



Disentangling the effect of hybrid interactions and of the constant effort hypothesis on ecological community stability

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In the last years, a remarkable theoretical effort has been made in order to understand the relation between stability and complexity in ecological communities. Yet, what maintains species diversity in real ecological communities is still an open question. The non-random structures of ecological interaction networks have been recognized as one key ingredient impacting the maximum number of coexisting species within the ecological community. However most of the earlier theoretical studies have considered communities with only one interaction type (either antagonistic, competitive or mutualistic). Recently, it has been proposed that multiple interaction types might stabilize ecosystems and that, in this hybrid case, increasing complexity increases stability. Here we show that these results depend on ad hoc hypothesis that the authors used in their model and we highlight the need to disentangle the role of multiple interaction types and constant interaction effort allocation on community stability. Indeed, we find that mixing of mutualistic and predator–prey interaction types does not stabilize the community dynamics and we demonstrate that a positive correlation between complexity and stability is observed only if a constant effort allocation is imposed in the ecological interactions.

Synthesis

In recent years a sparkling research has been devoted to the search of new theoretical mechanisms to explain way ecosystems may persist despite their complexity. Here we show that, contrary to what recently suggested (Mougi et al. 2012), the mismatch between theoretical results and empirical evidences on the stability of ecological community is still there also for communities with both mutualistic and antagonistic interactions, and the ‘complexity–stability’ paradox is still alive. Indeed, we demonstrate that their results arise as an artifact of the peculiar rescaling of the interaction strengths they imposed. Our study suggests that further theoretical studies and experimental evidences are still needed to better understand the role of interaction strengths in real ecological communities.

The relationship between ecosystems complexity or diversity and stability is one of the most debated issue by ecologists (May 1972, 1974, Pimm 1984, McCann 2000, Ives and Carpenter 2007, Allesina and Tang 2012). Complexity is defined as the product between the number of species S (also called diversity) and the connectance (C) – i.e. the ratio between actual and potential interactions in the ecological community. There are several definitions of stability (Ives and Carpenter 2007). Afterwards we will refer to community stability as the ability of the system to return to its rest state if a small perturbation drives the community away from its equilibrium state (McCann 2000). Assuming that the population dynamics for the species i is described by a non-linear differential equations $\dot{n}_i = f_i(\vec{n})$ – where f_i is a given non-linear function of \vec{n} – then the community stability is described by the linearized system equations $\delta\vec{n} = \Phi\vec{n}$ (where $\delta\vec{n} = \vec{n} - \vec{n}^*$ and \vec{n}^* is the fixed point of the community dynamics, i.e. $f_i(\vec{n}^*) = 0$).

In particular, the system is stable if all the real parts of the eigenvalues of Φ are negative (Ives and Carpenter 2007). Φ is known as the community matrix, and its elements Φ_{ij} are given by $\Phi_{ij} = (\partial f_i / \partial n_j)|_{\vec{n}}$.

Empirical evidences (Pimm 1984, Ives and Carpenter 2007) suggest a positive diversity – stability relationship, i.e. ecosystems with high biodiversity (e.g. tropical forests) are more stable and thus more resistant to perturbations. On the other hand, theoretical studies challenge this point of view and under some general assumptions they usually find that stability and diversity are negatively correlated (May 1972, Allesina and Tang 2012). These contrasting results and related discussions are commonly referred to as the diversity–stability debate or complexity–stability paradox (McCann 2000, Ives and Carpenter 2007, Allesina and Tang 2012). The discussion is heated since Robert May published his pioneer work (May 1972), which provided a quantitative relation between the stability of randomly

assembled communities, its number of species (S), – and the species interactions strength, that usually are unknown and therefore are described by random variables. Specifically, for species interactions strengths randomly drawn from a Gaussian distribution of zero mean and standard deviation σ , the ecosystem is stable if

$$\sigma\sqrt{CS} < 1 \quad (1)$$

This result rises the celebrated complexity–stability paradox: the community stability decreases for increasing complexity (i.e. larger $C \times S$) (May 1974). This important result suggests that real networks may have some non-random, stabilizing structures that allow ecosystems to persist despite their complexity (Fox 2006, Bascompte 2010). Indeed, in natural ecological communities species do not interact in a random way, rather emergent characteristic architecture structures in the species interaction networks can be detected (Pascual and Dunne 2006, Bascompte 2009, Suweis et al. 2013). For instance mutualistic ecosystems (e.g. pollinators and plants) seem to display a nested architecture (Bascompte and Jordano 2007): species interacting with specialist species (that have only few interacting partners) are also interacting with generalist species (that have several connections) (Bascompte et al. 2003). However, structure cannot be the solution: it has been shown that realistic architectures (e.g. nested structure) are less stable than random ones (Allesina and Tang 2012, Suweis et al. 2013).

Recent studies have also highlighted that the variety of interactions types (e.g. mutualistic, antagonistic, etc.) have indeed a remarkable impact on the stability profiles of ecosystem community dynamics (Bascompte and Jordano 2007, Allesina and Pascual 2008, Melian et al. 2009, Allesina and Tang 2012). In particular, it has been found that antagonistic systems are more stable with respect to random assembled community (Allesina and Tang 2012, Stouffer and Bascompte 2011), while mutualistic communities are not (Staniczenko et al. 2013, Suweis et al. 2013). However still for structured ecological communities stability decreases for increasing C and/or S (and fixed interaction strength).

A possible solution to the paradox has been recently proposed by Mougi and Kondoh (Mougi and Kondoh 2012, Boyd 2012). They conclude that ecological communities with multiple – both mutualistic and antagonist – interaction types (also called hybrid interactions) are more stable with respect to the less realistic case of ecosystem with interactions of a single type. Moreover it was found that in these systems with different types of interactions, complexity increases stability, in contrast with May’s result (May 1974) (Eq. 1). Here we question the core conclusions of their work by showing that the main findings presented by Mougi and Kondoh (2012) arise as an artifact of some specific hypothesis that are implicitly assumed in their equations. In particular we will present a theoretical framework to disentangle the effects of multiple interaction types and of the constant interaction effort hypothesis (for which generalist species interact more weakly than specialist species) on community stability.

The paper is organized as follows. We first show – using a mathematical approach based on random matrices (Allesina and Tang 2012) – that a mixture of interaction types does not have a stabilizing effect on community dynamics; rather stability decreases as the fraction of mutualistic links increase. We then demonstrate that the results obtained by Mougi and Kondoh do not hold if the hypothesis of constant interaction effort allocation occurs irrespective of interaction types. Finally we show that a positive complexity–stability effect for ecological communities is achieved if the hypothesis of constant interaction effort allocation is imposed in the interaction matrix driving the community dynamics. In fact this mechanism, which is unrelated to the mixing of interaction types, leads to an implicit rescaling of the interaction strengths causing a positive relationship between ecosystem complexity and stability.

Material and methods

Random matrices approach

We first analyze the effects of mixing mutualistic and predator–prey interactions on the ecosystem stability by extending to hybrid communities the analysis recently proposed by Allesina and Tang (Allesina and Tang 2012). This approach based, on random matrices, allows us to go beyond a specific model dynamics and illustrate some general results.

Consider the $S \times S$ community matrix Φ for the given community dynamics $\dot{n}_i = f_i(\bar{n})$ with $i = 1, \dots, S$. The matrix Φ for hybrid predator–prey and mutualistic interactions networks can be built in the following way (Allesina and Tang 2012). We first pick at random a pair $i-j$ of species. With probability C , these two species interact, otherwise they do not interact ($\Phi_{ij} = \Phi_{ji} = 0$). If $i-j$ are interacting species, then with probability $1-p_M$ species i preys species j , otherwise they are mutualistic partners. In the former case we set $\Phi_{ij} \sim |N(0, \sigma^2)|$ and $\Phi_{ji} \sim -|N(0, \sigma^2)|$, otherwise $\Phi_{ij} \sim |N(0, \sigma^2)|$ and $\Phi_{ji} \sim |N(0, \sigma^2)|$. is the normal distribution with mean μ and variance σ^2 , and determines the intensity of the interactions among species (with the notation $|N(0, \sigma^2)|$ we mean that a random number is taken from $N(0, \sigma^2)$ and its modulus is taken). Following this simple algorithm one can build community matrices with predator–prey (+–) interactions and with a desired fraction p_M of mutualistic (++) interactions. Fixing $p_M = 0$ we obtain ecological interaction matrices with pure antagonistic interactions, while if we set $p_M = 1$ we build ecological communities with pure mutualistic interactions.

Moreover it is easy to extend the above algorithm in order to superimpose a given structure to the interactions matrix (Allesina and Tang 2012). For instance in a predator–prey interaction matrix, we may impose a cascade structure (Cohen and Newman 1985), where species are ordered to form a hierarchy: from the species representing the top predator – that has negative column and positive row – to the species in the lowest trophic level (producer), which has positive column and negative row. For mutualistic ecosystems we build bipartite interaction matrices,

where plants species interact only with pollinator species, and vice versa (intra-species competition is turned off) (Allesina and Tang 2012).

To study the stability of the matrix Φ corresponding to a community with multiple interactions types, we analyze the corresponding eigenvalues: if the maximum real part of the eigenvalue is negative, then the system is stable. We can study the stability for several levels of complexity (C and S) and mixing of interaction types (p_M). This is the most general way to study the stability of ecosystem with hybrid interaction types, without considering specific ecological dynamics or hypothesis (e.g. constant interaction effort allocation).

Approach based on community dynamics models

Following Mougi and Kondoh (2012) we now present a different but complementary approach to study the stability of ecological networks as a function of their complexity and of p_M (that measures the ratio between mutualistic and antagonistic interaction types in the community). It consists in defining a particular function f that drives the community dynamics and in studying the stability of the corresponding community matrix Φ . For simplicity, we model the community dynamics through the classical Lotka–Volterra differential equations:

$$\dot{n}_i = f_i(\bar{n}) = n_i \left(r_i + \sum a_{ij} n_j \right) \quad (2)$$

where n_i is the abundance of species i , S is the number of species, r_i is the intrinsic rate of growth and a_{ij} describes the interaction between species i and species j while $a_{ii} = z_i$ represents the interaction among individuals of the same species (density dependent regulation) and it is uniformly distributed between 0 and 1 ($z_i \sim U_{[0,1]}$). The matrix a_{ij} contains all the information about the interactions between species. Therefore different ecological cases can be analyzed depending on the way a_{ij} is chosen. As before, we can impose a characteristic architecture on a . Additional ecological hypothesis can be considered as appropriate constraints to a .

Constant interacting effort hypothesis

The constant effort hypothesis in species interactions assumes that interaction strengths decrease with increasing resource species. In other words, it assumes that if a species is generalist and thus can positively interact with several different species, then the average interaction strength must be smaller than the one of specialist species that has only few resources. Even though, to our knowledge, there is no empirical study contradicting this relation, the hypothesis is biologically sound. Indeed this is clear if we consider that the interaction strength is proportional to the duration of the interaction between two species, i.e. there is a tradeoff between the number of interactions/contacts and the time spent in each one that a species may have.

The constraint of constant interaction effort can be incorporated in the modeling framework by imposing that species interaction a_{ij} is inversely proportional to the number of resources the species i has. To do that, we define the interaction matrix element a_{ij} as

$$a_{ij} = f_M e_{ij} \frac{A_{ij}}{\sum_{k \in m(i) \cup p(i)} A_{ik}} \quad (3)$$

$$a_{ji} = f_M e_{ji} \frac{A_{ji}}{\sum_{k \in m(j) \cup p(j)} A_{jk}}$$

while if species i has an antagonistic interaction with j (consider for instance i predator and j prey)

$$a_{ij} = f_A g_{ij} \frac{A_{ij}}{\sum_{k \in m(i) \cup p(i)} A_{ik}} \quad (4)$$

$$a_{ji} = -f_A \frac{A_{ji}}{\sum_{k \in m(i) \cup p(i)} A_{ik}} = -\frac{a_{ij}}{g_{ij}}$$

$m(i) \cup p(i)$ is the set of the resource species of the species i , i.e. both the mutualistic partners and preys of i . The matrix A describes the potential preference of a species in choosing its partner, f_A and f_M are, respectively, the relative strengths of the antagonistic and mutualistic interactions, while e_{ij} and g_{ij} quantifies the asymmetry of the interactions. Not all the species interact: only a fraction C of matrix elements A_{ij} is different from zero, of which a fraction p_M is mutualistic, while a fraction $1 - p_M$ is antagonistic.

Therefore in general we obtain that the assumption of constant interacting effort allocation is translated mathematically by rescaling the interactions as

$$a_{ij} \sim \frac{A_{ij}}{\sum_{k \in m(i) \cup p(i)} A_{ik}} \approx \frac{A_{ij}}{SC \left(p_M + \frac{1-p_M}{2} \right) E(A)} \quad (5)$$

where $E(\cdot)$ represents the expectation value, \approx denotes the approximation, that is valid when the product SC is large, and $m(i) \cup p(i)$ is the set of the resources species of the species i , i.e. both the mutualistic partners or preys of i .

For a given choice of: 1) the structure of the matrix A_{ij} (random, cascade or bipartite) (Allesina and Tang 2012); 2) the parameters f_A and f_M (that have not an a priori values range) and 3) randomly drawn values of e_{ij} and g_{ij} (uniformly distributed between 0 and 1), Eq. 3 and 4 lead to the interaction matrix a . By introducing a stationary point $\bar{n}^* = (n_1^*, \dots, n_S^*)$ – whose components are randomly drawn from a uniform distribution between 0 and 1 – and linearizing Eq. 2 around \bar{n}^* , one finally obtains the stability matrix Φ . If all eigenvalues of Φ have negative real parts, the system is stable. Otherwise it is unstable.

Constant interacting effort with an additional constraint

In Mougi and Kondoh (2012), the hypothesis of “constant interacting effort” is imposed with an additional constraint: the interacting effort spent *separately* in mutualistic and in antagonistic interactions are fixed to a constant. Indeed, in order to implement their constant interacting effort hypothesis, Mougi and Kondoh define the interaction matrix element a_{ij} as

$$a_{ij} = f_M e_{ij} \frac{A_{ij}}{\sum_{k \in m(i)} A_{ik}} \quad (6)$$

$$a_{ji} = f_M e_{ji} \frac{A_{ji}}{\sum_{k \in m(j)} A_{jk}}$$

for mutualistic interactions, while if species i has an antagonistic interaction with j (consider for instance i predator and j prey)

$$a_{ij} = f_A g_{ij} \frac{A_{ij}}{\sum_{k \in p(i)} A_{ik}} \quad (7)$$

$$a_{ji} = -f_A \frac{A_{ji}}{\sum_{k \in p(i)} A_{jk}} = -\frac{a_{ij}}{g_{ij}}$$

Equation 6–7 are different from Eq. 3–4. Indeed in Mougi and Kondoh (2012) it was also assumed that the average effort spent by a species in mutualistic or antagonistic interactions does not depend on p_M . In fact, in this case the total effort spent by species i to interact with its mutualistic partners is indeed

$$\sum_{j \in m(i)} a_{ij} \sim f_M \frac{E(e_{ij} A_{ij})}{E(A_{ij})} = f_M / 2 \quad (8)$$

and in the same way the effort spent by the species i as a predator is on average equal to $f_A/2$. We note that Eq. 8, contrarily to Eq. 5, does not depend on p_M . In other words, Mougi and Kondoh (2012) assume independently of the species composition in the community, that the time spent by a species in *mutualistic* interactions is fixed. Therefore Mougi and Kondoh (2012) do not only assumes that, 1) “interaction strengths decrease with increasing resource species, due to an allocation of interacting effort”, but also that, 2) the total interaction strengths spent in mutualistic (antagonistic) interactions does not depend on the number of mutualistic (antagonistic) interactions. 1) and 2) are described by Eq. 5 and 8, respectively.

This seemingly small additional constraint – that is biologically questionable and unrelated to the definition of hybrid community – has a dramatic impact on community stability. In fact, as we will see, the intriguing and non linear dependence on p_M of the observed increased stability in Mougi and Kondoh’s work (2012) is just a consequence of this specific additional constraint.

Discussion and results

Stability criteria for hybrid communities

If no constant allocation effort is considered, the random matrices approach shows that the mixing of interaction types have not – per se – a stabilizing effect on the community dynamics. On the contrary, adding mutualistic interactions in the ecological network tends to destabilize the community. Figure 1 shows that also for hybrid community the stability of the linearized dynamics described by Φ decreases as S and/or C increases, independently of p_M . Adding a

structure in the interaction network (cascade or bipartite) does not change these conclusions (Sommers et al. 1988, Allesina and Tang 2012).

Effect of the mixing of interaction types on the community dynamics stability

As we have explained in the Method section, from Eq. 2, 3 and 4 we can study the stability matrix $\Phi_{ij} = -n_i^* a_{ij}$ as a function of S , C and p_M when a constant interacting effort is considered (through Eq. 3 and 4).

Figure 2 shows that also in this case, and contrarily to the conclusions of Mougi and Kondoh (2012), the community stability decreases monotonically for increasing p_M . This result demonstrates that the mixing of interaction type does not stabilize ecological systems and that the stabilizing effect of intermediate values of p_M observed in Mougi and Kondoh (Fig. 1 in Mougi and Kondoh 2012) is solely due to the additional peculiar constraint discussed above.

Although the mixing of interaction types does not stabilize the system, there are two surprising facts that emerge from Fig. 2. In fact, from Fig. 2A we can see that the community stability increases for increasing connectance C , while from Fig. 2B a positive complexity–stability relationship for intermediate mixing level is observed. Do these results suggest that the mixing of interaction types promote a complexity–stability relationship? In the next section we will demonstrate that this is not the case.

Effect of the constant effort hypothesis: scaling of the interaction strengths

The apparent positive correlation between stability and complexity observed in Fig. 2 is due to the particular re-scaling of the interactions that is imposed so to accomplish the constant interacting effort allocation hypothesis (with or without additional constraint).

The general equation describing the maximum real part among the eigenvalues of a random matrix M is (Sommers et al. 1988, Allesina and Tang 2012).

$$-d + \max \left\{ E_1 S, -E_1 + \sqrt{S E_2 (1 + E_c)} \right\} \quad (9)$$

If this quantity is negative the system is stable, otherwise it is unstable. In this equation

- S is the number of species (i.e. the dimension of the matrix)
- d is the average of the diagonal elements,

$$E(M_{ij}) := \sum_{i=1}^S \frac{M_{ii}}{S}$$

- E_1 is the average of matrix elements,

$$E_1 := E(M_{ij}) := \sum_{i=1}^S \sum_{j=1}^S \frac{M_{ij}}{S(S-1)}$$

- E_2 is the variance of matrix elements, $E_2 := E(M_{ij}^2) - E_1^2$.
- E_c is the normalized correlation of opposed to diagonal matrix elements, i.e. $E_c := \frac{E(M_{ij} M_{ji}) - E_2^2}{E_2}$.

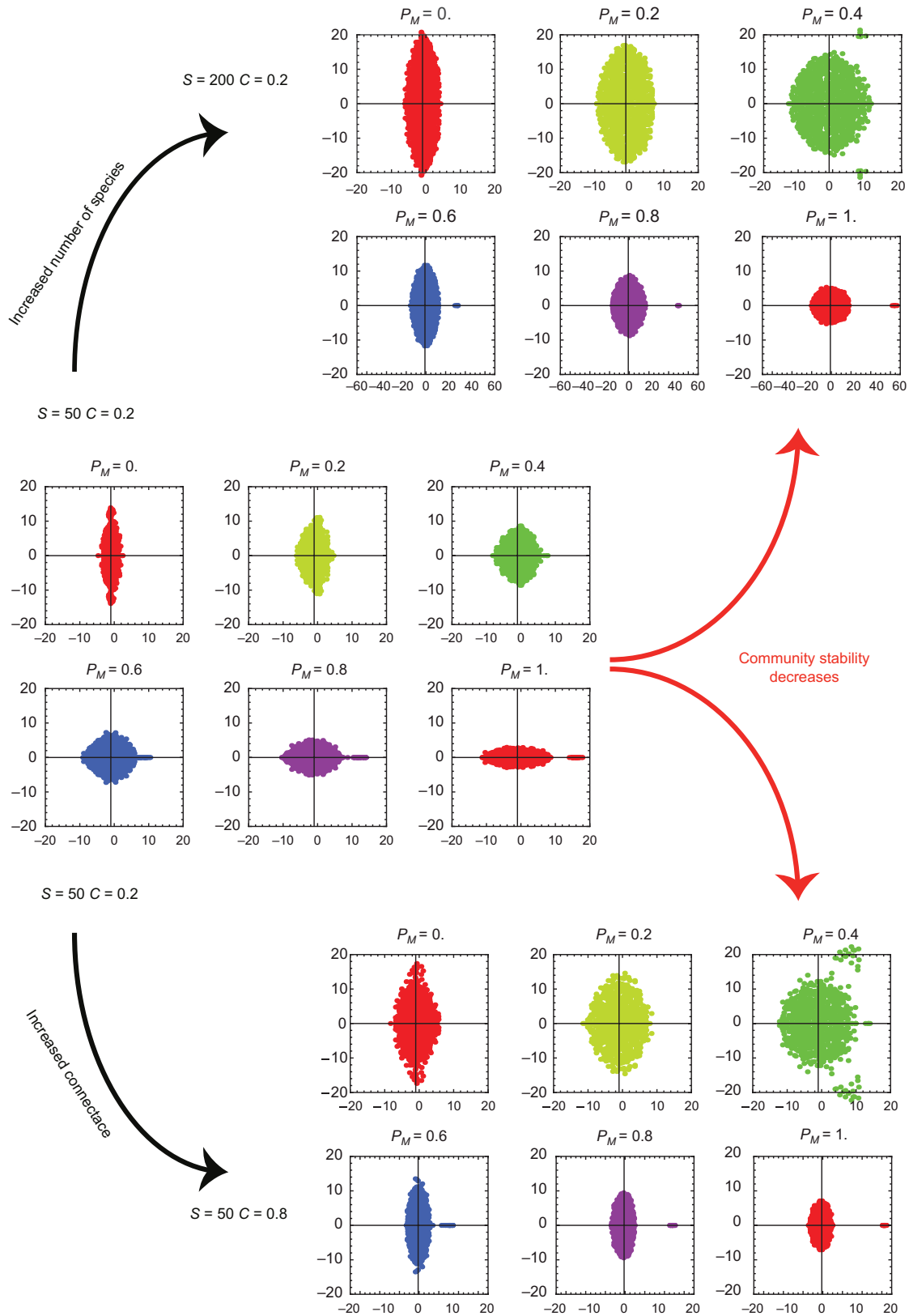


Figure 1. Stability profile of the stability matrix Φ in the model independent framework based on random matrices. In each plot, real and imaginary parts of the stability matrix eigenvalues are represented in the x-and y-axis, respectively. The profile of eigenvalues distribution in the complex plane, shows that increasing complexity decreases stability, i.e. the maximum real part of the eigenvalues of Φ increases for increasing S and/or C . Moreover the stability is not increased by the mixing of interaction types, but as expected (Allesina and Tang 2012) adding mutualistic links decreases stability. Interaction strengths have been drawn from the normal distribution with parameters $\mu = 0$ and $\sigma^2 = 1$ as described in the Methods section.

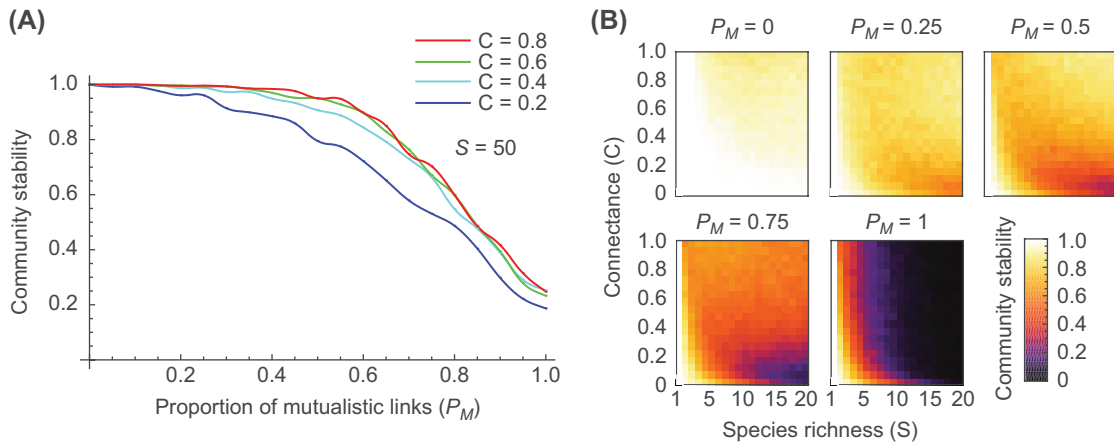


Figure 2. Relationship between complexity, stability and fraction of mutualistic links (p_M) for cascade networks with Holling type I linear response. The interaction strengths are rescaled by summing over both mutualistic partners and preys (Eq. 5). Panel (A) shows the community stability (measured as the probability that the linearized matrix is stable) versus the fraction of mutualistic links p_M . Colors indicate different values of connectance. S is fixed to 50, while $f_A = f_M = 0.5$. Panel (B) shows the complexity–stability relationship with varying p_M . Both the panels shows that, differently from what is claimed in previous works, (Boyd 2012, Mougi and Kondoh 2012), mixing of interaction type in the community dynamics model given by Eq. 5 does not increase stability. The parameters z_i , n_i^* , A_{ij} , g_{ij} and e_{ij} are drawn from a uniform distribution between 0 and 1, while $f_M = f_A = 1$.

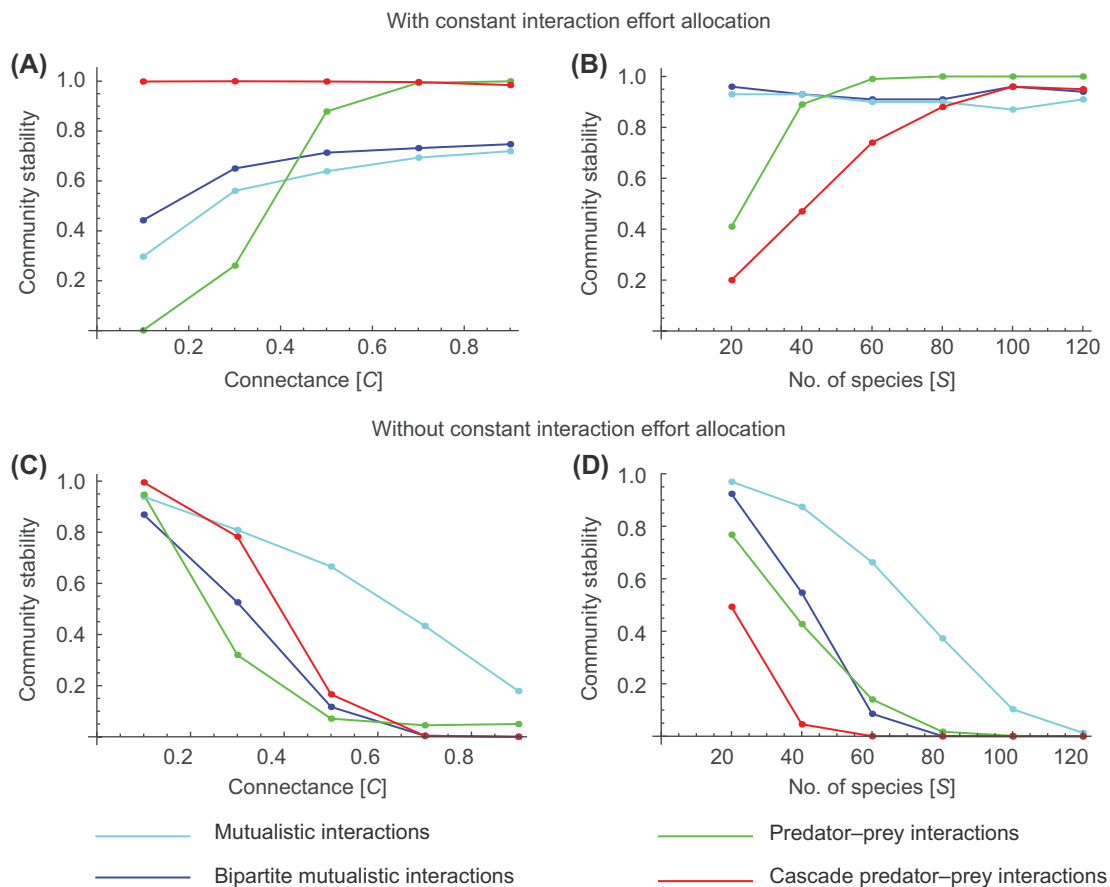


Figure 3. Panel (A) and (B) show the dependence of the stability on the connectance C and the number of species S , for ecological networks with a single interaction type and where constant interaction effort allocation is imposed (Eq. 3 and 4). Panel (C) and (D) give the community stability for the same single type interaction ecological networks, but any constant interaction effort is considered in the dynamics given by Eq. 2. The stability is measured as the probability to have a positive eigenvalues over 1000 realizations. Parameters used for the simulations are in (A) $S = 100$, $f_M = 0.25$, $f_A = 6$ ($f_A = 30$ in the cascade case); in (B) $C = 1$, $f_M = 0.15$, $f_A = 6$ ($f_A = 30$ in the cascade case); in (C) $S = 100$, $f_M = 0.02$, $f_A = 0.8$; in (D) $C = 1$, $f_M = 0.02$, $f_A = 1$.

We can rewrite the previous equation in terms of the connectance and of the moments of the distribution on non zero elements

$$-d + \max \left\{ \mu CS, -\mu C + \sqrt{SC} \frac{\sigma^2(1+\tau)+2\mu^2(1-C)}{\sqrt{\sigma^2+\mu^2(1-C)}} \right\} \quad (10)$$

where

- C is the connectance (i.e. the fraction of non-zero elements of the matrix).
- μ is the average of non-zero off-diagonal elements, i.e. $E_1 = C\mu$.
- σ is the variance of non-zero off-diagonal elements, i.e. $E_2 = C(\sigma^2 + (1-C)\mu^2)$.
- τ , is the normalized correlation of non zero elements, i.e. $E(M_{ij}M_{ji}) - E_1^2 = C(\sigma^2\tau + (1-C)\mu^2)$.

If we do not impose the constant interaction allocation hypothesis, then μ , σ and τ does not depend C and S , and Eq. 10 defines the relation between stability and complexity. As expected, in this case, if we increase S and C , then the stability of both mutualistic, antagonistic and hybrid communities decrease. In fact, in the large SC limit, the stability condition becomes,

$$\mu CS < d \text{ if } \mu > 0 \quad (11)$$

while

$$\sqrt{SC} \frac{\sigma^2(1+\tau)+2\mu^2(1-C)}{\sqrt{\sigma^2+\mu^2(1-C)}} < d \text{ if } \mu \leq 0 \quad (12)$$

In both cases, larger is SC less stable the is system. In the second case the direct dependence on connectance is less trivial and depends on the choice of μ , σ and τ .

If instead, we assume any constant effort allocation hypothesis on the interactions, then we are implicitly imposing also a dependence of the elements of the interaction matrix on S and C , as shown in Eq. 5. Specifically, in the large SC limit, the off-diagonal elements M_{ij} are proportional to $1/(SC)$. Therefore μ , σ and θ are no more independent of S and C . One can verify that in this case

$$\begin{aligned} \mu &= \frac{h_1}{CS} \\ \sigma &= \frac{h_2}{CS} \\ \tau &= h_3 \end{aligned} \quad (13)$$

where h_1 , h_2 and h_3 are independent of S and C . In the case of an hybrid community (Mougi and Kondoh 2012), these quantities will be suitable functions of p_M (and of the others parameters f_M and f_A). By substituting Eq. 13 in Eq. 10, one obtains the following stability condition

$$\max \left\{ h_1, -\frac{h_1}{S} + \frac{1}{\sqrt{SC}} \frac{h_2^2(1+h_3)+2h_1^2(1-C)}{\sqrt{h_2^2+h_1^2(1-C)}} \right\} < d \quad (14)$$

This equation implicitly incorporates a positive stability-complexity relationship. In fact, in the case of a positive average interaction ($\mu > 0$), then $h_1 > 0$ and therefore the stability condition simply becomes $h_1 < d$. While, in the case

of a negative or zero mean of interaction matrix ($\mu \leq 0$), then $h_1 < 0$, the second term in Eq. 11 dominates and the stability condition becomes

$$\frac{1}{\sqrt{SC}} \frac{h_2^2(1+h_3)+2h_1^2(1-C)}{\sqrt{h_2^2+h_1^2(1-C)}} < d \quad (15)$$

This condition has an inverse functional dependence on SC with respect to the well known May's criterion for stability (May 1972) given by Eq. 1 and its generalization of Eq. 12. This inverse relation is not a consequence of the mixing of interaction types, because it holds also for pure antagonistic communities ($p_M = 0$ and $\mu \leq 0$). It is important to note that the presented approach is valid in the limit of large SC . For intermediate values of S also others effects, which depends on the finite dimension of the matrix, may play an important role.

Therefore the key responsible of the observed positive complexity-stability relationship is the rescaling of the interaction strengths given by Eq. 5, rather than the mixing of interaction types. In other words, if constant effort is imposed, then a rescaling of the interaction strengths lead to Eq. 15 and thus introduce a positive correlation between stability and complexity.

To numerically confirm and stress this result, we show that also for non-hybrid ecological networks (with a single interaction type), if we impose the rescaling of interactions in order to accomplish the constant interaction effort allocation hypothesis, we find that the stability of the community matrix increases as complexity increases (Fig. 3). In fact, if we set $p_M = 1$ (i.e. we consider an ecosystem with pure mutualistic interactions), the stability condition in the large S limit becomes $h_1 < d$ (because $h_1(p_M = 1) > 0$). Note that in this case the stability condition is independent of S (Fig. 3A). Similarly, if we consider predator-prey ecological networks, i.e. $p_M = 0$, Eq. 15 reduces to $\frac{h_2^2(1+h_3)+2h_1^2(1-C)}{\sqrt{Ch_2^2+h_1^2C(1-C)}} < d\sqrt{S}$, and we indeed observe a

stabilizing effect for increasing number of species (Fig. 3B). Figure 3 also shows that these results do not change if we superimpose a particular architecture structure of the interaction network (bipartite or cascade).

On the other hand, if the constant interacting effort is not implemented in the modeling dynamics, then ecosystem stability is a decreasing function of the number of species S and connectance C , as expected in classical theoretical ecology (May 1972) (Fig. 3C–D). It is indeed the rescaling the interaction strengths – not the mixing of interaction types – that causes the apparent positive complexity stability relation observed in Fig. 2.

Conclusions

In this work we have shown that the mixing of mutualistic and predator-prey interaction types in ecological community does not per se stabilize the community dynamics. In particular, using a general approach based on random matrices (Allesina and Tang 2012) we find that community matrix stability decreases as the fraction p_M of mutualistic links increases. Furthermore these results do not change if the

assumption of constant interaction effort is incorporated in the model. Indeed, we have shown that also in this case the community stability decreases monotonically for increasing p_M . The stabilizing effect for intermediate p_M observed in Mougi and Kondoh (2012) is instead due to the additional constraint that the total effort spent by species in mutualistic and antagonistic interaction is independent of p_M . Finally, we have highlighted the importance to disentangle the effects of multiple interaction types and of the constant interaction effort hypothesis on community stability. In fact, we have demonstrated that the emergent positive relation between stability and complexity in this model is not due to the mixing of interaction types, rather it is a consequence of the hypothesis of constant interaction effort allocation: this condition is accomplished by rescaling the interactions strengths in a way that tacitly introduce a positive correlation between community matrix stability and SC . These results call for different principles beyond network structures and mixing of interaction types in order to understand the complexity and stability relationship in real ecological systems.

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