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The effects of space and diversity of interaction types on the stability of complex ecological networks

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Abstract The relationship between structure and stability in ecological networks and the effect of spatial dynamics on natural communities have both been major foci of ecological research for decades. Network research has traditionally focused on a single interaction type at a time (e.g. food webs, mutualistic networks). Networks comprising different types of interactions have recently started to be empirically characterized. Patterns observed in these networks and their implications for stability demand for further theoretical investigations. Here, we employed a spatially explicit model to disentangle the effects of mutualism/antagonism ratios in food web dynamics and stability. We found that increasing levels of plant-animal mutualistic interactions generally resulted in more stable communities. More importantly, increasing the

proportion of mutualistic vs. antagonistic interactions at the base of the food web affects different aspects of ecological stability in different directions, although never negatively. Stability is either not influenced by increasing mutualism—for the cases of population stability and species' spatial distributions—or is positively influenced by it—for spatial aggregation of species. Additionally, we observe that the relative increase of mutualistic relationships decreases the strength of biotic interactions in general within the ecological network. Our work highlights the importance of considering several dimensions of stability simultaneously to understand the dynamics of communities comprising multiple interaction types.

Keywords Cellular automata · Food web · Individual-based model · Meta-community dynamics · Mutualistic interactions · Network structure · Population dynamics · Predator-prey

Miguel Lurgi and Daniel Montoya contributed equally to this work.

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Introduction

Biodiversity and species interactions are key regulators of ecosystem stability and functioning (May 1972; Levins 1974; Pimm 1984; McCann 2000; Reiss et al. 2009; Loreau and de Mazancourt 2013). Research on the relationship between the architecture of species interaction networks and community stability has shown that, whereas high connectance and nestedness promote stability and increases species richness in communities made up exclusively of mutualistic interactions (but see (Allesina and Tang 2012; James et al. 2013; Staniczenko et al. 2013)), the stability of trophic networks is higher in modular and weakly connected architectures (Thebault and Fontaine 2010). Additionally, the strength of ecological interactions has also been shown to play a crucial role in community structure (Paine 1980; Neutel et al. 2002). Although these studies have improved our knowledge on

complexity-stability relationships, they have often focused on a single interaction type at a time and overlooked the fact that natural communities comprise different interaction types that operate simultaneously in space and time (Fontaine et al. 2011; Kéfi et al. 2012). Empirical work has started to address methodologies to incorporate different interaction types into a broader ecological network context, in which the creation of a ‘network of networks’ and its implications for different aspects of community organisation are considered (Melián et al. 2009; Olf et al. 2009; Fontaine et al. 2011; Kéfi et al. 2012).

These empirical studies have opened up a big theoretical challenge in complexity-stability research: exploring how interaction networks with different architectures and interaction types combine to shape stable networks of networks. A theoretical framework that incorporates these features will facilitate the understanding of the mechanisms behind the observed empirical patterns and of how multiple interaction types taken together affect ecosystem stability and functioning (Thebault and Fontaine 2010; Kéfi et al. 2012). Recent attempts to do so have shown that interaction type may affect community stability and its relationship with network architecture (Allesina and Tang 2012) and that the proportion of trophic vs. mutualistic interactions may influence the stability of natural communities (Mougi and Kondoh 2012). Mougi and Kondoh 2012 showed that, whereas the presence of a few mutualistic interactions destabilises predator-prey communities, a moderate mixture of antagonistic and mutualistic interactions could have a stabilising effect in ‘hybrid’ communities. More recently, the stabilising role of nestedness and modularity has been challenged when several interaction types are considered within the same network, arguably by the increasing importance of indirect effects in these networks of networks (Sauve et al. 2014).

Many of the organisational patterns of ecological communities that we observe in nature, including species-connectivity scaling laws in food webs, species-abundance distributions, complex fluctuations in population dynamics, and species-area relationships (Solé et al. 2002), can only be understood by acknowledging that populations move and interact in a spatial context (Durrett and Levin 1994; Tilman and Kareiva 1997; Solé et al. 2002). Further, the use of spatially explicit models has been fundamental to understand questions related to natural phenomena that are not detected in non-spatial or spatially implicit models, such as percolation thresholds (Neuhauser 1998; Solé and Bascompte 2006). Essentially, theoretical models that consider space explicitly include the range of dynamics found in spatially implicit models but with important constraints to movement and species interactions. This affects the spatial distribution and the mobility of species in the community, which in turn modulates the dynamics of interacting species through effects on the probability of encounter between individual predators and prey (Olesen and Jordano 2002; Burkle and Alarcon 2011), which ultimately determines the realisation of potential interactions. In other words, spatial processes such as species

distribution patterns, range dynamics and local dispersal abilities can affect community stability via the shaping of the network of interactions between species in the community. Constraints imposed by space are thus not only fundamental to understand patterns of diversity but also spatial processes alone can result in network architectures that resemble those observed in real networks (Morales and Vázquez 2008). However, despite important advances with single interaction types (Holt 2002; McCann et al. 2005; Fortuna et al. 2008), we still lack understanding on complexity-stability relationships in a spatially explicit context with different interaction types considered simultaneously.

In this work, we contribute to fill this gap by investigating the stability of ‘networks of networks’ that combine antagonistic and mutualistic consumer-resource interactions within a spatially explicit context using an individual-based, bioenergetic model. We ask whether different aspects of ecological stability are influenced by the proportion of mutualistic and antagonistic interactions (hereafter MAI ratio) within the overall species interaction network. Our aim is to explore the relationship between hybrid network architecture and community stability not only in terms of population dynamics and network structure but also introducing a novel analysis of spatial stability. The assessment of community stability from a spatial perspective allows for the quantification of the effect of community organisation on species distributions and range dynamics. Specifically, we address the following questions: (1) Do increasing levels of mutualism result in more stable communities? And, if so, (2) How do MAI ratios influence community stability in a spatial context?

Material and methods

We developed an individual-based, spatially explicit, bioenergetic model of species interaction networks. Network architecture was obtained using the niche model (Williams and Martinez 2000). The dynamics of the system are governed by local rules of interactions between individuals in a simulated, spatially explicit environment. Models of this type, although simple in terms of the nature of individual’s interactions, successfully reproduce relevant ecological patterns (Durrett and Levin 1994; Solé et al. 2002; Morales and Vázquez 2008). Individuals’ state is determined by several bioenergetic constraints. For the analysis of model outcomes, we employ network metrics that are traditionally used for the characterisation of food webs and mutualistic interaction networks. We also calculate different metrics of community stability to create a comprehensive picture of stability based on several dimensions (*sensu* (Donohue et al. 2013)). The model allows us to test the relationship between different mutualistic vs. antagonistic interactions (MAI) ratios and several network and stability properties. We ran 275 replicates of experiments

consisting of model communities generated using different MAI ratios and letting them evolve through time.

Generation of species interactions networks

Food web architecture was obtained using the niche model (Williams and Martinez 2000). This model requires two input parameters: (1) the number of species (S) and (2) connectance, defined as the fraction of realised links ($C=L/S^2$) within the network. The niche model describes trophic niche occupancy between consumers and resources along a resource axis and successfully generates network structures that approximate well the central tendencies and the variability of a number of food web properties (Williams and Martinez 2000; Dunne et al. 2002; Stouffer et al. 2005). Because it arranges consumers and resources along a resource axis, the niche model can be applied to other types of consumer-resource interactions (aside from antagonistic predator-prey). We thus used the niche model to define mutualistic interactions simply by substituting some herbivore links by mutualistic ones while keeping connectance and species richness constant. The model for network construction selected, however, should not affect our results, as long as realistic food web architectures are produced.

We created food webs comprising 60 species and with connectance values of 0.08 (values well within the range of those found for real food webs (Dunne et al. 2002)) for MAI ratios ranging from 0 to 1.0 with steps of 0.1: [0, 0.1, 0.2, 0.3 ... 1], making up a total of 11 different MAI ratios, from communities with no mutualistic interactions to communities with only mutualistic links and no herbivores (see Appendix S1 in Supporting Information for more details on network construction). We classified species into six categories (i.e. trophic groups) according to their position within the overall food web: (1) non-mutualistic plants, (2) mutualistic plants, (3) animal mutualists or mutualistic consumers, (4) herbivores, (5) primary predators and (6) top or apex predators (Fig. 1).

Individual-based spatially explicit dynamics

Individual-based models (IBMs) have been used to tackle different problems in ecology, although not very frequently to simulate complex ecosystems comprising large numbers of species (Grimm and Railsback 2005). We implemented an IBM that simulates dynamics typical of two-dimensional cellular automata (CA) (Ulam 1952; Durrett and Levin 1994) but based on ecological rules of interaction. This CA represents our simulated community in space. Space in the CA is represented as a 2D lattice. Cells in the lattice can be occupied by a maximum of two individuals at any given time, provided that one of them belongs to a plant and the other one to an animal species. Cells in the lattice can thus be in one of four states: (i) empty, (ii) harbouring a plant individual or (iii) an animal individual, and (iv) harbouring a plant and an animal individuals. Torus boundary

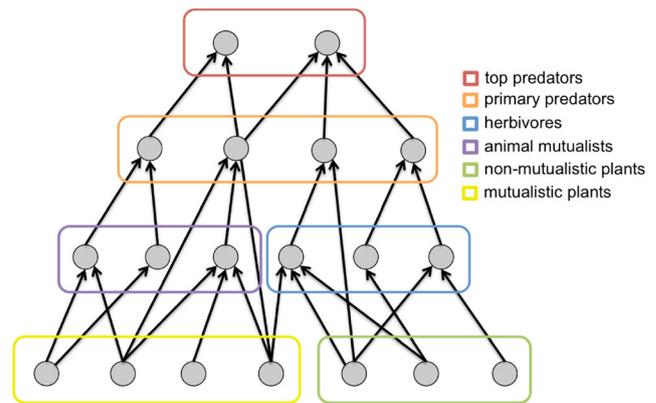


Fig. 1 Schematic representation of the species interaction networks generated. *Nodes* correspond to taxonomic species and *arrows* to trophic links from resources to consumers. The six different categories (i.e. functional groups) of species, according to their position, that result from the process of network generation are shown (see text)

conditions were used for the 2D lattice in order to reduce possible edge effects due to the loss of individuals. Individuals change their internal state (or not) during each iteration of model simulations not only according to their interactions but also as a function of a number of bioenergetic constraints (Table S1). CA-type rules represent demographic processes, foraging actions, and inter/intraspecific interactions of individuals in our IBM. These rules, by which individuals (and hence the CA) change their state through time, are detailed in Appendix S1.

In summary, the macroscopic dynamics of the CA emerge from the local interactions occurring between individuals occupying cells in a 2D lattice (Fig. 2). These dynamics will determine not only the spatial distribution of species (states of the CA) but also the temporal dynamics of their populations. Persistence/extinction dynamics are determined by individual energetics, which in turn affect demographic processes at the individual level (see Table S1 for description of bioenergetic parameters). This individual-based, bioenergetic model is more realistic than previous models of complex food web dynamics (e.g. (Pimm 1979; McCann et al. 2005; Brose et al. 2006)) in the following aspects: (i) individuals within species have different extinction rates, which are not dependant on stochastic events, thus eliminating the need to define fixed extinction probabilities for all species in the community (e.g. (Solé and Montoya 2006; Fortuna et al. 2013)); (ii) more complex demographic processes such as reproductive ability and immigration based on available space are taken into account; and (iii) bioenergetic constraints such as energy gathering efficiency and energy loss at the individual level are driving population dynamics.

During model simulations, spatial communities evolve through time following constraints imposed by bioenergetic parameters (see Table S1), spatial constraints (similar to all individuals) and the interactions between species determined by network architecture. After 5000 time steps, which include an initial period of transient dynamics, the communities are

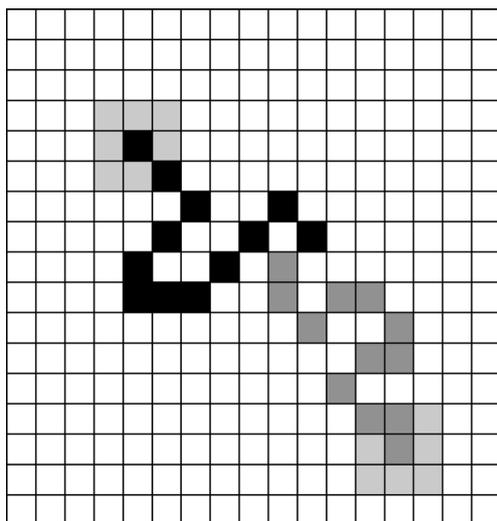


Fig. 2 Example of a 2D grid (17×17 cells) showing a fraction of the landscape where digital organisms in the individual-based model coexist and interact. Trajectories of two sample individuals until they encounter each other are represented by black and dark grey squares. Light grey squares represent the neighbourhood of each of the two individuals at the beginning of their respective current paths. At the end of both paths, each individual finds itself inside the other's neighbourhood. Depending on other individuals present on a given individual's neighbouring cells (shown as light grey cells for the starting position of each of the two individuals in the figure) or whether these are available, the 'state' in this complex cellular automaton will change following certain rules and constraints (see text and Supporting Information)

analysed in terms of diversity (species richness and abundances), network properties and stability.

Diversity and food web properties

Several statistical properties of the network of species interactions were measured after transient dynamics. In particular, we measured the number of species (S), number of links (L), connectance ($C=L/S^2$), the standard deviation of generality ($GenSD$) and vulnerability ($VulSD$)—the last two quantify diet breadth variability and predation pressure variability across species, respectively (Williams and Martinez 2000). Additionally, we obtained quantitative indices that consider the strength of species interactions including: H'_2 —a measure of mutualistic specialisation—(Blüthgen et al. 2006), which was calculated for the mutualistic part of the web, since it is only meaningful for bipartite interaction networks; and quantitative measures of generality (G_q) and vulnerability (V_q) (Bersier et al. 2002). Table 1 presents the full set of metrics calculated over the networks and their mathematical definitions, including those mentioned above.

In addition to properties related to network architecture, we also measured community diversity using the Shannon diversity and evenness indexes (Begon et al. 2006). These indexes were calculated both at the community level and within each trophic group (Fig. 1).

Community stability

Theoretical studies on the relationship between network architecture and stability of hybrid communities often define stability as the proportion of stable communities following May's stability criterion (e.g. (Allesina and Tang 2012; Mougi and Kondoh 2012)). May concluded that a complex ecosystem would be stable if, and only if, it complied with the following condition: $\langle \lambda \rangle (SC)^{1/2} < 1$ (May 1972), where $\langle \lambda \rangle$ is the mean strength of the interactions between species in the community—the strength of the interaction between species i and j is the effect of species i on the population growth rate of j . S and C correspond to the number of species in the community and its connectance, respectively. Although, due to the nature of our modelling approach, our communities are not amenable to this type of analysis, May's criterion is useful in our case because we have communities with constant S and C values. A good indicator of community stability in our communities is thus the average interaction strength among their constituent species: the lower the $\langle \lambda \rangle$, the more stable our communities will be because of less fluctuating dynamics. This attribute has also been identified as distinctive feature of more stable natural communities (McCann 2000; Neutel et al. 2002).

We estimated the interaction strength between a predator j and its prey i as:

$$\alpha_{ij} = \frac{b_{ij}}{N_i \times N_j}$$

where b_{ij} is the total biomass flowing from prey species i to predator species j —quantified here as the total number of individuals (or fractions of it, in the case of plants) from species i eaten by individuals of species j . N_i and N_j are the total number of individuals of species i and j at the time of the calculation of the index, respectively. This way of calculating interaction strengths quantifies the per-capita effect of a predator species over its prey, and it is thus analogous to Paine's index and Lotka-Volterra interaction coefficients (Neutel et al. 2002; Berlow et al. 2004). This allows us to employ these values to assess and understand community stability based on the strengths of ecological interactions.

We additionally looked at three other measures of community stability. First, temporal variability, which quantifies population variability as the average of the coefficient of variation (CV) of species population abundances through time (Pimm 1984). Second, spatial variability, which corresponds to the CV of the location of the centroid of each species range through time (see Appendix S1). And third, aggregation stability, measured as the degree of clustering (i.e. spatial correlation) of individuals within each species in space (i.e. Moran's I and Geary's C indexes described in Appendix S1). This metric is linked to reproductive stability because the likelihood of finding a reproductive partner in the neighbourhood is higher in more

Table 1 Metrics applied over the interaction networks to obtain information about their structural and quantitative properties

| Property | Formula |
|---|---|
| C: connectance, fraction of realised links out of the possible ones | L/S^2 |
| GenSD is the standard deviation of the normalised number of prey G_i across species | $G_i = \frac{1}{L/S} \sum_{j=1}^S a_{ij}$, where a_{ij} is 1 if there exists a trophic link between prey j and predator i , and 0 otherwise |
| VulSD is the standard deviation of the normalised number of predators V_i across species | $V_i = \frac{1}{L/S} \sum_{j=1}^S a_{ij}$, where a_{ij} is 1 if there exists a trophic link between prey i and predator j , and 0 otherwise |
| Compartmentalisation is the degree to which species share common neighbours across the web (Pimm and Lawton 1980) | $C = \frac{1}{S(S-1)} \sum_i \sum_{j \neq i} c_{ij}$, where c_{ij} is the number of species with which both i and j interact divided by the number of species with which either i or j interact |
| Nestedness: the extent to which the diets of specialist species are proper subsets of more generalist ones | Calculated using the nestedness metric based on overlap and decreasing fill (NODF) proposed by Almeida-Neto et al. (Almeida-Neto et al. 2008). This metric was only calculated for the mutualistic sub-web |
| H'_2 : two-dimensional standardised Shannon entropy, as proposed by (Blüthgen et al. 2006) | $H'_2 = (H_{2\max} - H_2) / (H_{2\max} - H_{2\min})$, where $H_{2\max}$ and $H_{2\min}$ are maximum and minimum H_2 for the particular network over which the index is being calculated [see (Blüthgen et al. 2006) for details]. $H_2 = -\sum_{i=1}^r \sum_{j=1}^c (p_{ij} \cdot \ln p_{ij})$, where r and c are resources and consumers in the mutualistic web respectively. p_{ij} is the proportion of the total number of interactions in the network that occur between resource species i and consumer species j . This metric was calculated over our networks using the bipartite package in R (Dormann et al. 2009), and only for the mutualistic sub-web |
| G_q : weighted (quantitative) generality, as proposed by Bersier et al. 2002 | $G_q = \sum_{k=1}^S \frac{b_k}{b..} n_{N,k}$, where b_k is the total amount of biomass going into species k , and $b..$ is the total amount of biomass flowing through the entire food web. $n_{N,k}$ is the number of prey that predator k has. Here, the biomass flowing from one species to another was calculated as the number of individuals of a given prey species eaten by individuals of predator species k (Bersier et al. 2002) |
| V_q : weighted (quantitative) vulnerability, as proposed by Bersier et al. 2002 | $V_q = \sum_{k=1}^S \frac{b_k}{b..} n_{P,k}$, where b_k is the total biomass emanating from species k . $b..$ is the total biomass flowing through the entire food web. $n_{P,k}$ is the number of predator species that feed upon prey species k . Here, the biomass flowing from one species to another was calculated as the number of individuals of prey species k eaten by a given predator species (Bersier et al. 2002) |

spatially aggregated distributions. Collectively, more stable communities will be characterised by lower temporal and spatial variability, higher reproductive stability and lower average interaction strengths. This framework allowed for the exploration of the relationships between network properties and the stability metrics in our communities by looking at how temporal and spatial stability changed as MAI ratio increased.

Experimental simulations

We generated networks with 11 different MAI ratios in order to study the effects of different combinations of antagonistic and mutualistic interactions on community stability. The individual-based model described above was employed to perform a series of simulations of the dynamics of the system through time and space. Simulations were set up by placing a given community,

made up of artificial individuals belonging to each of the species in the interaction network defined by the niche model, on a landscape that consists of a 200×200 square lattice with identical cells. Each cell can be occupied at any given time by at most two individuals, yielding a maximum of 80,000 individuals. At the beginning of the simulations, only 40% of the landscape was occupied and populated with the same number of individuals of each species randomly across the lattice. Communities were allowed to evolve for 5000 iterations. Diversity and network properties were constantly monitored.

We performed 25 replicates for each of the 11 MAI ratios, each of them representing different sets of initial conditions not only in terms of the initial configuration of the simulated landscape but also regarding the network of interactions. For each of these 25 replicates, the initial distributions of individuals across the landscape varied by placing individuals randomly

across the landscape for each replicate as detailed above. The network of interactions for each of these replicates was generated independently by running different instances of the niche model with the same S and C values and choosing the mutualistic links following the heuristic described in Appendix S1. We kept S and C constant across our simulations because our aim is to evaluate the effect of varying MAI ratios on community stability rather than the effects of changes in species richness or connectivity. This process effectively produced different interaction networks for each run with the same number of species and connectivity. Each of the 25 communities simulated for each MAI ratio was thus independent, and the architecture of the ecological network was different from replicate to replicate. This yielded a total of $25 \times 11 = 275$ replicates.

Linear models (LM) were used to analyse the relationship between MAI ratios and the properties of the communities and their interaction networks as well as their effect on stability. The IBM used here was developed using Python v2.7 (www.python.org), while statistical analyses were performed in R 2.15.2 (R Core Development Team 2012). Sensitivity analyses were carried out to assess the robustness of our results to differences in species richness, landscape lattice size and number of generated communities. See Appendix S1 for a description of these analyses. The model presented here incorporates a total of 17 free parameters (see Table S1), over which sensitivity analyses have also been performed. We have modified individually every parameter of the model (i.e. those described in Table S1). In doing so, we have changed the original value reported in Table S1 by $\pm 10\%$ and used GLMs to test whether significant changes on the relationship between MAI ratios and network properties/stability metrics analysed exist. Results are summarised in Tables S2 and S3. In general, no significant differences were observed for any of the parameters modified, suggesting our results are not very sensitive, and hence robust, at least for a given section of the parameter space, whose full exploration is not feasible to tackle given the complexity of the model used.

Results

Community structure

After a period of transient dynamics, the resulting simulated communities and their associated interactions networks displayed patterns similar to those found in empirical multitrophic assemblages. Population dynamics showed oscillations typical of predator-prey and mutualistic interactions in multispecies systems, with all species in the community persisting through time. The rank-abundance and degree distributions of the simulated communities followed lognormal (Fig. S2) and exponential (Fig. 3, p value < 0.001 for all fits to exponential models) patterns, respectively, typical of natural

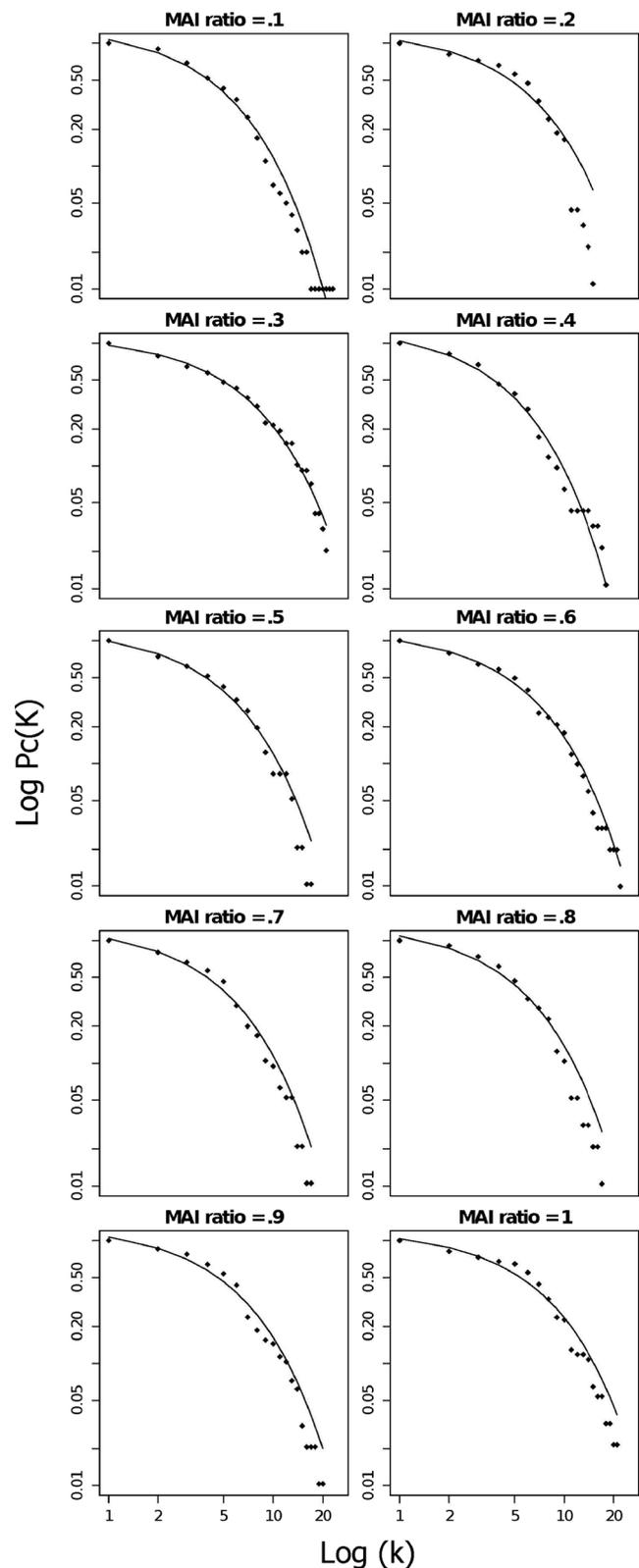


Fig. 3 Cumulative degree distributions from 10 sample communities with different MAI ratios. Lines represent a fit of each dataset to an exponential distribution (p values for all fits < 0.001)

communities (Montoya et al. 2006). Therefore, we can conclude that the model successfully generates communities displaying empirically observed patterns.

Diversity metrics changed as expected by an increase in MAI ratios. Although the level of mutualism did not affect total species richness, communities with larger MAI ratios hosted a larger number of individuals ($F_{(1273)}=98.69, p<0.001$) (Fig. 4). In spite of a decline in the abundance of non-mutualistic primary producers and herbivores with increasing MAI ratios (as expected due to a larger fraction of mutualistic species), the increase in mutualistic plants and animals overcompensated for this loss, causing an overall increase in abundance. This overcompensation was due to mutualistic plants becoming more abundant than non-mutualistic ones since mutualistic consumers do not consume as much resources from them and are, additionally, beneficial for their reproduction. Increased MAI ratios caused a significant decline in Shannon diversity index (Fig. 4, $F_{(1273)}=71.47, p<0.001$). This result is in line with our previous observation reporting an increased overall abundance of individuals following a systematic increase in mutualistic plant and animal abundances. The proportion of mutualistic species in the community had a profound effect on diversity and evenness, making model communities more biased towards the dominance of mutualistic species.

Most network properties were not significantly affected by the degree of mutualism vs. antagonism. However, some of them

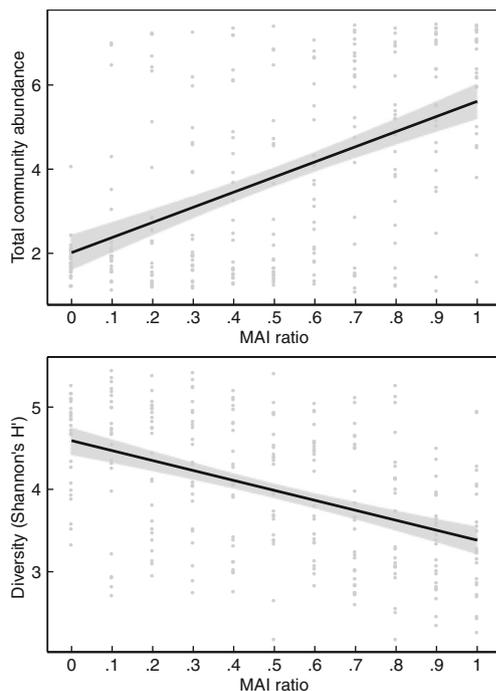


Fig. 4 Total abundance of individuals in the community and Shannon diversity index at the level of the total community vs. MAI ratio. Total numbers of individuals are represented in tens of thousands. *Points* show index values for each replicate. *Line* and *shadow* on each plot represent the fit of a linear model to the data and the standard error of the mean, respectively. p value <0.001 for linear model fits to each data set

did show a monotonic relationship with MAI ratio. Quantitative generality (G_q) was significantly lower in communities with higher MAI ratio ($F_{(1273)}=59.49, p<0.001$, Fig. 5), whereas specialisation (H'_2) within the mutualistic sub-web decreased ($F_{(1248)}=25.91, p<0.001$, Fig. 5). These results combined indicate that a larger fraction of mutualistic interactions resulted in more generalised mutualistic interactions within a more specialised overall network. It is important to note that we are referring here to quantitative metrics. This means that, with increasing MAI ratios, binary network architecture remained constant—not significant differences in modularity, nestedness or connectance across MAI ratios—but interactions at the overall network level became weaker in general, with only a few strong interactions. On the mutualistic sub-web, interactions became more homogeneous in terms of strength due to a weakening of the interactions in general, which made it less specialised (lower H'_2) by increasing the relative importance of weak links.

Community stability

Based on the interaction strengths criterion for community stability (see “Methods”), we found that MAI ratios enhanced dynamic stability in our model communities. We observed a significant reduction in $\langle i \rangle$ —the average interaction strength—as MAI ratio increased, evidenced by a shift in the distribution of interactions strengths towards lower values

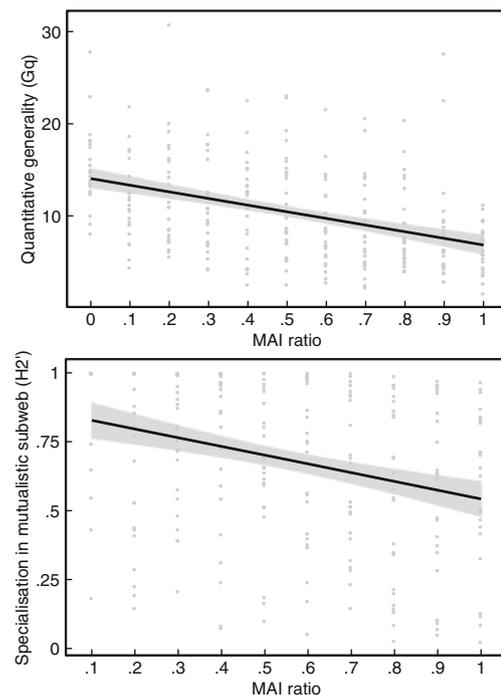


Fig. 5 Quantitative generality (G_q) and specialisation degree (H'_2) values as a function of MAI ratio. *Points* show index values for each replicate. *Line* and *shadow* on each plot represent the fit of a linear model to the data and the standard error of the mean, respectively. p value <0.001 for linear model fits to each data set

with MAI ratio (Fig. 6, $p < 0.001$ for all pairwise comparisons between distributions). This result suggests that mutualistic interactions make communities more stable by lowering the average strength of ecological relationships between species.

MAI ratios did not affect temporal stability (i.e. population variability through time), spatial stability (as measured by the change in the centroid of the species' spatial range) or the area and density of species populations. In contrast, higher MAI ratios resulted in significantly higher and lower Moran's I and Geary's C indexes, respectively (correlation tests using linear models yielded $F_{(1273)} = 29.06$, $p < 0.01$ for Moran's I and $F_{(1273)} = 24.35$, $p < 0.01$ for Geary's C against MAI ratios), revealing more spatially aggregated populations with increasing MAI ratios (Fig. S3). Increases in spatial aggregation were different across trophic levels both at global (Moran's I) and local (Geary's C) scales. For example, whereas predators and plants got significantly more aggregated as MAI ratio increased, the aggregation of mutualistic animals and herbivores was either not affected or only weakly affected by changing MAI ratios, respectively (Fig. 7 and S4). We argue that more spatially aggregated populations can be associated with higher reproductive potential stability, as the likelihood of finding a reproductive partner in the neighbourhood is higher. From this perspective, communities in general, and plant and predator species in particular, were thus more stable in terms of species reproductive potential as the MAI ratio increased (Fig. 7, S3 and S4).

Discussion

The consideration of different interaction types simultaneously within the same ecological network has consistent and predictable effects on community organisation and stability across a gradient of antagonistic vs. mutualistic interactions. We have shown that increasing levels of mutualisms result in

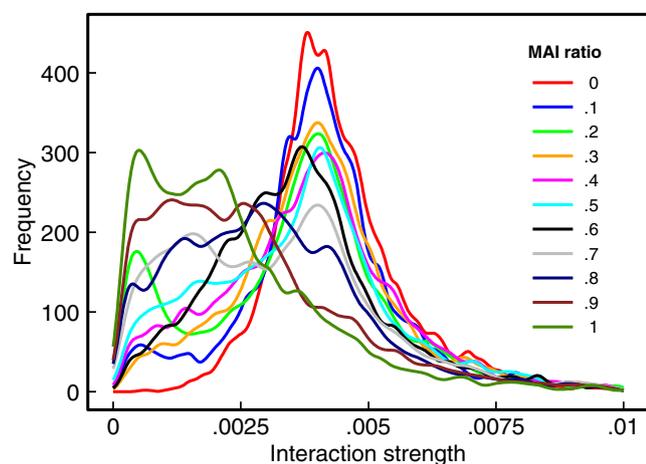


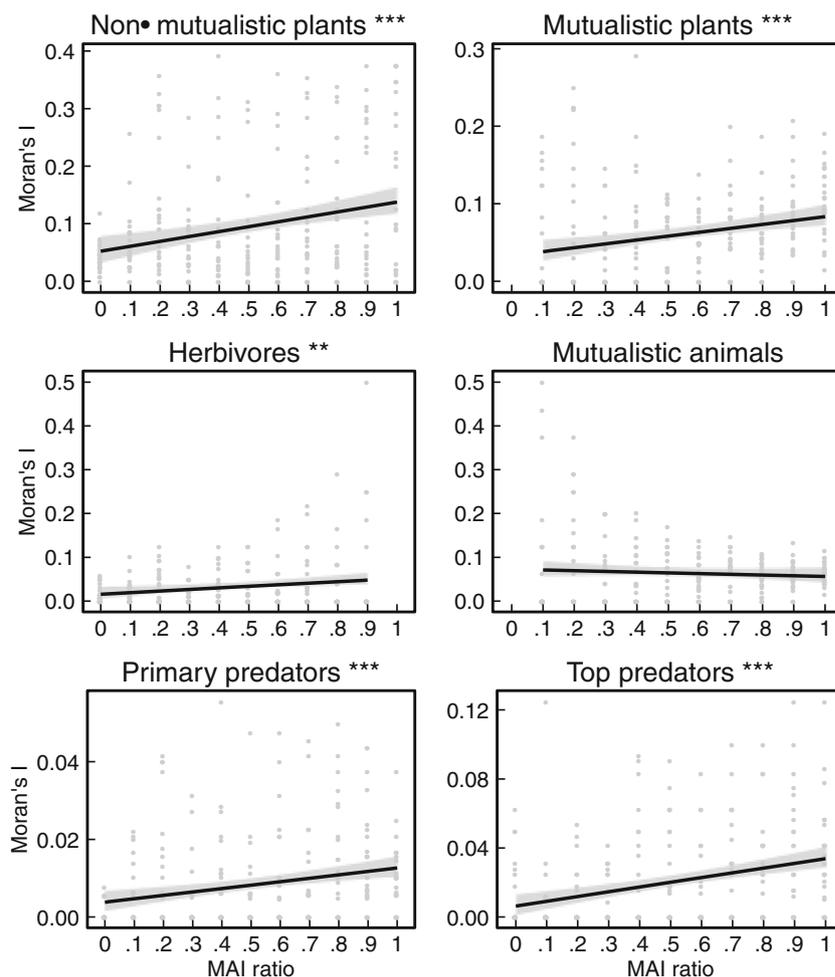
Fig. 6 Frequency distributions of interaction strengths in the overall ecological network across different values of MAI ratio

more stable communities. More importantly, increasing the proportion of mutualistic vs. antagonistic interactions (i.e. MAI ratios) influences different dimensions of ecological stability in different ways, although never negatively. Stability was either not influenced by increasing mutualism—in the cases of population stability and species' spatial distributions—or was positively influenced by them—spatial aggregation, distribution of interaction strengths. The question arising is: why were some components of stability affected by MAI ratios and others were not?

Stability of our model communities in terms of the variability in the population dynamics of their constituent species was not affected by the MAI ratio. This could be a consequence of the stabilising effect of space on complex communities, as has been previously demonstrated (e.g. (Solé and Bascompte 2006)), regardless of the type of interaction considered. Several mechanisms that could yield these stability patterns due to spatial arrangements within communities, such as metapopulation dynamics and refugee effects, are in place in our model. Metapopulation dynamics, via the exchange of individuals among local populations, could be an important factor determining the fate of species, preventing them from going extinct (Hanski 1998). Metapopulation structure in our model communities emerges as a property of the system from organisation of individuals at the local scale. Also, the refugee effect created by highly aggregated populations (see Fig. 7), which prevents predators from attacking individuals at the core of these populations, could drive stability at the population level. Collectively, these factors could have profound impacts on the ability of predators to capture prey as mutualisms increase. It is possible however that the opposite pattern could arise, whereas a more aggregated prey distribution would allow predator individuals to find the 'next' prey to attack more readily. This would result in higher attack rates. The emergence of this pattern would make communities displaying it less able to persist through time since the predator would force their prey into an extinction vortex. This suggests that a good balance between prey aggregation and attack rate must be found to enhance persistence. The key to this balance could lie on the strength of ecological interactions.

Our results showed that increasing MAI ratios results in model communities with a lower quantitative generality (G_q). Because quantitative generality measures the generality of consumers, this indicates that predators, even when keeping all of their prey species as MAI increases, are becoming more specialised (i.e. they are more likely to interact with some of their prey species than with others). Since our model does not enforce any kind of prey preference or selection, this is exclusively a consequence of an increased abundance of those 'preferred' prey species. A higher proportion of mutualistic interactions promotes the dominance of certain prey species that are becoming relatively more abundant. As a result and in parallel to this pattern, some of the interactions of generalist

Fig. 7 Moran's I spatial aggregation index per trophic level as a function of MAI ratio. Points show index values for each replicate. Line and shadow on each plot represent the fit of a linear model to the data and the standard error of the mean, respectively. ** and *** correspond to p values <0.01 and 0.001 for linear models fit to each data set, respectively



species are becoming weaker (those with less abundant prey). This could in turn cause a shift in the distribution of the strengths of interactions towards lower values, a distinctive feature of more stable communities (McCann 2000; Neutel et al. 2002). Interestingly, the distribution of interaction strengths at the community level was largely affected by MAI ratios, with weaker interactions becoming more common in communities with higher MAI ratios. Therefore, a higher fraction of mutualistic species promotes community stability by shifting the distribution of interaction strengths towards lower values.

The likely mechanism behind the observed changes in interaction strength patterning is a differential spatial aggregation of species per trophic level. Both global (Moran's I) and local (Geary's C) aggregation metrics were positively influenced by MAI ratios at the whole community level, with some trophic groups displaying a stronger relationship than others. The populations of basal species (plants) were more aggregated at higher MAI ratios. This higher spatial aggregation of primary producers is likely due to the fact that mutualistic consumers take up fewer resources from their interaction partners. Populations of mutualistic plants can thus remain more

aggregated due to decreased mortality and hence increased local reproduction. Additionally, given that there are less herbivore species as MAI ratio increases, non-mutualistic plants remain more clustered. Regardless of the mechanisms behind the aggregation of basal species (e.g. decreased mortality, increased local reproduction, herbivory release), the effects of this aggregation percolates up through the food chains, possibly by inducing herbivores (and mutualistic animals) to remain near aggregated food sources, and hence predator species become more clustered as MAI ratio increases. In summary, spatial aggregation offers a potential explanation to why interactions in the community are becoming weaker in general, as suggested by the decrease in G_q . Consumers will be more likely to interact with the same prey species if they are aggregated around them, in detriment of their other potential interactions as defined in the niche model.

Our results seem to contradict those of Mougi and Kondoh 2012, who found that higher levels of mutualisms have a destabilising effect on the communities with a mixture of antagonistic and mutualistic interactions. Even though space has an important influence on the stability of ecological communities (whether natural or artificial), we should not overlook

the fact that the results by Mougi and Kondoh were obtained from communities where mutualistic interactions were arranged randomly across the interaction network. In the present study, we only allow mutualistic interactions between basal (plant) and first-order consumer (herbivores) species, mimicking plant-animal mutualisms. Besides, the ‘proportion of mutualistic interactions’ in our study refers to the proportion in relation to herbivore links rather to the whole set of interactions in the community, as in Mougi and Kondoh’s. Thus, MAI ratios of 1 (or 100 % mutualism) in this study correspond to low-to-intermediate values of mutualism in their study, range in which they found the most stable communities. These observations suggest that both studies might actually be consistent with each other. Also recently, Sauve et al. 2014 found that in model communities, network properties that were previously associated to community stability in ecological networks with a single interaction type—nestedness for mutualistic networks and modularity for food webs—are no longer good predictors of stability in ‘hybrid’ communities. These properties were not affected by MAI ratios in our model communities. By extending community stability analysis to spatial networks with a mixture of interaction types, our results further supports Sauve et al.’s findings by confirming that modularity and nestedness (network properties that do not change with MAI ratio) are not related to community stability (which increases with MAI ratio). However, the mechanisms are not clear. The increase in the importance of indirect effects on hybrid communities, together with the associated unpredictability that indirect effects have on community dynamics (Yodzis 1988; Montoya et al. 2009; Novak et al. 2011), is likely to reduce the importance of network topology for stability. In addition, the spatial distribution of individuals across trophic levels by ultimately affecting interaction strengths is also diminishing the importance of these two network properties for community dynamics.

Conclusion

Ecological stability has several components (Pimm 1984) and considering different aspects of stability in community analyses benefits the exploration of complexity-stability relationships (Donohue et al. 2013). In this study, we have made three major developments in the understanding of complexity-stability relationships in complex food webs by (1) exploring the effects of antagonistic and mutualistic interactions operating simultaneously and across a gradient, (2) including interactions at the individual level and (3) considering space explicitly. We showed that the proportion of mutualistic vs. antagonistic interactions largely affects spatial stability. This is a key advance for understanding how spatial processes such as dispersal, aggregation, or habitat loss and fragmentation affect community stability. The ‘network of networks’ approach

adopted here and increasingly claimed for in network research allows for a more comprehensive exploration of the relationship between network architecture and community stability.

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Author contributions All authors designed the research. ML performed modelling work, ran the simulations and analysed output data. DM also analysed output data. All authors discussed the results. ML wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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