



Swansea University
Prifysgol Abertawe



Cronfa - Swansea University Open Access Repository

This is an author produced version of a paper published in:

Theoretical Ecology

Cronfa URL for this paper:

<http://cronfa.swan.ac.uk/Record/cronfa50165>

Paper:

Lurgi, M., Montoya, D. & Montoya, J. (2016). The effects of space and diversity of interaction types on the stability of complex ecological networks. *Theoretical Ecology*, 9(1), 3-13.

<http://dx.doi.org/10.1007/s12080-015-0264-x>

This item is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Copies of full text items may be used or reproduced in any format or medium, without prior permission for personal research or study, educational or non-commercial purposes only. The copyright for any work remains with the original author unless otherwise specified. The full-text must not be sold in any format or medium without the formal permission of the copyright holder.

Permission for multiple reproductions should be obtained from the original author.

Authors are personally responsible for adhering to copyright and publisher restrictions when uploading content to the repository.

<http://www.swansea.ac.uk/library/researchsupport/ris-support/>

1 **Title:** The effects of space and diversity of interaction types on the stability of complex
2 ecological networks

3
4 **Running title:** Interaction types, space & network stability

5
6 **Authors:** Miguel Lurgi¹⁺ (miguel.lurgi@creaf.uab.es), Daniel Montoya²⁺
7 (daniel.montoya@bristol.ac.uk) and José M. Montoya^{1,3,*} (montoya@icm.csic.es)

8
9 **Affiliations:**

10 ¹ CREAM, Cerdanyola del Vallès, Barcelona, Spain

11
12 ² School of Biological Sciences, Life Science Building, University of Bristol, Bristol, UK

13
14 ³ Ecological Networks and Global Change Group, Experimental Ecology Station, CNRS,
15 09200, Moulis, France

16
17 ⁺ Both authors contributed equally to this work

18
19 **Keywords:** cellular automata, food web, individual-based model, meta-community
20 dynamics, mutualistic interactions, network structure, population dynamics, predator-prey

21
22 **Author contributions.** All authors designed the research. ML performed modeling work, ran
23 the simulations and analyzed output data. DM analyzed output data. All authors discussed
24 results. ML wrote the first draft of the manuscript, and all authors contributed substantially to
25 revisions

26
27 **Words in abstract:** 213

28
29 **Words in main text:** 5133

30
31 **References:** 51

32
33 **Figures:** 7

34
35 **Tables:** 1

36
37 * Corresponding author: José M. Montoya

38
39 Ecological Networks and Global Change Group, Experimental Ecology Station, Centre
40 National de la Recherche Scientifique, 09200 Moulis, France

41 E-mail: montoya@icm.csic.es

44 **Abstract**

45 The relationship between structure and stability in ecological networks, and the effect of
46 spatial dynamics on natural communities have both been major foci of ecological research for
47 decades. Network research has traditionally focused on a single interaction type at a time
48 (e.g., food webs, mutualistic networks). Networks comprising different types of interactions
49 have recently started to be empirically characterized. Patterns observed in these networks and
50 their implications for stability demand for further theoretical investigations. Here we
51 employed a spatially explicit model to disentangle the effects of mutualism:antagonism ratios
52 in food web dynamics and stability. We found that increasing levels of plant-animal
53 mutualistic interactions generally resulted in more stable communities. More importantly,
54 increasing the proportion of mutualistic vs. antagonistic interactions at the base of the food
55 web affects different aspects of ecological stability in different directions, although never
56 negatively. Stability is either not influenced by increasing mutualism - for the cases of
57 population stability and species' spatial distributions - or is positively influenced by it - for
58 spatial aggregation of species. Additionally, we observe that the relative increase of
59 mutualistic relationships decreases the strength of biotic interactions in general within the
60 ecological network. Our work highlights the importance of considering several dimensions of
61 stability simultaneously to understand the dynamics of communities comprising multiple
62 interaction types.

63

64 **Introduction**

65 Biodiversity and species interactions are key regulators of ecosystem stability and
66 functioning (May 1972; Levins 1974; Pimm 1984; McCann 2000; Reiss et al. 2009; Loreau
67 & de Mazancourt 2013). Research on the relationship between the architecture of species
68 interaction networks and community stability has shown that, whereas high connectance and
69 nestedness promote stability and increases species richness in communities made up
70 exclusively of mutualistic interactions (but see (Allesina & Tang 2012; James et al. 2013;
71 Staniczenko et al. 2013)), the stability of trophic networks is higher in modular and weakly
72 connected architectures (Thebault & Fontaine 2010). Additionally, the strength of ecological
73 interactions has also been shown to play a crucial role in community structure (Paine 1980;
74 Neutel et al. 2002). Although these studies have improved our knowledge on complexity-
75 stability relationships, they have often focused on a single interaction type at a time and
76 overlooked the fact that natural communities comprise different interaction types that operate
77 simultaneously in space and time (Fontaine et al. 2011; Kéfi et al. 2012). Empirical work has
78 started to address methodologies to incorporate different interaction types into a broader
79 ecological network context, in which the creation of a ‘network of networks’ and its
80 implications for different aspects of community organisation are considered (Melián et al.
81 2009; Olff et al. 2009; Fontaine et al. 2011; Kéfi et al. 2012).

82 These empirical studies have opened up a big theoretical challenge in complexity-
83 stability research: exploring how interaction networks with different architectures and
84 interaction types combine to shape stable networks of networks. A theoretical framework that
85 incorporates these features will facilitate the understanding of the mechanisms behind the
86 observed empirical patterns and of how multiple interaction types taken together affect
87 ecosystem stability and functioning (Thebault & Fontaine 2010; Kéfi et al. 2012). Recent
88 attempts to do so have shown that interaction type may affect community stability and its

89 relationship with network architecture (Allesina & Tang 2012), and that the proportion of
90 trophic versus mutualistic interactions may influence the stability of natural communities
91 (Mougi & Kondoh 2012). Mougi & Kondoh (2012) showed that, whereas the presence of a
92 few mutualistic interactions destabilises predator-prey communities, a moderate mixture of
93 antagonistic and mutualistic interactions could have a stabilising effect in 'hybrid'
94 communities. More recently, the stabilizing role of nestedness and modularity has been
95 challenged when several interaction types are considered within the same network, arguably
96 by the increasing importance of indirect effects in these networks of networks (Sauve et al.
97 2014).

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

114 interactions between species in the community. Constraints imposed by space are thus not
115 only fundamental to understand patterns of diversity, but also spatial processes alone can
116 result in network architectures that resemble those observed in real networks (Morales &
117 Vázquez 2008). However, despite important advances with single interaction types (Holt
118 2002; McCann et al. 2005; Fortuna et al. 2008), we still lack understanding on complexity-
119 stability relationships in a spatially explicit context with different interaction types considered
120 simultaneously.

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

133

134 **Material and Methods**

135 We developed an individual-based, spatially explicit, bio-energetic model of species
136 interaction networks. Network architecture was obtained using the niche model (Williams &
137 Martinez 2000). The dynamics of the system are governed by local rules of interactions
138 between individuals in a simulated, spatially explicit environment. Models of this type,

139 although simple in terms of the nature of individual's interactions, successfully reproduce
140 relevant ecological patterns (Durrett & Levin 1994; Solé et al. 2002; Morales & Vázquez
141 2008). Individuals' state is determined by several bio-energetic constraints. For the analysis
142 of model outcomes we employ network metrics that are traditionally used for the
143 characterisation of food webs and mutualistic interaction networks. We also calculate
144 different metrics of community stability to create a comprehensive picture of stability based
145 on several dimensions (*sensu* (Donohue et al. 2013)). The model allows us to test the
146 relationship between different mutualistic vs. antagonistic interactions (MAI) ratios and
147 several network and stability properties. We ran 275 replicates of experiments consisting of
148 model communities generated using different MAI ratios and letting them evolve through
149 time.

150 *Generation of species interactions networks*

151 Food web architecture was obtained using the niche model (Williams & Martinez
152 2000). This model requires 2 input parameters: (1) the number of species (S), and (2)
153 connectance, defined as the fraction of realised links ($C=L/S^2$) within the network. The niche
154 model describes trophic niche occupancy between consumers and resources along a resource
155 axis, and successfully generates network structures that approximate well the central
156 tendencies and the variability of a number of food web properties (Williams & Martinez
157 2000; Dunne et al. 2002; Stouffer et al. 2005). Because it arranges consumers and resources
158 along a resource axis, the niche model can be applied to other types of consumer-resource
159 interactions (aside from antagonistic predator-prey). We thus used the niche model to define
160 mutualistic interactions simply by substituting some herbivore links by mutualistic ones
161 while keeping connectance and species richness constant. The model for network
162 construction selected however, should not affect our results, as long as realistic food web
163 architectures are produced.

164 We created food webs comprising 60 species and with connectance values of 0.08
165 (values well within the range of those found for real food webs (Dunne et al. 2002)) for MAI
166 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
167 different MAI ratios, from communities with no mutualistic interactions to communities with
168 only mutualistic links and no herbivores (see Appendix S1 in Supporting Information for
169 more details on network construction). We classified species into 6 categories (i.e., trophic
170 groups) according to their position within the overall food web: (1) non-mutualistic plants,
171 (2) mutualistic plants, (3) animal mutualists or mutualistic consumers, (4) herbivores, (5)
172 primary predators, and (6) top or apex predators (Fig. 1).

173 *Individual-based spatially explicit dynamics*

174 Individual-based models (IBMs) have been used to tackle different problems in
175 ecology, although not very frequently to simulate complex ecosystems comprising large
176 numbers of species (Grimm & Railsback 2005). We implemented an IBM that simulates
177 dynamics typical of two-dimensional cellular automata (CA) (Ulam 1952; Durrett & Levin
178 1994) but based on ecological rules of interaction. This CA represents our simulated
179 community in space. Space in the CA is represented as a 2D lattice. Cells in the lattice can be
180 occupied by a maximum of two individuals at any given time, provided that one of them
181 belongs to a plant and the other one to an animal species. Cells in the lattice can thus be in
182 one of four states: (i) empty, (ii) harbouring a plant individual or (iii) an animal individual,
183 and (iv) harbouring a plant and an animal individuals. Torus boundary conditions were used
184 for the 2D lattice in order to reduce possible edge effects due to the loss of individuals.
185 Individuals change their internal state (or not) during each iteration of model simulations, not
186 only according to their interactions but also as a function of a number of bio-energetic
187 constraints (Table S1). CA-type rules represent demographic processes, foraging actions, and
188 inter/intra -species interactions of individuals in our IBM. These rules, by which individuals

189 (and hence the CA) change their state through time, are detailed in Appendix S1.

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

204 During model simulations spatial communities evolve through time following
205 constraints imposed by bio-energetic parameters (see Table S1), spatial constraints (similar to
206 all individuals), and the interactions between species determined by network architecture.
207 After 5000 time steps, which include an initial period of transient dynamics, the communities
208 are analysed in terms of diversity (species richness and abundances), network properties and
209 stability.

210 *Diversity and food web properties*

211 Several statistical properties of the network of species interactions were measured after
212 transient dynamics. In particular, we measured the number of species (S), number of links
213 (L), connectance ($C=L/S^2$), the standard deviation of generality ($GenSD$) and vulnerability

214 (*VulSD*) - the last two quantify diet breadth variability, and predation pressure variability
215 across species, respectively (Williams & Martinez 2000). Additionally, we obtained
216 quantitative indices that consider the strength of species interactions including: H'_2 - a
217 measure of mutualistic specialisation - (Blüthgen et al. 2006), which was calculated for the
218 mutualistic part of the web, since it is only meaningful for bipartite interaction networks; and
219 quantitative measures of generality (G_q) and vulnerability (V_q) (Bersier et al. 2002). Table 1
220 presents the full set of metrics calculated over the networks and their mathematical
221 definitions, including those mentioned above.

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

225 *Community stability*

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

239 been identified as distinctive feature of more stable natural communities (McCann 2000;
240 Neutel et al. 2002).

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

$$242 \quad \alpha_{ij} = \frac{b_{ij}}{N_i * N_j}$$

243 where b_{ij} is the total biomass flowing from prey species i to predator species j -quantified
244 here as the total number of individuals (or fractions of it, in the case of plants) from species i
245 eaten by individuals of species j -. N_i and N_j are the total number of individuals of species i
246 and j at the time of the calculation of the index, respectively. This way of calculating
247 interaction strengths quantifies the per-capita effect of a predator species over its prey, and it
248 is thus analogous to Paine's index and Lotka-Volterra interaction coefficients (Neutel et al.
249 2002; Berlow et al. 2004). This allows us to employ these values to assess and understand
250 community stability based on the strengths of ecological interactions.

251 We additionally looked at 3 other measures of community stability. First, temporal
252 variability, which quantifies population variability as the average of the coefficient of
253 variation (CV) of species population abundances through time (Pimm 1984). Second, spatial
254 variability, which corresponds to the CV of the location of the centroid of each species range
255 through time (see Appendix S1). And third, aggregation stability, measured as the degree of
256 clustering (i.e., spatial correlation) of individuals within each species in space (i.e., Moran's I
257 and Geary's C indexes described in Appendix S1). This metric is linked to reproductive
258 stability because the likelihood of finding a reproductive partner in the neighbourhood is
259 higher in more spatially aggregated distributions. Collectively, more stable communities will
260 be characterised by lower temporal and spatial variability, higher reproductive stability, and
261 lower average interaction strengths. This framework allowed the exploration of the
262 relationships between network properties and the stability metrics in our communities by
263 looking at how temporal and spatial stability changed as MAI ratio increased.

264 *Experimental simulations*

265 We generated networks with 11 different MAI ratios in order to study the effects of
266 different combinations of antagonistic and mutualistic interactions on community stability.
267 The individual-based model described above was employed to perform a series of
268 simulations of the dynamics of the system through time and space. Simulations were set up
269 by placing a given community, made up of artificial individuals belonging to each of the
270 species in the interaction network defined by the niche model, on a landscape that consists of
271 a 200x200 square lattice with identical cells. Each cell can be occupied at any given time by
272 at most two individuals, yielding a maximum of 80,000 individuals. At the beginning of the
273 simulations only 40 per cent of the landscape was occupied and populated with the same
274 number of individuals of each species randomly across the lattice. Communities were
275 allowed to evolve for 5,000 iterations. Diversity and network properties were constantly
276 monitored.

277 We performed 25 replicates for each of the 11 MAI ratios, each of them representing
278 different sets of initial conditions, not only in terms of the initial configuration of the
279 simulated landscape but also regarding the network of interactions. For each of these 25
280 replicates the initial distributions of individuals across the landscape varied by placing
281 individuals randomly across the landscape for each replicate as detailed above. The network
282 of interactions for each of these replicates was generated independently by running different
283 instances of the niche model with the same S and C values, and choosing the mutualistic links
284 following the heuristic described in Appendix S1. We kept S and C constant across our
285 simulations because our aim is to evaluate the effect of varying MAI ratios on community
286 stability rather than the effects of changes in species richness or connectivity. This process
287 effectively produced different interaction networks for each run with the same number of
288 species and connectivity. Each of the 25 communities simulated for each MAI ratio was thus

289 independent, and the architecture of the ecological network was different from replicate to
290 replicate. This yielded a total of $25 \times 11 = 275$ replicates.

291 Linear models (LM) were used to analyse the relationship between MAI ratios and the
292 properties of the communities and their interaction networks as well as their effect on
293 stability. The IBM used here was developed using Python v2.7 (www.python.org), while
294 statistical analyses were performed in R 2.15.2 (R Core Development Team, 2012).
295 Sensitivity analyses were carried out to assess the robustness of our results to differences in
296 species richness, landscape lattice size, and number of generated communities. See Appendix
297 S1 for a description of these analyses. The model presented here incorporates a total of 17
298 free parameters (see Table S1), over which sensitivity analyses could be performed. Our aim
299 however, was to use realistic values that would result in dynamically stable communities in
300 terms of species richness and trophic level abundances. For some parameter combinations,
301 after a short number of iterations of the model, several species in the system went extinct,
302 making the analysis of stability proposed in this work unfeasible. Additionally, we were not
303 interested in parameter combinations able to produce stable dynamics but based on
304 unrealistic parameter combinations, because their applicability to reality is questionable. Our
305 approach was thus to use a single parameter combination with realistic values for all of the
306 parameters while at the same time able to reproduce persistent communities.

307 **Results**

308 *Community structure*

309 After a period of transient dynamics, the resulting simulated communities and their
310 associated interactions networks displayed patterns similar to those found in empirical
311 multitrophic assemblages. Population dynamics showed oscillations typical of predator-prey
312 and mutualistic interactions in multispecies systems, with all species in the community
313 persisting through time. The rank-abundance and degree distributions of the simulated

314 communities followed lognormal (Fig. S2) and exponential (Fig. 3, p-value < 0.001 for all
315 fits to exponential models) patterns, respectively, typical of natural communities (Montoya et
316 al. 2006). Therefore, we can conclude that the model successfully generates communities
317 displaying empirically-observed patterns.

318 Diversity metrics changed as expected by an increase in MAI ratios. Although the level
319 of mutualism did not affect total species richness, communities with larger MAI ratios hosted
320 a larger number of individuals ($F_{(1,273)} = 98.69$, $p < 0.001$) (Fig. 4). In spite of a decline in the
321 abundance of non-mutualistic primary producers and herbivores with increasing MAI ratios
322 (as expected due to a larger fraction of mutualistic species), the increase in mutualistic plants
323 and animals overcompensated for this loss, causing an overall increase in abundance. This
324 over-compensation was due to mutualistic plants becoming more abundant than non-
325 mutualistic ones since mutualistic consumers do not consume as much resources from them
326 and are, additionally, beneficial for their reproduction. Increased MAI ratios caused a
327 significant decline in Shannon diversity index (Fig. 4, $F_{(1,273)} = 71.47$, $p < 0.001$). This result
328 is in line with our previous observation reporting an increased overall abundance of
329 individuals following a systematic increase in mutualistic plant and animal abundances. The
330 proportion of mutualistic species in the community had a profound effect on diversity and
331 evenness, making model communities more biased towards the dominance of mutualistic
332 species.

333 Most network properties were not significantly affected by the degree of mutualism vs.
334 antagonism. However, some of them did show a monotonic relationship with MAI ratio.
335 Quantitative generality (G_q) was significantly lower in communities with higher MAI ratio
336 ($F_{(1,273)} = 59.49$, $p < 0.001$, Fig. 5), whereas specialisation (H'_2) within the mutualistic sub-
337 web decreased ($F_{(1,248)} = 25.91$, $p < 0.001$, Fig. 5). These results combined indicate that a
338 larger fraction of mutualistic interactions resulted in more generalised mutualistic interactions

339 within a more specialised overall network. It is important to note that we are referring here to
340 quantitative metrics. This means that, with increasing MAI ratios, binary network architecture
341 remained constant –not significant differences in modularity, nestedness or connectance
342 across MAI ratios-, but interactions at the overall network level became weaker in general,
343 with only a few strong interactions. On the mutualistic sub-web, interactions became more
344 homogeneous in terms of strength due to a weakening of the interactions in general, which
345 made it less specialised (lower H'_2) by increasing the relative importance of weak links.

346 *Community stability*

347 Based on the interaction strengths criterion for community stability (see Methods), we
348 found that MAI ratios enhanced dynamic stability in our model communities. We observed a
349 significant reduction in $\langle i \rangle$ -the average interaction strength- as MAI ratio increased,
350 evidenced by a shift in the distribution of interactions strengths towards lower values with
351 MAI ratio (Fig. 6, $p < 0.001$ for all pairwise comparisons between distributions). This result
352 suggests that mutualistic interactions make communities more stable by lowering the average
353 strength of ecological relationships between species.

354 MAI ratios did not affect temporal stability (i.e., population variability through time),
355 spatial stability (as measured by the change in the centroid of the species' spatial range) or the
356 area and density of species populations. In contrast, higher MAI ratios resulted in
357 significantly higher and lower Moran's I and Geary's C indexes, respectively (correlation tests
358 using linear models yielded $F_{(1,273)} = 29.06$, $p < 0.01$ for Moran's I and $F_{(1,273)} = 24.35$, $P <$
359 0.01 for Geary's C against MAI ratios), revealing more spatially aggregated populations with
360 increasing MAI ratios (Fig. S3). Increases in spatial aggregation were different across trophic
361 levels both at global (Moran's I) and local (Geary's C) scales. For example, whereas
362 predators and plants got significantly more aggregated as MAI ratio increased, the
363 aggregation of mutualistic animals and herbivores was either not affected or only weakly

364 affected by changing MAI ratios, respectively (Figs. 7 and S4). We argue that more spatially
365 aggregated populations can be associated with higher reproductive potential stability, as the
366 likelihood of finding a reproductive partner in the neighbourhood is higher. From this
367 perspective, communities in general, and plant and predator species in particular, were thus
368 more stable in terms of species reproductive potential as the MAI ratio increased (Figs. 7, S3,
369 and S4).

370 **Discussion**

371 The consideration of different interaction types simultaneously within the same
372 ecological network has consistent and predictable effects on community organisation and
373 stability across a gradient of antagonistic vs. mutualistic interactions. We have shown that
374 increasing levels of mutualisms result in more stable communities. More importantly,
375 increasing the proportion of mutualistic vs. antagonistic interactions (i.e., MAI ratios)
376 influences different dimensions of ecological stability in different ways, although never
377 negatively. Stability was either not influenced by increasing mutualism - in the cases of
378 population stability and species' spatial distributions - or was positively influenced by them -
379 spatial aggregation, distribution of interaction strengths-. The question arising is: why were
380 some components of stability affected by MAI ratios and others not?

381 Stability of our model communities in terms of the variability in the population
382 dynamics of their constituent species was not affected by the MAI ratio. This could be a
383 consequence of the stabilising effect of space on complex communities, as has been
384 previously demonstrated (e.g., (Solé & Bascompte 2006)), regardless of the type of
385 interaction considered. Several mechanisms that could yield these stability patterns due to
386 spatial arrangements within communities, such as metapopulation dynamics and refuge
387 effects, are in place in our model. Metapopulation dynamics, via the exchange of individuals
388 among local populations, could be an important factor determining the fate of species,

389 preventing them from going extinct (Hanski 1998). Metapopulation structure in our model
390 communities emerges as a property of the system from organisation of individuals at the local
391 scale. Also, the refugee effect created by highly aggregated populations (see Fig. 7), which
392 prevents predators from attacking individuals at the core of these populations, could drive
393 stability at the population level. Collectively, these factors could have profound impacts on
394 the ability of predators to capture prey as mutualisms increase. Is it possible however that the
395 opposite pattern could arise, whereas a more aggregated prey distribution would allow
396 predator individuals to find the ‘next’ prey to attack more readily. This would result in higher
397 attack rates. The emergence of this pattern would make communities displaying it less able to
398 persist through time since the predator would force their prey into an extinction vortex. This
399 suggests that a good balance between prey aggregation and attack rate must be found to
400 enhance persistence. The key to this balance could lie on the strength of ecological
401 interactions.

402 Our results showed that increasing MAI ratios results in model communities with a
403 lower quantitative generality (G_q). Because quantitative generality measures the generality of
404 consumers, this indicates that predators, even when keeping all of their prey species as MAI
405 increases, are becoming more specialised (i.e., they are more likely to interact with some of
406 their prey species than with others). Since our model does not enforce any kind of prey
407 preference or selection, this is exclusively a consequence of an increased abundance of those
408 ‘preferred’ prey species. A higher proportion of mutualistic interactions promotes the
409 dominance of certain prey species that are becoming relatively more abundant. As a result
410 and in parallel to this pattern, some of the interactions of generalist species are becoming
411 weaker (those with less abundant prey). This could in turn cause a shift in the distribution of
412 the strengths of interactions towards lower values, a distinctive feature of more stable
413 communities (McCann 2000; Neutel et al. 2002). Interestingly, the distribution of interaction

414 strengths at the community level was largely affected by MAI ratios, with weaker interactions
415 becoming more common in communities with higher MAI ratios. Therefore, a higher fraction
416 of mutualistic species promotes community stability by shifting the distribution of interaction
417 strengths towards lower values.

418 The likely mechanism behind the observed changes in interaction strength patterning is
419 a differential spatial aggregation of species per trophic level. Both global (Moran's I) and
420 local (Geary's C) aggregation metrics were positively influenced by MAI ratios at the whole
421 community level, with some trophic groups displaying a stronger relationship than others.
422 The populations of basal species (plants) were more aggregated at higher MAI ratios. This
423 higher spatial aggregation of primary producers is likely due to the fact that mutualistic
424 consumers take up fewer resources from their interaction partners. Populations of mutualistic
425 plants can thus remain more aggregated due to decreased mortality and hence increased local
426 reproduction. Additionally, given that there are less herbivore species as MAI ratio increases,
427 non-mutualistic plants remain more clustered. Regardless of the mechanisms behind the
428 aggregation of basal species (e.g., decreased mortality, increased local reproduction,
429 herbivory release), the effects of this aggregation percolates up through the food chains,
430 possibly by inducing herbivores (and mutualistic animals) to remain near aggregated food
431 sources, and hence predator species become more clustered as MAI ratio increases. In
432 summary, spatial aggregation offers a potential explanation to why interactions in the
433 community are becoming weaker in general, as suggested by the decrease in G_q . Consumers
434 will be more likely to interact with the same prey species if they are aggregated around them,
435 in detriment of their other potential interactions as defined in the niche model.

436 Our results seem to contradict those of Mougi and Kondoh (2012), who found that
437 higher levels of mutualisms have a destabilising effect on the communities with a mixture of
438 antagonistic and mutualistic interactions. Even though space has an important influence on

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

463 *Conclusion*

464 Ecological stability has several components (Pimm 1984), and that considering
465 different aspects of stability in community analyses benefits the exploration of complexity-
466 stability relationships (Donohue et al. 2013). In this study, we have made three major
467 developments in the understanding of complexity-stability relationships in complex food
468 webs by (1) exploring the effects of antagonistic and mutualistic interactions operating
469 simultaneously and across a gradient, (2) including interactions at the individual level, and
470 (3) considering space explicitly. We showed that the proportion of mutualistic versus
471 antagonistic interactions largely affects spatial stability. This is a key advance for
472 understanding how spatial processes such as dispersal, aggregation, or habitat loss and
473 fragmentation affect community stability. The ‘network of networks’ approach used here and
474 increasingly claimed for in network research allows for a more comprehensive exploration of
475 the relationship between network architecture and community stability.

476

477 **Acknowledgements**

478 Miguel Lurgi was supported by Microsoft Research, through its PhD Scholarship
479 programme. DM was supported by the European Commission
480 (MODELECORESTORATION - FP7 Marie Curie Intra-European Fellowship for Career
481 Development [301124]).

482 **References**

- 483 Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems *Nature*, 483, 205–
484 208.
- 485 Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Jr, Loyola, R.D. & Ulrich, W. (2008). A
486 consistent metric for nestedness analysis in ecological systems: reconciling concept and
487 measurement. *Oikos*, 117, 1227–1239.
- 488 Begon, M., Townsend, C.R. & Harper, J.L. (2006). *Ecology: From Individuals to*
489 *Ecosystems*. 4th edn. John Wiley & Sons, Oxford, UK.
- 490 Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M.C., et
491 al. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of Animal*
492 *Ecology*, 73, 585–598.
- 493 Bersier, L.-F., Banašek-Richter, C. & Cattin, M. (2002). Quantitative descriptors of food-web
494 matrices. *Ecology*, 83, 2394–2407.
- 495 Blüthgen, N., Menzel, F. & Blüthgen, N. (2006). Measuring specialization in species
496 interaction networks *BMC Ecology*, 6.
- 497 Brose, U., Williams, R.J. & Martinez, N.D. (2006). Allometric scaling enhances stability in
498 complex food webs. *Ecology Letters*, 9, 1228–1236.
- 499 Burkle, L.A. & Alarcon, R. (2011). The future of plant-pollinator diversity: Understanding
500 interaction networks across time, space, and global change. *American Journal of Botany*,
501 98, 528–538.
- 502 Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., McNally, L., Viana, M., et al.
503 (2013). On the dimensionality of ecological stability. *Ecology Letters*, 16, 421–429.
- 504 Dormann, C.F., Fründ, J., Blüthgen, N. & Gruber, B. (2009). Indices, graphs and null models:
505 analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24.
- 506 Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002). Food-web structure and network

507 theory: The role of connectance and size. *PNAS*, 99, 12913–12916.

508 Durrett, R. & Levin, S.A. (1994). Stochastic spatial models: a user's guide to ecological
509 applications. *Philosophical Transactions of the Royal Society of London B: Biological*
510 *Sciences*, 343, 329–350.

511 Fontaine, C., Guimarães, P.R., Jr, Kéfi, S., Loeuille, N., Memmott, J., Van Der Putten, W.H.,
512 et al. (2011). The ecological and evolutionary implications of merging different types of
513 networks. *Ecology Letters*, 14, 1170–1181.

514 Fortuna, M.A., García, C., Guimarães, P.R., Jr & Bascompte, J. (2008). Spatial mating
515 networks in insect-pollinated plants. *Ecology Letters*, 11, 490–498.

516 Fortuna, M.A., Zaman, L., Wagner, A.P. & Ofria, C. (2013). Evolving digital ecological
517 networks *PLoS Computational Biology*, 9, e1002928.

518 Grimm, V. & Railsback, S.F. (2005). *Individual-based Modeling and Ecology (Princeton*
519 *Series in Theoretical and Computational Biology)*. Princeton University Press, Princeton,
520 New Jersey.

521 Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396.

522 Holt, R.D. (2002). Food webs in space: On the interplay of dynamic instability and spatial
523 processes. *Ecological Research*, 17, 261–273.

524 James, A., Pitchford, J.W. & Plank, M.J. (2013). Disentangling nestedness from models of
525 ecological complexity. *Nature*, 487, 227–230.

526 Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., et al.
527 (2012). More than a meal... integrating non-feeding interactions into food webs. *Ecology*
528 *Letters*, 15, 291–300.

529 Levins, R. (1974). Discussion paper: The qualitative analysis of partially specified systems.
530 *Annals of the New York Academy of Sciences*, 231, 123–138.

531 Loreau, M. & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of

532 underlying mechanisms. *Ecology Letters*, 16, 106–115.

533 May, R.M. (1972). Will a Large Complex System be Stable *Nature*, 238, 413–414.

534 McCann, K.S. (2000). The diversity–stability debate. *Nature*, 405, 228–233.

535 McCann, K.S., Rasmussen, J.B. & Ulanowicz, R.E. (2005). The dynamics of spatially
536 coupled food webs. *Ecology Letters*, Spatially coupled food webs, 8, 513–523.

537 Melián, C.J., Bascompte, J., Jordano, P. & Bascompte, J. (2009). Diversity in a complex
538 ecological network with two interaction types. *Oikos*, 118, 122–130.

539 Montoya, J.M., Pimm, S.L. & Solé, R.V. (2006). Ecological networks and their fragility.
540 *Nature*, 442, 259–264.

541 Montoya, J.M., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009). Press perturbations
542 and indirect effects in real food webs. *Ecology*, 90, 2426–2433.

543 Morales, J.M. & Vázquez, D.P. (2008). The effect of space in plant–animal mutualistic
544 networks: insights from a simulation study. *Oikos*, 117, 1362–1370.

545 Mougi, A. & Kondoh, M. (2012). Diversity of Interaction Types and Ecological Community
546 Stability. *Science*, 337, 349–351.

547 Neuhauser, C. (1998). Habitat destruction and competitive coexistence in spatially explicit
548 models with local interactions. *Journal of Theoretical Biology*, 193, 445–463.

549 Neutel, A.-M., Heesterbeek, J.A.P. & De Ruiter, P.C. (2002). Stability in Real Food Webs:
550 Weak Links in Long Loops. *Science*, 296, 1120–1123.

551 Novak, M., Wootton, J.T., Doak, D.F., Emmerson, M., Estes, J.A. & Tinker, M.T. (2011).
552 Predicting community responses to perturbations in the face of imperfect knowledge and
553 network complexity. *Ecology*, 92, 836–846.

554 Olesen, J.M. & Jordano, P. (2002). Geographic patterns in plant-pollinator mutualistic
555 networks. *Ecology*, 83, 2416–24162424.

556 Olf, H., Alonso, D., Berg, M.P., Eriksson, B.K., Loreau, M., Piersma, T., et al. (2009).

557 Parallel ecological networks in ecosystems. *Philosophical Transactions of the Royal*
558 *Society B: Biological Sciences*, 364, 1755–1779.

559 Paine, R.T. (1980). Food Webs: Linkage, Interaction Strength and Community Infrastructure.
560 *Journal of Animal Ecology*, 49, 666–685.

561 Pimm, S.L. (1979). Complexity and stability: another look at MacArthur's original
562 hypothesis. *Oikos*, 33, 351–357.

563 Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.

564 Pimm, S.L. & Lawton, J.H. (1980). Are food webs divided into compartments *JAE*, 49, 879–
565 898.

566 Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009). Emerging horizons in
567 biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution*, 24,
568 505–514.

569 Sauve, A.M.C., Fontaine, C. & Thébault, E. (2014). Structure-stability relationships in
570 networks combining mutualistic and antagonistic interactions. *Oikos*, 123, 378–384.

571 Solé, R.V. & Bascompte, J. (2006). *Self-Organization in Complex Ecosystems*. Princeton
572 University Press, New Jersey, USA.

573 Solé, R.V. & Montoya, J.M. (2006). Ecological network meltdown from habitat loss and
574 fragmentation. In: *Ecological Networks: Linking structure to dynamics in food webs*
575 (Pascual, M. & Dunne, J.A. eds.). Oxford University Press, Oxford, UK, p. 386.

576 Solé, R.V., Alonso, D. & Mckane, A. (2002). Self-organized instability in complex
577 ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357,
578 667–681.

579 Staniczenko, P.P.A., Kopp, J.C. & Allesina, S. (2013). The ghost of nestedness in ecological
580 networks. *Nature Communications*, 4, 1–6.

581 Stouffer, D.B., Camacho, J., Guimera, R., Ng, C. & Nunes Amaral, L. (2005). Quantitative

582 patterns in the structure of model and empirical food webs. *Ecology*, 86, 1301–1311.

583 Thebault, E. & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture
584 of Mutualistic and Trophic Networks. *Science*, 329, 853–856.

585 Tilman, D. & Kareiva, P. (Eds.). (1997). *Spatial Ecology: The Role of Space in Population*
586 *Dynamics and Interspecific Interactions*. Princeton University Press, New Jersey, USA.

587 Ulam, S.M. (1952). Random processes and transformations. In: *International Congress of*
588 *Mathematicians*. Presented at the International Congress of Mathematicians, Cambridge,
589 MA, USA, pp. 264–275.

590 Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404,
591 180–183.

592 Yodzis, P. (1988). The Indeterminacy of Ecological Interactions as Perceived Through
593 Perturbation Experiments. *Ecology*, 69, 508–515.

594

595 **Table 1.** Metrics applied over the interaction networks to obtain information about its
 596 structural and quantitative properties.
 597

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.	$G_i = \frac{1}{L/S} \sum_{j=1}^S a_{ji}$, where a_{ji} 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 & Lawton 1980)	$C = \frac{1}{S(S-1)} \sum_{i=1}^S \sum_{\substack{j=1 \\ j \neq i}}^S c_{ij}$, 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 Bluthgen 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).	$G_q = \sum_{k=1}^S \frac{b_{\cdot k}}{b_{\cdot\cdot}} n_{N,k}$, where $b_{\cdot k}$ is the total amount of biomass going into species k , and $b_{\cdot\cdot}$ 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).	$V_q = \sum_{k=1}^S \frac{b_{k\cdot}}{b_{\cdot\cdot}} n_{P,k}$, where $b_{k\cdot}$ is the total biomass emanating from species k . $b_{\cdot\cdot}$ 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).

598

599 **Figure Legends**

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

604

605 **Figure 2.** Example of a 2D grid (17x17 cells) showing a fraction of the landscape where
606 digital organisms in the individual-based model co-exist and interact. Trajectories of two
607 sample individuals until they encounter each other are represented by black and dark grey
608 squares. Light grey squares represent the neighbourhood of each of the two individuals at the
609 beginning of their respective current paths. At the end of both paths, each individual finds
610 itself inside the other's neighbourhood. Depending on other individuals present on a given
611 individual's neighbouring cells (shown as light grey cells for the starting position of each of
612 the two individuals in the figure) or whether these are available, the 'state' in this complex
613 cellular automaton will change following certain rules and constraints (see text and
614 Supporting Information).

615

616 **Figure 3.** Cumulative degree distributions from 10 sample communities with different MAI
617 ratios. Lines represent a fit of each dataset to an exponential distribution (p-values for all fits
618 < 0.001).

619

620 **Figure 4.** Total abundance of individuals in the community and Shannon diversity index at
621 the level of the total community versus MAI ratio. Total numbers of individuals are
622 represented in tens of thousands. Points show index values for each replicate. Line and
623 shadow on each plot represent the fit of a linear model to the data and the standard error of

624 the mean respectively. p-value < 0.001 for linear model fits to each data set.

625

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

630

631 **Figure 6.** Frequency distributions of interaction strengths in the overall ecological network
632 across different values of MAI ratio.

633

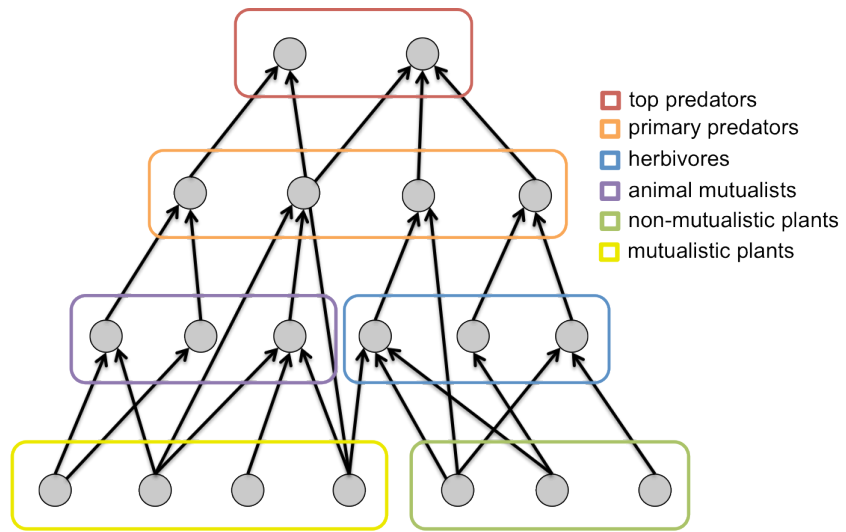
634 **Figure 7.** Moran's I spatial aggregation index per trophic level as a function of MAI ratio.
635 Points show index values for each replicate. Line and shadow on each plot represent the fit of
636 a linear model to the data and the standard error of the mean respectively. ** and ***
637 correspond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

638

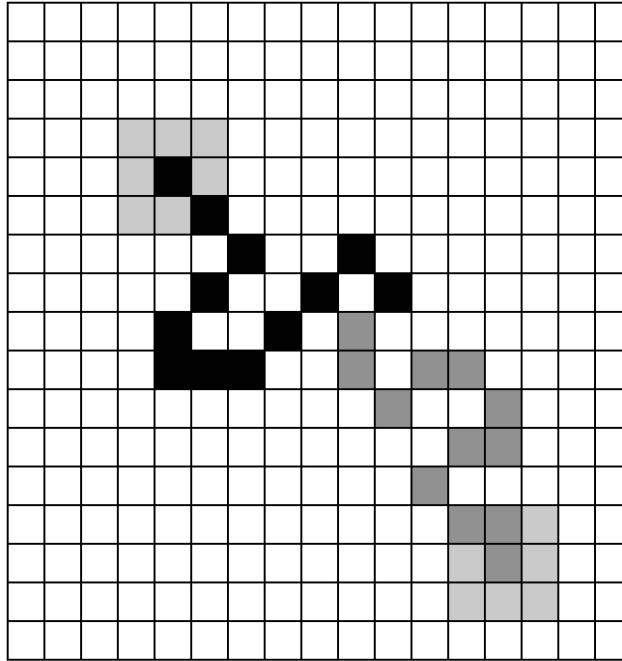
639

640 **Figures**

641 **Figure 1**



644 **Figure 2**

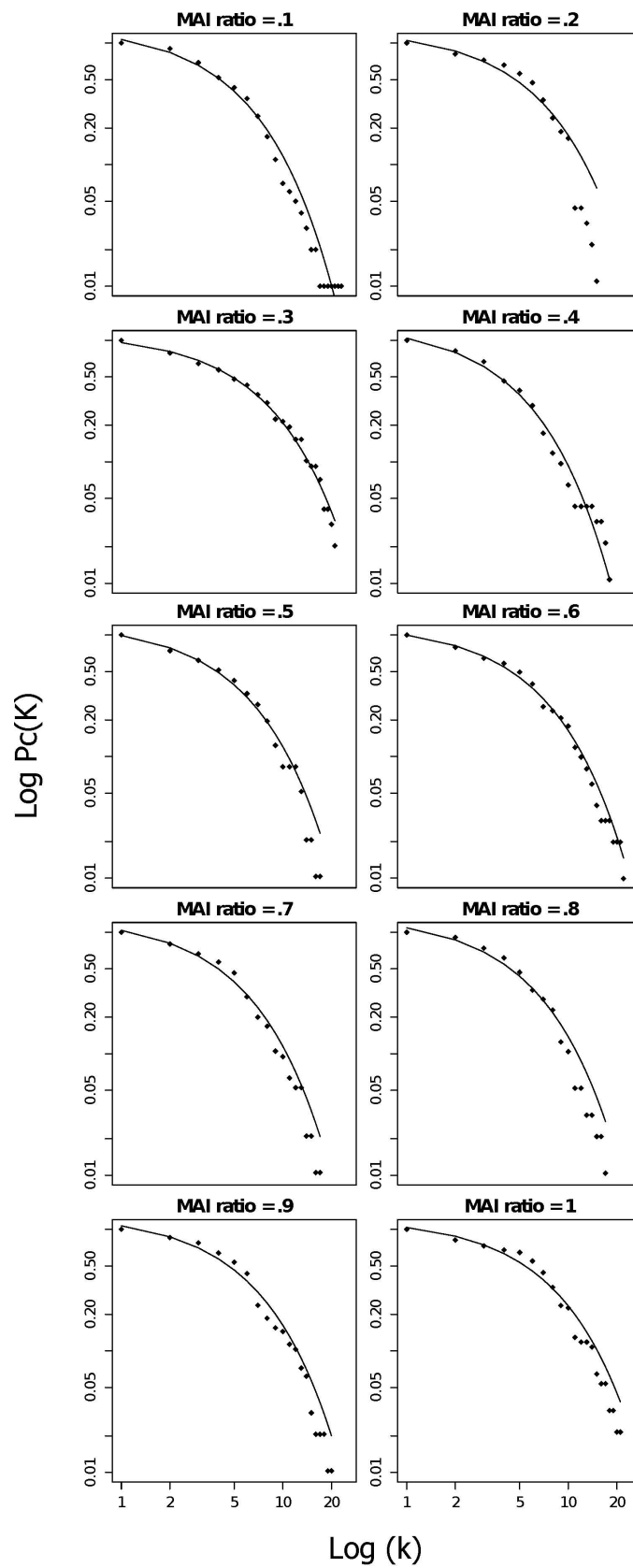


645

646

647

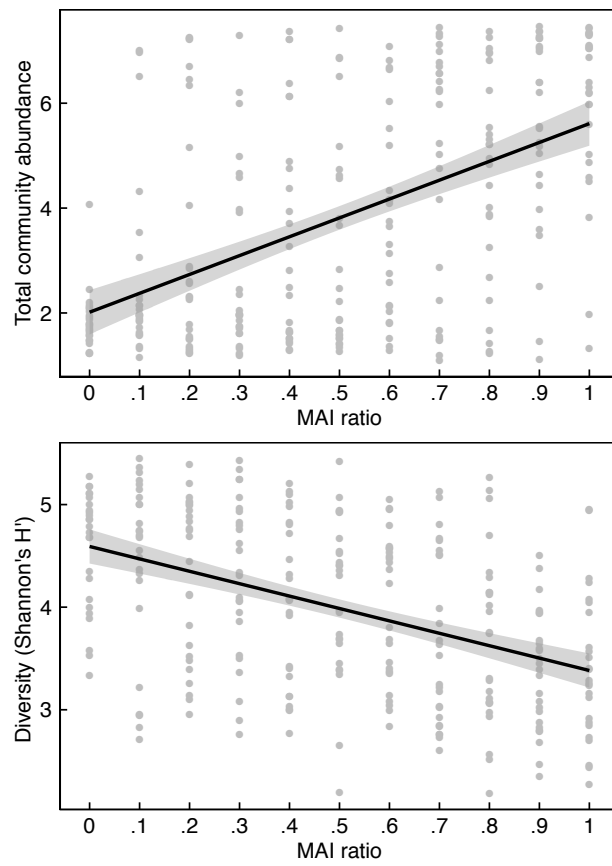
648



650

651

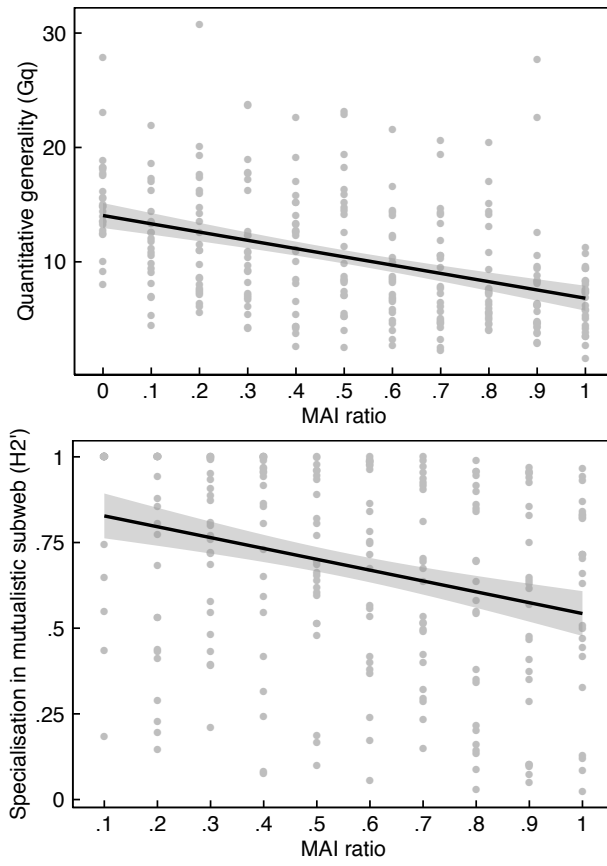
652 **Figure 4**



653

654

655 **Figure 5**

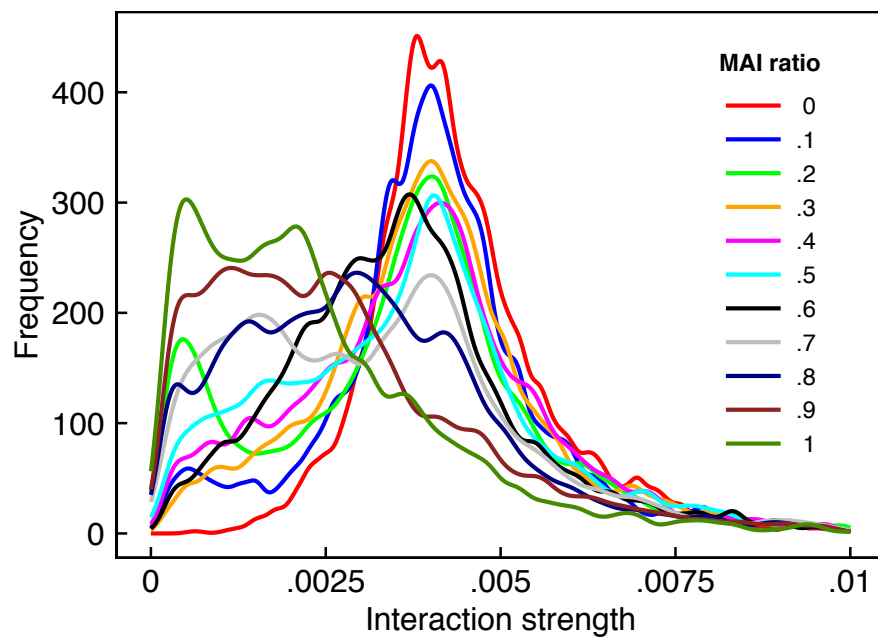


656

657

658

659 **Figure 6**



660

661

662

663

