three species (15, 16). These studies have shown that dispersal can stabilize pairwise trophic interactions (15), tritrophic food chains (11), and competitive interactions (17). Similarly, another source of multispecies stability is induced by the action of predators (18, 19).

Models at the module level have been very useful at providing a bridge between the complexity of entire communities and the simplicity of pairwise interactions (20). To go a step farther into closing the circle, a few theoretical papers have begun to study the role of spatial processes in models of entire ecological networks (13, 14, 21, 22). Here, we follow the same avenue, focusing on bitrophic ecological networks such as those networks describing pollination or herbivory between plants and insects. Our aim is to understand to what degree network structure affects the metacommunity dynamics of the two interacting groups.

We will use the neutral metacommunity model in the work by Hubbell (4) as our baseline reference. This minimal model encapsulates the combined role of dispersal limitation and stochasticity in metacommunity dynamics. Next, we will extend this framework by adding a deterministic component emerging from the nonrandom structure of bitrophic interaction networks.

Comparing the outputs of the extended model and the neutral one will allow us to assess the impact of bitrophic interactions on the composition and dynamics of the metacommunity.

When they act differentially among community members, bitrophic interactions induce fitness differences among individuals. For instance, if pollinators preferentially pollinate flowers with short corollas, flowers with long corollas will tend to produce fewer seeds and will be progressively filtered out of the plant community. Phrased in the terms of metacommunity theory, bitrophic interactions act as an environmental filter for some community members if these members suffer greater damages from antagonists or benefit less from mutualists than their competitors (23–25). Bitrophic interactions should, thus, decrease species richness.

However, bitrophic interactions can stabilize the coexistence of different species if different community members partition biotic resources (mutualists) or threats (antagonists) by having different specialized interactions. For instance, assume that plant species A is locally abundant and sustains a large population of herbivore species B. If such species B exclusively feeds on plants of species A, then individuals of a rare plant species C may have a competitive advantage against individuals of species A in suffering less from herbivory (18, 26, 27). Herbivory should now stabilize the coexistence of the two plant species. Inversely, the diversity of plants creates a diversity of food sources for the animals. This diversity can also increase the likelihood of coexistence of different animal species (28). More generally, bitrophic interactions are likely to affect the composition of a trophic group (e.g., plants) just like abiotic conditions (29). Their overall effect on community richness will depend on a balance between their filtering and stabilizing (niche partitioning) effects. This overall impact of bitrophic interactions on community richness is, thus, likely to depend on the architecture of the interaction network, just as the heterogeneity in the abiotic environment contributes to the assembly of each trophic group.

Here, we first perform extensive individual-based simulations to explore how interactions between two trophic groups can alter their composition and dynamics (Box 1). We consider two types of interactions independently: mutualistic (e.g., plants and their pollinators) and antagonistic (e.g., plants and their insect herbivores). Each trophic group experiences stochastic lottery-like dynamics (30) in a lattice of patches connected by dispersal. Interactions between the trophic groups are controlled by two trait-based rules used in isolation or combined: a threshold rule and a matching rule (31) (Box 1). Exploring a wide range of combinations of model parameters, we investigate under which circumstances bitrophic interactions have an overall positive or

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negative effect on community richness and other community characteristics.

After assessing the potential range of effects of bitrophic interactions, we confront our theoretical findings to real data of ecological networks. We, hence, develop a statistical method based on approximate Bayesian computation (ABC) (32, 33) (Box 2) to fit our model to 54 bipartite networks (23 plant–pollinator networks, 16 plant–fungi networks, and 15 plant–insect

herbivore networks) (SI Appendix). This procedure consists in simulating the model with a wide range of parameter values and retaining the parameter values that produce interaction networks that are closest to real ones. The combination of our theoretical exploration and empirical testing enables us to determine the likely impact of community-wide bitrophic interactions on community structure in nature and pinpoint knowledge gaps where efforts should be concentrated in the near future.

**Box 1. Description of the Model**

We model the dynamics of two trophic groups: plants and animals. The groups occupy a regular grid of  $l \times l$  patches. Each patch contains  $N_p$  plants and  $N_a$  animals and follows stochastic dynamics with dispersal from the four neighboring patches at rates  $m_p$  and  $m_a$  and long distance dispersal from a pool of species at rates  $\mu_p$  and  $\mu_a$  (SI Appendix, Fig. S1). We consider that the patches are constantly saturated, and therefore at each generation,  $N_p$  and  $N_a$  descendants are drawn at random in a lottery manner (30) and replace their parents. For plants (similarly for animals replacing subindex p by a), the descendants of a patch P can come from either the present patch P, from one of the four neighboring patches, or from the regional pool. The respective probabilities of these three scenarios are  $1/(1 + m_p + \mu_p)$ ,  $m_p/(1 + m_p + \mu_p)$ , and  $\mu_p/(1 + m_p + \mu_p)$ , respectively. We use regional pools of 300 species with equal species regional abundances. Immigrants from the regional pool, hence, belong to a randomly drawn species (of 300). Immigrants from the neighboring patches have the species identity of a randomly drawn individual in the neighboring patches. Descendants coming from the local patch have a species identity drawn at random with a probability proportional to the product of the local species abundance and its seed (egg) production. This seed (egg) production is affected, in part, by the local interaction with the other group as defined next.

**Case 1: Mutualistic Interactions.** For the group of plants (animals), the seed (egg) production  $f_i^p$  ( $f_i^a$ ) of an individual of species  $i$  is equal to

$$f_i^p = (1 - c_p) + c_p \frac{\sum_{j=1}^{S_a} n_j^a I_{ij}}{\sum_{k=1}^{S_p} \left( \frac{n_k^p}{N_p} \sum_{l=1}^{S_a} n_l^a I_{kl} \right)} \quad [1]$$

and

$$f_i^a = (1 - c_a) + c_a \frac{\sum_{j=1}^{S_p} n_j^p I_{ji}}{\sum_{k=1}^{S_a} \frac{n_k^a}{N_a} I_{jk}} \quad [2]$$

where  $c_p$  ( $c_a$ ) is the component of seed (egg) production that depends on the interaction with the other trophic group,  $n_i^p$  ( $n_i^a$ ) is the number of individuals of species  $i$  in the group of plants (animals), and  $I_{ij}$  is the interaction strength between plant  $i$  and animal  $j$ .

For plants, the term  $1 - c_p$  in Eq. 1 means that seed production is partially uncoupled from the interaction with animals (e.g., because of selfing). Eq. 1 also describes that plants compete to attract animals: a plant  $i$  interacts with animals at a total rate of  $\sum_{j=1}^{S_a} n_j^a I_{ij}$ . It will then receive a fraction of plant–animal interactions proportional to the term after  $c_p$ .

For animals, Eq. 2 is similarly constituted of two terms: the uncoupled egg production  $1 - c_a$  and the coupled one,

where the term after  $c_a$  describes the competition among animals to obtain the reward offered by plants. An animal  $i$  will receive from a plant  $j$  a fraction of its reward proportional to  $I_{ji}/[\sum_{k=1}^{S_a} (n_k^a/N_a) I_{jk}]$ . This animal  $i$  will, thus, obtain a total reward from the plants given by the term after  $c_a$  (SI Appendix).

If  $c_p$  and  $c_a$  equal zero or if interactions between plants and animals are equivalent among species (i.e.,  $I_{ij}$  is constant), the dynamics of plants and animals are purely neutral and uncoupled.

**Case 2: Antagonistic Interactions.** For antagonistic interactions, the seed production  $f_i^p$  is similarly modeled by

$$f_i^p = \sup \left\{ 0; 1 - c_p \frac{\sum_{j=1}^{S_a} n_j^a I_{ij}}{\sum_{k=1}^{S_p} \left( \frac{n_k^p}{N_p} \sum_{l=1}^{S_a} n_l^a I_{kl} \right)} \right\} \quad [3]$$

where  $\sup\{0; x\}$  equals zero if  $x < 0$  and  $x$  otherwise.  $f_i^a$  is given by Eq. 2.

**Interaction Rules.** Each species has a set of  $T$  independent trait values randomly drawn from the interval  $[0, 1]$  according to a uniform probability density function. These trait values determine the interaction strength between plants and animals. For each of the  $T$  traits, one of two interaction rules is used.

The first interaction rule is a threshold rule: an animal  $j$  with trait value  $t_j^a$  can interact with a plant  $i$  with trait value  $t_i^p$  only if  $t_j^a \geq t_i^p$ . This rule increases the nestedness of the network: animals with low trait values are more specialist and interact with the subset of plants that have low trait values, whereas animals with large trait values are more generalist and interact with a larger subset of plants having both low and large trait values (45). Similarly, plants with large trait values are specialists and interact only with animals with large trait values, whereas plants with low trait values interact with a larger subset of animals.

The second interaction rule is a matching rule: an animal  $j$  with trait value  $t_j^a$  interacts with a plant  $i$  with trait value  $t_i^p$  with a probability proportional to  $\exp[-(t_j^a - t_i^p)^2/2\sigma^2]$ , where  $\sigma$  is a parameter measuring the specificity of the interaction. This rule increases the specificity of plant–animal interactions: plants and animals interact more if they have similar trait values. Consequently, plants (animals) with different trait values tend to interact with different subsets of animals (plants). In this rule, the smaller  $\sigma$  is, the more specific the interactions will be; with these two interaction rules and less than four independent traits, various topological properties of real ecological networks can be reproduced as shown by ref. 31.

Our model formulation presents several advantages (directly comparable with a neutral model, simulation speed, and control of community size) (SI Appendix), but it also makes a number of assumptions that need to be taken into account (Discussion).

## Box 2. ABC Procedure

We compared our model to real data using an approximate Bayesian computation (ABC) (32, 33). The ABC procedure is represented in Fig. 1. It consists in replacing the computation of the model likelihood by simulations of this model (*SI Appendix*). This approximation is useful when likelihood formulas are unavailable as in the present case.

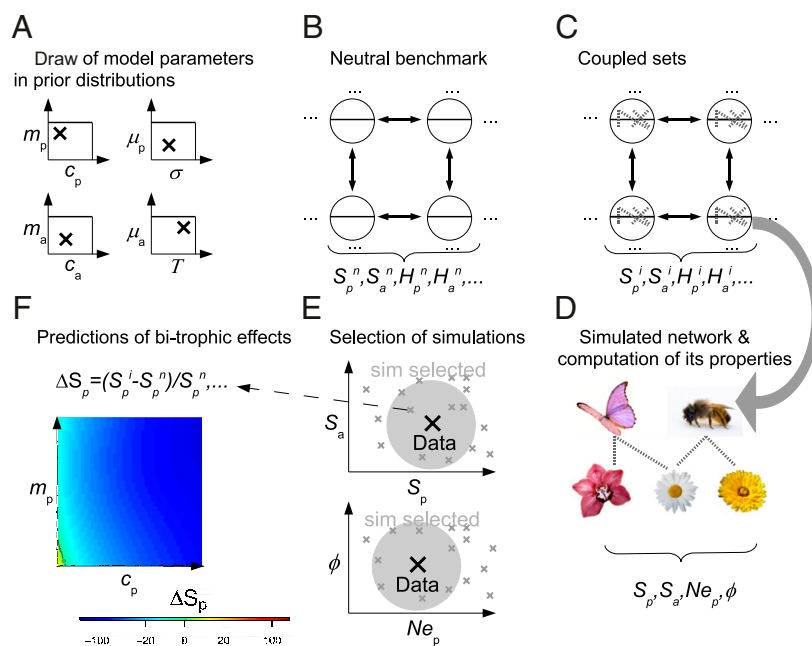
The ABC procedure consists in simulating the model multiple times. For each one of these replicates, we draw the parameter values in prior (here flat) distributions (Fig. 1*A* and *SI Appendix*, Table S5). At the end of each simulation, a network of interactions between plants and animals is simulated (Fig. 1*D*). To this end, we first choose at random a patch out of the  $l \times l$  simulated patches. In this patch,  $N_n$  animals are drawn at random, and for each of them, the plant with which it interacts is also drawn at random with probability proportional to  $n_i^p I_{ij}$ , where  $n_i^p$  is the abundance of plant species  $i$  in the patch and  $I_{ij}$  is the interaction strength between plant species  $i$  and animal species  $j$ .

Four network properties are then computed: the number of both plant  $S_p^s$  and animal  $S_a^s$  species sampled by this procedure, the nestedness index of plants  $Ne_p$  (35), and an index of specialization  $\phi$  defined as  $\phi = 1 - \langle H_i / \langle H_i \rangle \rangle$ , where  $H_i = -\sum n_{ij} \ln(n_{ij})$  and  $n_{ij}$  is the number of interactions between plant  $i$  and animal  $j$  divided by the total number of interactions ( $\langle H_i \rangle$  is the average of  $H_i$  computed in 100 randomized networks). The null model used consists in

randomly drawing an interaction network with the same total number of plants, animals, and interactions and having each interaction independently placed between a plant  $i$  and an animal  $j$  with probability  $I_{ij} = \sum_i n_{ij} \sum_j n_{ij}$ . Note that  $1 - \phi$  is close to the  $H'_2$  value in the work by Blüthgen et al. (46), but the null model used here is different in that it does not constrain the number of interactions per plant and animal species. We use these last two indices to capture the effect of the different interaction rules on network structure: threshold rules tend to increase  $Ne_p$ , whereas matching rules tend to increase  $\phi$ .

The properties of the simulated network are then compared with the ones of the real network, and therefore, the closest simulations according to these properties are retained (Fig. 1*E*).

These retained simulations are then used to quantify the impact of bi-trophic interactions on the composition and dynamics of the plant and animal groups. This quantified effect depends on badly fitted model parameters, mainly on  $m_p$  ( $m_a$ ) and  $c_p$  ( $c_a$ ), which are not well-fitted because of the limited information content of the data used (Figs. 1*F* and 3 and *SI Appendix*, Figs. S7–S9). Note that we used the ABC procedure to perform an approximate Bayesian model averaging. The goal here is neither to compare the different interaction rules (with threshold and/or matching rules) nor obtain precise model parameter estimates but constrain our simulations so that they fit observed network properties.



**Fig. 1.** Approximate Bayesian computation (ABC) procedure. (A) Model parameter values (symbolized by x) are randomly drawn in flat prior distributions (symbolized by rectangles). (B) A neutral metacommunity is simulated to form the benchmark. A grid of patches (circles) is connected by dispersal (arrows). Plants and animals (lower and upper semicircles, respectively) coexist in the patches, but they do not interact. Various community statistics are computed in this neutral benchmark ( $S_p^n, S_a^n, H_p^n, H_a^n, \dots$ ). (C) The metacommunity dynamics are pursued including the bitrophic interactions (dotted lines between the half circles) this time. Various community statistics are computed in this coupled metacommunity ( $S_p^i, S_a^i, H_p^i, H_a^i, \dots$ ). (D) A network of bitrophic interactions is simulated in a randomly chosen patch of the metacommunity, and its properties are computed ( $S_p, S_a, Ne_p, \phi$ ). (E) The properties of the simulated networks (small gray x) are compared with those properties of the real data (large black x), and the simulations with the best match are selected (gray circles). (F) Selected simulations are used to assess the effect of bitrophic interactions. This assessment is done by comparing the final metacommunity structure in the simulation (C) with the one of the neutral benchmark (B). These bitrophic effects are plotted against the two model parameters explaining the bulk of their variation:  $m_p$  and  $c_p$  for plants and  $m_a$  and  $c_a$  for animals.

## Results

In this section, we will use the term animal to designate a plant's interactor, although it can be a fungus in the datasets studied.

**Model Results.** Our simulations show that mutualistic and antagonistic interactions can either increase or decrease local plant and animal species richness (Fig. 2 and *SI Appendix, Fig. S4*) depending on the balance between biotic filtering and niche partitioning. This balance, in turn, depends on the model parameters describing the structure of the interaction network, the dispersal rate across patches ( $m_p$  and  $m_a$ ), and the strength of the interactions (i.e., the component of seed or egg production— $c_p$  and  $c_a$ , respectively—accounted by the interaction with the other trophic group) (*SI Appendix, Tables S1 and S2*).

The stabilizing effect (34) of biotrophic interactions is induced, for plants, by the heterogeneity among animals in their plant preferences and for animals, by the diversity of plant resources. It can be detected by looking at the variance in trait values among community members. Communities tend to gain species with overdispersed traits during the coupled dynamics (*SI Appendix, Variance Test*).

The other effect of biotrophic interactions is to filter out community members by producing fitness differences among individuals. We detect this filtering effect by computing the average interaction strength between plant and animal individuals. When mutualistic interactions have a negative impact on plant (animal) species richness, the average interaction strength increases compared with the neutral case. The surviving plants (animals) are those plants that encounter more mutualists. For antagonistic interactions, the average interaction strength decreases (increases) for plants (animals) when biotrophic interactions have a negative impact on plant (animal) species richness. The surviving plants are

those plants that encounter fewer antagonists, whereas the surviving animals are those animals that have many interactions (*SI Appendix, Coupling Test*).

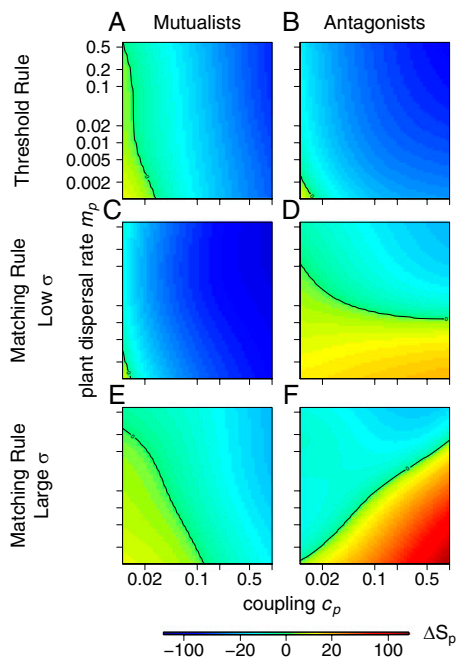
Bitrophic interactions, however, principally affect rare species: in 96% of the cases, the similarity in species composition between trophically coupled and uncoupled plant sets is larger when an abundance-weighted measure is used (*SI Appendix*).

Fig. 2 illustrates how the net effect of biotrophic interactions on local plant richness  $S_p$  depends on the plant dispersal rate  $m_p$  and the component of seed production dependent on biotrophic interactions  $c_p$ . In Fig. 2, various extremes of network structure are illustrated. These contrasting network architectures are produced with a threshold rule, a matching rule with high trait specificity, and a matching rule with low trait specificity, respectively. They result in nested, specialized, and generalized networks, respectively (Box 1 has details on these interaction rules and the resulting network structures).

Two points arising from Fig. 2 are worth mentioning. First, in the limits of low dispersal (low  $m_p$ ) and weak interactions (low  $c_p$ ), we recover the results shown in the work by Bastolla et al. (35)—namely, that nested networks tend to increase plant local richness (Fig. 2A, bottom left). Second, there is a strong interaction in the effect of the different model parameters on the outcome of biotrophic interactions. This finding means that, with such a relatively simple model, one can already produce very complex outcomes, and therefore, the effects of biotrophic interactions on metacommunity structure and dynamics are likely to be case-specific. A detailed interpretation of the patterns observed in Fig. 2 as well as the effect on biotrophic interactions on other community characteristics, including the animal group, can be found in *SI Appendix*.

**Application to Real Networks.** Because the theoretical exploration of our model revealed a rich variety of possible outcomes, we proceeded by assessing what specific patterns would emerge when the model was fitted to real data. We, therefore, developed a statistical technique to fit our biotrophic metacommunity model to local networks compiled in the literature. This fitting procedure is based on ABC (32, 33) (Box 2). The information available in the data was not sufficient to fully parameterize our metacommunity model and hence, precisely quantify the effect of biotrophic interactions on plant and animal richness in these datasets. It was, however, sufficient to greatly constrain our simulations, and therefore, the remaining variation in biotrophic effects on plant (animal) richness was highly dependent on two noninferred parameters: the plant (animal) dispersal rate between patches  $m_p$  ( $m_a$ ) and the proportion of seed (egg) production  $c_p$  ( $c_a$ ), which depends on trophic interactions (average  $R^2 = 61\%$  and  $23\%$ , respectively) (Fig. 3).

We found that biotrophic interactions are likely to decrease local plant species richness in the three types of networks (Fig. 3A, C, and E), producing an increase in  $\beta$ -diversity (*SI Appendix, Fig. S2*). The sole exception is for very weak interactions and very low dispersal rates, where our model predicts an increase in local diversity. In plant–pollinator networks, we can estimate  $c_p$  with the index of pollen limitation, which compares the fruit set of freely pollinated flowers with the fruit set of encapsulated flowers. The average of reported indices of pollen limitation for angiosperms in the metaanalysis in the work by Larson and Barrett (36) is  $c_p = 0.4$ . This value is an order of magnitude higher than the value required for a positive effect of pollinators on local richness ( $c_p < 0.02$ ). In plant–fungi and plant–herbivore networks,  $c_p$  is more difficult to relate to any direct empirical measure. However, even in these cases, we can use available information to set up some general limits to the potential range of variability in this parameter. In the case of herbivores, for example, defoliation, flower, and fruit consumption attributable to insects represent above 5% each of the corresponding biomass (37). It is then likely that  $c_p$  is generally well above 0.02 in real settings.



**Fig. 2.** Relative variation (in percentage) of plant  $\alpha$ -diversity between trophically coupled and uncoupled communities.  $\alpha$ -Diversity is measured as the local plant species richness  $S_p$ . A positive value means that trophically coupled communities are species-richer than uncoupled ones. Different panels show results for the threshold model with one trait (A and B), the matching model with one trait and  $\sigma = 0.015$  (C and D), and the matching model with one trait and  $\sigma = 1$  (E and F). A, C, and E correspond to mutualistic interactions, whereas B, D, and F correspond to antagonistic interactions. Parameter values are  $\mu_p = \mu_a = 0.004$ ,  $m_a = 0.625$ , and  $c_a = 0.16$ .



the limitations of our approach, it illustrates how complex questions and models can be statistically compared with real world data through an ABC approach. It also points out that, to elaborate and test more complicated models of spatial network dynamics, new types of data should be concurrently gathered, informing us on the mechanisms of network assembly, the dispersal rates of organisms, and the impact of trophic interactions on organisms' fitness.

## Materials and Methods

**Model Outputs.** The two trophic groups are initialized fixing  $c_p$  and  $c_a$  to zero. They are, thus, at a neutral dispersal–drift dynamic equilibrium that can be simulated quickly by coalescence (44). The coalescence procedure consists of tracing backward in time the genealogy of the individuals in the present. Because all individuals ultimately have a unique common ancestor, the number of individuals to simulate progressively decreases, making the computation quicker. Starting from this reference neutral point obtained by coalescence, the trophically coupled dynamics of the two groups are simulated forward in time during 100 generations (with  $c_p$  and  $c_a$  different from zero). Species richness in both a single patch (local) and all of the patches together (metacommunity) and species diversity (measured as Shannon's index) are recorded for both plants and animals and both before and after coupling the two trophic groups. The turnover in plant and animal composition from one generation to the next is also recorded (*SI Appendix, Temporal Turnover*). We measure the effect of the bitrophic interactions by the relative variation of plant and animal species richness between the coupled and uncoupled scenarios  $\Delta S_p = (S_p^i - S_p^n) / S_p^n$  and  $\Delta S_a = (S_a^i - S_a^n) / S_a^n$  (the superscripts  $i$  and  $n$  indicate with and without trophic interaction, respectively). We also monitor the relative variation of the other summary statistics in the same way.

**Effect of the Interactions and Role of the Different Parameters.** We performed simulations on a grid of parameter values:  $\mu_p$  and  $\mu_a$  in {0.0005, 0.004},  $m_p$  and

$m_a$  in {0.001, 0.005, 0.025, 0.125, 0.625}, and  $c_p$  and  $c_a$  in {0.01, 0.04, 0.16, 0.64, 1}. Eight different interaction rules were used based on a combination of zero, one, or two threshold rules and zero, one, or two matching rules, and each rule applies to independent and uncorrelated traits (hence, the number of traits  $T$  ranged between one and four depending on the interaction rule). Matching rules were used with  $\sigma$  in {0.015, 0.125, 1, 8}. For each interaction rule and set of parameter values, 10 independent communities were simulated, leading to a total of 1,300,000 simulations. We used  $l = 5$ ,  $N_p = 1,000$ , and  $N_a = 200$ . The results were qualitatively similar with other choices of  $N_a$  and  $l$  (*SI Appendix*). Simulations were run with periodic boundary conditions. Results were similar in simulations with zero-flux boundary conditions and lost migrants at the boundary (*SI Appendix*). A detailed analysis of the effect of each model parameter as well as some community properties on the impact of bitrophic interactions are provided in *SI Appendix*.

To assess the robustness of our results to the specific choice of the component of seed (egg) production because of the trophic interaction, we studied an additional model where Eq. 2 is similar to Eq. 1, finding similar results (*SI Appendix*).

**Compilation of Ecological Networks.** Datasets were included based on two criteria: they had to be quantitative and built from a single study site (7). In the majority of cases, there is little information on the spatial dimension of these sampled networks, and here, we will be assuming that they correspond in our model to a single patch.

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