

# Avoiding artifacts when varying the number of species in ecological network models

Pablo Moisset de Espanés<sup>1</sup>, Rodrigo Ramos-Jiliberto <sup>2\*</sup>, and José A. Soto<sup>3,4</sup>

<sup>1</sup>Centro de Biotecnología y Bioingeniería, Universidad de Chile, Chile. E-mail: pmoisset@ing.uchile.cl

<sup>2</sup>GEMA Center for Genomics, Ecology & Environment, Faculty of Interdisciplinary Studies, Universidad Mayor, Chile. \*E-mail: rodrigo.ramos@umayor.cl

<sup>3</sup>Centro de Modelamiento Matemático, FCFM, Universidad de Chile, Chile

<sup>4</sup>Departamento de Ingeniería Matemática, FCFM, Universidad de Chile, Chile. E-mail: jsoto@dim.uchile.cl

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**Corresponding author:** Rodrigo Ramos-Jiliberto. Camino La Pirámide 5750 Huechuraba, Santiago, Chile. Tel: +56 2 2518 9262, E-mail: rodrigo.ramos@umayor.cl

## **Abstract**

Ecological theory recognizes the importance of the variety of species for maintaining the functioning of ecosystems and their derived services. We assert that when studying the effects of shifts in biodiversity levels using mathematical models, their dynamics must be sensitive to the variety of species traits but not to raw species numbers, a property that we call scale-invariance. We present a testing procedure for verifying scale-invariance of ecological network models —with or without trait adaptation— expressed as ODEs. Furthermore, we applied our test to several influential models used for evaluating biodiversity effects on ecosystem functioning. In most of the surveyed studies the equations failed our test. This raises doubts about the validity of previous results and calls for revisiting the theory derived from these studies. Our results foster the creation of artifact-free models, a necessary step towards building a more robust theory of biodiversity-driven ecosystem functioning.

## INTRODUCTION

Few questions in ecology have received such a great attention over decades and have been so fertile in promoting research, like the one about the relation between species diversity and ecosystem stability (McCann, 2000). This is of particular concern in the context of current biodiversity loss. The importance of this matter encompasses both the theoretical understanding of ecosystems and the more pragmatic issue of conservation of ecosystem services, which are vital for human well-being. In the early '90s, the more general biodiversity–ecosystem functioning (BEF) paradigm emerged. It extended the concept of stability beyond that of species populations, towards aggregated ecosystem properties. Due to the inherent complexity of ecological systems, much of this research relies on the use of mathematical models.

Concerning biodiversity, BEF relations are driven by more than the raw number of species (i.e. the quantity of species, irrespective of their variety). For example, at a fixed species richness, different community composition of key functional traits governs resource exploitation, and species interactions (Gagic *et al.*, 2015; Aubree *et al.*, 2020). Therefore, we expect that increasing species richness without modifying *functional diversity*, expressed as variety of functional traits and responses to environmental changes, should not drive changes in ecosystem functioning (Yachi & Loreau, 1999; Naeem & Wright, 2003; Loreau & De Mazancourt, 2013). Moreover, functional trait composition within the community is subject to temporal changes due to ecological and adaptive dynamics. These changes are known to have a strong influence on ecosystem productivity (Cadotte & Tucker, 2017), stability (Loreau & De Mazancourt, 2013), and resistance and tolerance to invasions (Hector *et al.*, 2001). Ecosystems are currently facing environmental perturbations, and their communities are constantly experiencing adaptation due to phenotypic/behavioral plasticity and genetic evolution. However, we have a poor

understanding of the role of adaptation in BEF. This turns the process of creating models for eco–evolutionary systems into a challenging endeavor.

Besides capturing key biological features, it has been noted that ecosystem models should exhibit some fundamental forms of logical consistency (Arditi & Michalski, 1996; Kuang, 2002). As argued below, proper models for studying BEF should show different dynamics in response to changes in functional diversity but not to changes in the raw number of species. In this article, we will say a model is *scale-sensitive* (as opposed to *scale-invariant*) if its dynamics are modified by changes in the raw number of species. We will formalize these concepts later. A scale-sensitive model would impede identifying the effect of incorporating new species with their own biological features to an ecosystem, due to the confounding effect of scale-sensitivity. This point, which is crucial for the BEF study, has scarcely been considered. Our literature survey, included in this paper, lists a number of influential published models of ecological networks that exhibit scale-sensitivity, as well as a few that do not. The fact that such high visibility research is liable to produce misleading results as a consequence of the mentioned artifacts highlights the need for a model design procedure that avoids scale-sensitivity pitfalls.

In this article, after presenting the problem of scale-sensitivity, we will state formal criteria to detect it in ecological network models. Following canonical definitions (e.g. Newman (2018)) ecological networks are a collection of —one or more— species populations linked in pairs by ecological interactions. In ecological network models, species abundances, trait values, interaction intensities and the network topology could vary with time. If a model is being used for studying BEF relations, especially if it includes adaptive trait dynamics, it should probably be discarded if it fails our scale-invariance criteria. We also suggest ways to fix the equations to obtain and use ecological network models that exhibit scale-invariance. We achieve this by identifying model features that introduce the scale-sensitivity and are frequently found in the ecological literature.

# THE PROBLEM OF SCALE-SENSITIVITY IN ECOLOGICAL NETWORK MODELS

The usual theoretical procedure to study the BEF relation in ecological networks is to conduct an *in silico* controlled experiment. First, ecological networks with different diversity levels are obtained, usually by means of an algorithm generating quasi-empirical webs such as the cascade (Cohen *et al.*, 2012) or the niche model (Williams & Martinez, 2000). Different diversity levels are most commonly obtained through varying species richness in the network. Second, a dynamic population model is added to each of the interacting species, typically by using ordinary differential equations (ODEs). Third, the model community is run for a given time lapse, after which system functioning is assessed through appropriate measures, such as stability metrics (Pascual & Dunne, 2006), biomass or productivity. Finally, the association between species richness and system functioning is evaluated by using visualization or statistical tools.

Ecological network models used to evaluate the BEF relation must be able to capture system responses to biodiversity changes. However, they must be insensitive to changes in raw number of species that preserve functional diversity. For example, consider an initial population of  $x(0)$  individuals belonging to species  $X$ . Then, suppose we arbitrarily *count* a fraction  $p$  of  $x(0)$  (with  $x_1(0) = px(0)$ , see Fig. 1) as if it belonged to a species  $Q$ . The remaining fraction  $1 - p$  of  $x(0)$  (with  $x_2(0) = (1 - p)x(0)$ ) is counted as if it belonged to another species  $R$ . Then, the sum of individuals belonging to pseudo-species  $Q$  and  $R$  should behave exactly the same as the population  $X$ . In other words, artificially splitting species  $X$  into pseudo-species  $Q$  and  $R$  should not bring any consequence for the dynamics of the community, since the behavior of  $x(t)$  should be recovered exactly by the behavior of  $x_1(t) + x_2(t)$ . Conversely, the existence of a  $t$  at which  $x_1(t) + x_2(t) \neq x(t)$  would imply that a mere nominal split of  $X$  into  $Q$  and  $R$  changed the community dynamics. In this case,

the model outcomes are altered by a spurious increase in the raw number of species, which reveals an experimental artifact in the procedure. This artifact has a crucial importance for understanding the effects of biodiversity changes through modifying the number of functionally different species. Splitting a species is equivalent to adding a new species functionally identical to an existing one. In the context of ODE based studies, two species are considered functionally identical if their equations have the same form, and the values of corresponding equation parameters are the same. Population level model parameters (e.g, handling times, intrinsic growth rates) will be the same if both species exhibit the same values for individual level traits. This hierarchical organization of trait definitions is shared by Violle *et al.* (2007) and Cadotte *et al.* (2011). Theoretical studies, such as Ceulemans *et al.* (2019), have adopted this perspective. Note that under our approach, it is perfectly valid to add functionally distinct species to a model community (e.g. with different values of their competition coefficients) but the model must be invariant in the limiting case of addition of identical species (e.g. when their competition coefficients are set to identical values). This is a necessary condition for any model used for evaluating the consequences of biodiversity shifts.

To explain the concept of scale-invariance we will present examples based on Kondoh (2003). We start from a system composed of a prey species of abundance  $P$  and a predator species of abundance  $A$ .

$$\begin{aligned}\dot{P} &= P \cdot (\rho - \beta P - \varphi \alpha A) \\ \dot{A} &= A \cdot (\sigma - \gamma A + \epsilon \varphi \alpha P)\end{aligned}\tag{1}$$

where we use  $\dot{P}$  as a shorthand for  $dP/dt$  and so forth. The ecological interaction represented in Eq. (1) depicts the killing rate of prey by predators  $\varphi \alpha A P$ , with consumer preference  $\alpha = 1/\#\text{prey species} = 1$ . Parameter  $\varphi$  is the predation rate coefficient,  $\epsilon$  is the conversion efficiency of killed prey into consumer abundance,  $\rho$  and  $\sigma$  are the intrinsic growth rate of preys and predators, respectively. Finally,  $\beta$  and  $\gamma$  are self-interference

terms, due to intraspecific competition. All parameters are positive constants. If we increased the system's species richness by adding, for example, a new prey species *while preserving the form of the model equations in* Kondoh (2003), we would obtain

$$\dot{P}_1 = P_1 \cdot (\rho_1 - \beta_1 P_1 - \varphi_1 \alpha_1 A) \quad (2)$$

$$\dot{P}_2 = P_2 \cdot (\rho_2 - \beta_2 P_2 - \varphi_2 \alpha_2 A) \quad (3)$$

$$\dot{A} = A \cdot (\sigma - \gamma A + \epsilon_1 \varphi_1 \alpha_1 P_1 + \epsilon_2 \varphi_2 \alpha_2 P_2) \quad (4)$$

with predator preferences  $\alpha_1 + \alpha_2 = 1$ . Species  $P_1$  and  $P_2$  are functionally identical if and only if  $\alpha_1 = \alpha_2 = 1/2$ ,  $\rho_1 = \rho_2$ ,  $\beta_1 = \beta_2$ ,  $\varphi_1 = \varphi_2$  and  $\epsilon_1 = \epsilon_2$ . To test whether this system is scale-invariant, let us imagine that the original prey species in Eq. (1) was *artificially* split into two new species (Eqs. (2) and (3)), which are functionally identical. It remains to check whether the dynamics of  $P_1 + P_2$  is identical to the dynamics of  $P$  in Eq. (1). Note that by omitting competition between  $P_1$  and  $P_2$  we reduced the average competition effects in the system. To see the consequences of this, we obtain the dynamics of  $P = P_1 + P_2$  by adding Eq. (2) and (3).

$$\dot{P} = \dot{P}_1 + \dot{P}_2 = P_1 \cdot (\rho_1 - \beta_1 P_1 - \varphi_1 \alpha_1 A) + P_2 \cdot (\rho_2 - \beta_2 P_2 - \varphi_2 \alpha_2 A) \quad (5)$$

In general, we cannot express the right hand side of Eq. (5) and Eq. (4) as functions of  $P$  and  $A$  only. We call this feature lack of “species addability,” which we define precisely in the next section. However, if  $P_1(t) = P_2(t)$  we can combine  $P_1$  and  $P_2$  into a single variable  $P$ . This equality is true for all  $t$  if we choose  $P_1(0) = P_2(0)$  because of the symmetry between  $P_1$  and  $P_2$  in Eqs. (2) though (4). Then we obtain the *reduced* system

$$\begin{aligned} \dot{P} &= P \cdot \left( \rho - \beta \frac{P}{2} - \varphi \frac{A}{2} \right) \\ \dot{A} &= A \cdot \left( \sigma - \gamma A + \epsilon \varphi \frac{P}{2} \right) \end{aligned} \quad (6)$$

where  $\rho = \rho_1 = \rho_2$ ,  $\beta = \beta_1 = \beta_2$ ,  $\varphi = \varphi_1 = \varphi_2$  and  $\epsilon = \epsilon_1 = \epsilon_2$ . Since Eq. (6) is not the same as Eq. (1), we conclude that the dynamics are altered by artificially splitting species and therefore the model is scale-sensitive. Furthermore, it can be shown that Eq. (6) presents equilibrium population densities greater than those obtained from Eq. (1).

### Scale-sensitivity and BEF

Artificially splitting a species into identical copies can affect the dynamics of the system. Now we will show that some important measures of ecosystem functioning can also be affected. Still considering model (1), assume that the predator population is split into  $D$  functionally identical copies with equal abundance. Adding the equations for these copies we obtain the reduced system

$$\begin{aligned}\dot{P} &= P \cdot \left( \rho - \beta \frac{P}{D} - \varphi \frac{A}{D} \right) \\ \dot{A} &= A \cdot \left( \sigma - \gamma A + \epsilon \varphi \frac{P}{D} \right).\end{aligned}\tag{7}$$

Notice that  $D$  appears explicitly in the right-hand side of the equations. This immediately implies that the model is scale-sensitive. Moreover, the following quantitative ecosystem functioning metrics are dependent on  $D$ : population equilibria, total community biomass at equilibrium, ecosystem production, and community resilience. Qualitative metrics, such as feasibility (existence of positive equilibria) and asymptotic stability, are also dependent on  $D$ . We also analyzed a competitive system based on (7) and we obtained similar conclusions. A detailed derivation of these results can be found in Appendix S1.

## SCALE-INVARIANCE CRITERIA FOR NETWORKS

We will present a test to determine if a given ODE based model is scale-invariant. To make the presentation more amenable, in this section we will restrict our analysis to systems



where each population abundance is represented by a single real variable, and the state of the system is defined only by these variables. This precludes the use of systems with stage or spatial structure, or with trait adaptation. In a later section, we will extend our method to include systems with adaptation.

For this study, and given an ecological network characterized by a set of species and parameters that describe the interactions among them, we will make the following two assumptions. The first one is that there is an unambiguous procedure to translate the network into a set of ODEs. The second one is that there is a well defined operation for adding a species to a network  $G$ , yielding a network  $G'$ . We are especially interested in the case where the species being added (call it  $s'$ ) is identical to another species (call it  $s$ ) that is already in  $G$ . This is conceptually equivalent to splitting the original species  $s$  in  $G$  into two identical pseudo-species  $s$  and  $s'$  in  $G'$ . Duplicating a species should not alter the dynamics of the system since the combined population of species  $s$  and  $s'$  in  $G'$  should behave exactly like the population of  $s$  in  $G$ . For all species  $i$  in  $G$ , the ODEs will have the form

$$\dot{x}_i = x_i \cdot f_i(\mathbf{x}) \quad (8)$$

with initial conditions  $x_i(0)$ . For  $G'$ , the equations will have the form

$$\dot{\tilde{x}}_i = \tilde{x}_i \cdot \tilde{f}_i(\tilde{\mathbf{x}}) \quad (9)$$

and initial conditions should fulfill  $\tilde{x}_s(0) + \tilde{x}_{s'}(0) = x_s(0)$ , and  $\tilde{x}_i(0) = x_i(0)$  for all other species. We demand that for all  $t > 0$

$$\begin{aligned} \tilde{x}_s(t) + \tilde{x}_{s'}(t) &= x_s(t) \\ \tilde{x}_i(t) &= x_i(t) \quad \text{for all other species} \end{aligned} \quad (10)$$

The last two equations simply mean that the species abundances through time should behave in exactly the same way in the  $G$  network ( $x_i$  variables) as the  $G'$  network ( $\tilde{x}_i$  variables). For the particular case of species  $s$  in  $G$ , its abundance should be exactly as the summed abundances of species  $s$  and  $s'$  in  $G'$ .

### Defining *species addability*

Consider the model:

$$\dot{\tilde{x}}_i = \tilde{x}_i \cdot \tilde{g}_i(\tilde{x}_0, \tilde{x}_1, \dots, \tilde{x}_n) \quad (11)$$

where the  $\tilde{x}_i$ 's represent the abundances of  $n + 1$  species and, for convenience, they are indexed from zero. We will assume the  $\tilde{g}_i$  functions are “well-behaved.” For example, the  $\tilde{g}_i$ 's being continuously differentiable is enough to guarantee the existence and uniqueness of solutions (at least locally). It is usually the case in population dynamics models that both existence and uniqueness of the solution extend globally to the  $[0, \infty)$  interval. Thus, Eq. (11) is general enough to capture most popular ODE based models in the ecological literature.

Suppose that we identify two variables that seem to represent identical species. Since we can rename variables, without loss of generality we can assume that these two variables are  $\tilde{x}_0$  and  $\tilde{x}_1$ . If they represented identical species, and we fixed the values for  $\tilde{x}_2, \dots, \tilde{x}_n$ , then  $\dot{\tilde{x}}_0 + \dot{\tilde{x}}_1$  would depend only on  $\tilde{x}_0 + \tilde{x}_1$ . Similarly, the values of  $\dot{\tilde{x}}_2, \dots, \dot{\tilde{x}}_n$  would depend exclusively on  $\tilde{x}_0 + \tilde{x}_1$ . Thus, if only the sum  $\tilde{x}_0 + \tilde{x}_1$  matters, it is natural to combine these two variables into a new one by simple addition. More formally, we will say a function  $\tilde{g}_i$  is *sum-dependent* if and only if it satisfies the following condition for all  $\tilde{x}_i \geq 0$  ( $i = 0, 1, \dots, n$ ), and for all  $\lambda \in [0, 1]$ :

$$\tilde{g}_i(\tilde{x}_0, \tilde{x}_1, \dots, \tilde{x}_n) = \tilde{g}_i(\lambda \cdot (\tilde{x}_0 + \tilde{x}_1), (1 - \lambda)(\tilde{x}_0 + \tilde{x}_1), \tilde{x}_2, \tilde{x}_3, \dots, \tilde{x}_n) \quad (12)$$

An equivalent way to state the rule described in Eq. (12) is

$$\tilde{g}_i(\tilde{x}_0, \tilde{x}_1, \dots, \tilde{x}_n) = \tilde{g}_i(\tilde{x}_0 + \beta, \tilde{x}_1 - \beta, \tilde{x}_2, \tilde{x}_3, \dots, \tilde{x}_n) \quad (13)$$

for all  $\tilde{x}_i \geq 0$  ( $i = 0, 1, \dots, n$ ), and for all  $\beta$  such that  $0 \leq \tilde{x}_0 + \beta$  and  $0 \leq \tilde{x}_1 - \beta$ . Intuitively, we should be able to transfer an arbitrary amount of “mass”  $\beta$  from species 1 to species 0 without affecting the values of any per capita effect  $\tilde{g}_i$ .

If per capita growth rates of species 0 and 1 are the same, i.e.

$$\tilde{g}_0(\tilde{x}_0, \tilde{x}_1, \dots, \tilde{x}_n) = \tilde{g}_1(\tilde{x}_0, \tilde{x}_1, \dots, \tilde{x}_n) \quad (14)$$

for all  $\tilde{x}_i \geq 0$  ( $i = 0, 1, \dots, n$ ), and also all  $\tilde{g}_i$ ’s are sum-dependent, we can show that  $\tilde{x}_0$  and  $\tilde{x}_1$  can be combined into a single variable  $x_1 = \tilde{x}_0 + \tilde{x}_1$  (see Appendix S2 for details and for alternative formulations of the test for addability). Therefore, we will say species 0 and 1 are *addable* if and only if either Eq. (12) or (13), and Eq. (14) are satisfied. Concisely, if two species are addable, then we can combine them and write a reduced system. Also note that we can group more than two species by using the same technique repeatedly. Thus it is enough to define addability for two species only. Addability will serve as a building block to define the scale-invariance test.

### The scale-invariance test

Conceptually, the test consists of applying, for all possible networks of interest and species of those networks, a sequence of a few steps we summarize in Fig. 2. The set  $\mathcal{R}$  of networks of interest depends on the particular study being carried out. Typical choices include bipartite, acyclic, and unconstrained networks. Consider an arbitrary  $G \in \mathcal{R}$  and a species  $s$  in  $G$ . Write the differential equations for all species in  $G$ . Then, replace  $s$  by two identical pseudo-species we will call  $s_1$  and  $s_2$ , yielding a new network  $G'$ . Write the

differential equations for  $G'$ . Now test for addability of  $s_1$  and  $s_2$  using any of the formulas given in section *Defining species addability* or in Appendix S2. If they are addable, define  $s = s_1 + s_2$  and reduce the system. Test if all the equations in the reduced system match those written for  $G$ . A model is *scale-invariant* if, for all networks  $G$  and for all species  $s$  in  $G$ , duplicating  $s$  and then reducing the system yields the same equations as those written for  $G$ .

### Example applications of the test

We will show three applications of the scale-invariance test. The first one is on the classic Lotka–Volterra system:

$$\dot{x}_i = x_i \cdot \left( r_i + \sum_{j=1}^n a_{ij} x_j \right) \quad \text{for } i = 1, 2, \dots, n \quad (15)$$

Say we wish to duplicate species with index number 1 into two identical species and, therefore, with identical parameter values. Introducing variables  $\tilde{x}_0$  and  $\tilde{x}_1$  to represent their abundances we obtain

$$\begin{aligned} \dot{\tilde{x}}_0 &= \tilde{x}_0 \cdot \left( r_1 + \sum_{j=2}^n a_{1j} \tilde{x}_j + a_{11} \tilde{x}_0 + a_{11} \tilde{x}_1 \right) \\ \dot{\tilde{x}}_1 &= \tilde{x}_1 \cdot \left( r_1 + \sum_{j=2}^n a_{1j} \tilde{x}_j + a_{11} \tilde{x}_0 + a_{11} \tilde{x}_1 \right) \\ \dot{\tilde{x}}_i &= \tilde{x}_i \cdot \left( r_i + \sum_{j=2}^n a_{ij} \tilde{x}_j + a_{i1} \tilde{x}_0 + a_{i1} \tilde{x}_1 \right) \quad \text{for } i = 2, 3, \dots, n \end{aligned} \quad (16)$$

with  $\tilde{x}_i = x_i$  for  $i = 2, 3, \dots, n$ , and assuming we preserve the values of all the  $a_{ij}$  and  $r_i$  coefficients. This ends the splitting part. We can see that Eq. (12) and Eq. (14) are satisfied by Eq. (16); therefore, species 0 and 1 are addable. Then, by creating a new variable with value  $\tilde{x}_0 + \tilde{x}_1$  and reducing the system, we obtain equations identical to

Eq. (15). Since this holds for all species, we conclude that Eq. (15) is *scale-invariant*.

The second application, to show a negative example, is on Eq. (1). Copying the only plant species gives

$$\dot{\tilde{P}}_1 = \tilde{P}_1 \cdot (\rho - \beta \tilde{P}_1 - \varphi \alpha \tilde{A}) \quad (17)$$

$$\dot{\tilde{P}}_2 = \tilde{P}_2 \cdot (\rho - \beta \tilde{P}_2 - \varphi \alpha \tilde{A}) \quad (18)$$

It is immediate that the equations fulfill neither Eq. (12) because the per capita growth rates are non sum-dependent, nor Eq. (14) because the per capita growth rates are different. Therefore this model fails our test for scale-invariance, which was expected after our analysis of Eq. (6).

Finally, we will apply our test to a more complex example. Thébault & Fontaine (2010) proposed the food web model

$$\begin{aligned} \dot{P}_i &= P_i \cdot \left( r_i - I_i P_i - \sum_{j=1}^m \frac{c_{ij} A_j \beta_{ij}}{1 + \beta_{ij} \sum_{k, \beta_{kj} > 0} P_k} \right) & \text{for } i = 1, 2, \dots, n \\ \dot{A}_j &= A_j \cdot \left( -q_j - E_j A_j + \sum_{i=1}^n \frac{c_{ij} P_i \beta_{ij}}{1 + \beta_{ij} \sum_{k, \beta_{kj} > 0} P_k} \right) & \text{for } j = 1, 2, \dots, m \end{aligned} \quad (19)$$

To test for scale-invariance, we apply our procedure, replicating species 1.

$$\begin{aligned} \dot{\tilde{P}}_0 &= \tilde{P}_0 \cdot \left( r_0 - I_0 \tilde{P}_0 - \sum_{j=1}^m \frac{c_{0j} \tilde{A}_j \beta_{0j}}{1 + \beta_{0j} \sum_{k, \beta_{kj} > 0} \tilde{P}_k} \right) \\ \dot{\tilde{P}}_1 &= \tilde{P}_1 \cdot \left( r_1 - I_1 \tilde{P}_1 - \sum_{j=1}^m \frac{c_{1j} \tilde{A}_j \beta_{1j}}{1 + \beta_{1j} \sum_{k, \beta_{kj} > 0} \tilde{P}_k} \right) \\ \dot{\tilde{P}}_i &= \tilde{P}_i \cdot \left( r_i - I_i \tilde{P}_i - \sum_{j=1}^m \frac{c_{ij} \tilde{A}_j \beta_{ij}}{1 + \beta_{ij} \sum_{k, \beta_{kj} > 0} \tilde{P}_k} \right) & \text{for } i = 2, 3, \dots, n \\ \dot{\tilde{A}}_j &= \tilde{A}_j \cdot \left( -q_j - E_j \tilde{A}_j + \sum_{i=1}^n \frac{c_{ij} \tilde{P}_i \beta_{ij}}{1 + \beta_{ij} \sum_{k, \beta_{kj} > 0} \tilde{P}_k} \right) & \text{for } j = 1, 2, \dots, m \end{aligned} \quad (20)$$

No matter what positive values we assign to  $I_0$  and  $I_1$ , the per-capita growth rates of  $\tilde{P}_0$  and  $\tilde{P}_1$  are not sum-dependent (Eq. (12)). This is apparent in the limiting case  $A_j = 0$  for all  $j$ . Therefore, the model (19) is scale-sensitive.

It is possible to add direct interspecific competition terms to model (19) and make it scale-invariant. To show the consequences of this model feature that affects scale-sensitivity, we ran some numerical experiments using the original model in Thébault & Fontaine (2010) and using the scale-invariant version of it. We summarize the results for both treatments in the BEF relations shown in Fig. 3. We observe qualitative differences, i.e. different shapes of BEF curves, in herbivore biomass, plant biomass, herbivore persistence and quantitative differences in plant persistence. Note that Eq. (19) allows indirect interspecies competition via shared resources, but this is not enough to prevent scale-sensitivity. For details and additional experiments see Appendix S3. For an extension of the test to discrete time systems see Appendix S4.

### Scale-invariance in models with trait adaptation

Equation (11) is not general enough to capture ecological models with evolutionary or behavioral adaptation. Typically, trait adaptation is represented by adding extra variables. A real variable  $\alpha_{ij}$  may represent the preference of individuals of predator species  $i$  for prey species  $j$ . It could be a probability of attack or a fraction of time devoted to hunting that particular prey. Commonly, the values of  $\alpha$ 's are constrained. This will be important when specifying the test for species addability. If  $\alpha_{ij}$  represents the fraction of time individuals of species  $i$  spends foraging on a resource  $j$  or a fraction of available energy allocated to a task, then we must have that  $\sum_j \alpha_{ij} = 1$ . This constraint must be preserved by the differential equations for all time. In this case, we say the system is *normalized*. A well known normalized model is the *replicator equation*. A *non-normalized* system is the classic *optimal diet model* (Stephens & Krebs, 1986). Here, it is only re-

quired that  $0 \leq \alpha_{ij} \leq 1$ , as the  $\alpha$ 's are probabilities. In this paper, we will handle both scenarios.

To represent this adaptation process, in addition to the  $x_i$  variables that model species abundances, we introduce new variables  $\alpha_{ij}$ , whose time evolution will be described by new equations. To simplify the notation, we will express the state variables in vector form. Let  $\mathbf{x} = [x_1, x_2, \dots, x_n]^T$ , where  $n$  is the number of species in the network. Similarly, let  $\mathcal{A} = [\alpha_{ij}]$  be an  $n \times n$  matrix. Consider:

$$\begin{aligned}\dot{x}_i &= x_i \cdot g_i(\mathbf{x}, \mathcal{A}) \\ \dot{\alpha}_{ij} &= f_{ij}(\mathbf{x}, \mathcal{A})\end{aligned}\tag{21}$$

To generalize the scale-invariance test for Eq. (21), we just have to extend the conditions for species addability. We will split our analysis into the non-normalized and normalized cases.

### Addability in non-normalized systems

In this case we do not impose any constraints on the values for the  $\alpha$ 's. After splitting species 1 into species 0 and 1 we obtain equations of the form

$$\begin{aligned}\dot{\tilde{x}}_i &= \tilde{x}_i \cdot \tilde{g}_i(\tilde{\mathbf{x}}, \tilde{\mathcal{A}}) \\ \dot{\tilde{\alpha}}_{ij} &= \tilde{f}_{ij}(\tilde{\mathbf{x}}, \tilde{\mathcal{A}})\end{aligned}\tag{22}$$

Note that  $\tilde{\mathbf{x}}$  has  $n + 1$  elements, while  $\tilde{\mathcal{A}}$  is an  $(n + 1) \times (n + 1)$  matrix. Also note that elements in  $\tilde{\mathbf{x}}$  are indexed from zero. Rows and columns of  $\tilde{\mathcal{A}}$  are also indexed from zero. For brevity, we can define  $\tilde{\mathcal{F}} = [\tilde{f}_{ij}]$  and write Eq. (22) as

$$\begin{aligned}\dot{\tilde{x}}_i &= \tilde{x}_i \cdot \tilde{g}_i(\tilde{\mathbf{x}}, \tilde{\mathcal{A}}) \\ \dot{\tilde{\mathcal{A}}}_{ij} &= \tilde{\mathcal{F}}(\tilde{\mathbf{x}}, \tilde{\mathcal{A}})\end{aligned}\tag{23}$$

For an arbitrary matrix  $M$  we will write  $M^{(k)}$  and  $M_{(k)}$  to denote the  $k$ -th column and  $k$ -th row of  $M$  respectively.

If species 0 and 1 are the result of nominally splitting an original species, then their trait values for interaction with an arbitrary species  $j$ , must be the same for all time. This means that we have the time invariants  $\tilde{\alpha}_{0j}(t) = \tilde{\alpha}_{1j}(t)$  and  $\tilde{\alpha}_{i0}(t) = \tilde{\alpha}_{i1}(t)$ . This is exactly the same as saying  $\tilde{\mathcal{A}}^{(0)}(t) = \tilde{\mathcal{A}}^{(1)}(t)$  &  $\tilde{\mathcal{A}}_{(0)}(t) = \tilde{\mathcal{A}}_{(1)}(t)$ .

The conditions for addability, i.e. for reducing the system by combining variables  $\tilde{x}_0$  and  $\tilde{x}_1$ , are:

1. Initial conditions must fulfill:

$$\tilde{\mathcal{A}}^{(0)}(0) = \tilde{\mathcal{A}}^{(1)}(0) \text{ \& } \tilde{\mathcal{A}}_{(0)}(0) = \tilde{\mathcal{A}}_{(1)}(0). \quad (24)$$

Informally, for the two identical species, their trait values for interaction with all other species must be the same at time zero.

2. Fixing  $\tilde{\mathcal{A}}$ , define  $\gamma_{i,\tilde{\mathcal{A}}}(\tilde{\mathbf{x}}) = \tilde{g}_i(\tilde{\mathbf{x}}, \tilde{\mathcal{A}})$  and  $\varphi_{i,j,\tilde{\mathcal{A}}}(\tilde{\mathbf{x}}) = \tilde{f}_{ij}(\tilde{\mathbf{x}}, \tilde{\mathcal{A}})$ . The second condition is:

$$\forall \tilde{\mathcal{A}} \left[ \tilde{\mathcal{A}}^{(0)} = \tilde{\mathcal{A}}^{(1)} \text{ \& } \tilde{\mathcal{A}}_{(0)} = \tilde{\mathcal{A}}_{(1)} \implies \gamma_{i,\tilde{\mathcal{A}}} \text{ and } \varphi_{i,j,\tilde{\mathcal{A}}} \text{ are sum-dependent} \right] \quad (25)$$

for all  $i$  and  $j$ . This is analogous to condition Eq. (12) for systems without adaptation.

3. Finally,

$$\forall \tilde{\mathbf{x}} \geq \mathbf{0} \forall \tilde{\mathcal{A}} \left[ \tilde{\mathcal{A}}^{(0)} = \tilde{\mathcal{A}}^{(1)} \text{ \& } \tilde{\mathcal{A}}_{(0)} = \tilde{\mathcal{A}}_{(1)} \implies \tilde{g}_0(\tilde{\mathbf{x}}, \tilde{\mathcal{A}}) = \tilde{g}_1(\tilde{\mathbf{x}}, \tilde{\mathcal{A}}) \text{ \& } \quad (26)$$

$$\tilde{\mathcal{F}}^{(0)}(\tilde{\mathbf{x}}, \tilde{\mathcal{A}}) = \tilde{\mathcal{F}}^{(1)}(\tilde{\mathbf{x}}, \tilde{\mathcal{A}}) \text{ \& } \quad (27)$$

$$\tilde{\mathcal{F}}_{(0)}(\tilde{\mathbf{x}}, \tilde{\mathcal{A}}) = \tilde{\mathcal{F}}_{(1)}(\tilde{\mathbf{x}}, \tilde{\mathcal{A}}) \right]. \quad (28)$$



Equation. (26) is analogous to Eq. (14). Since the  $\tilde{F}^{(0)}$ ,  $\tilde{F}^{(1)}$ ,  $\tilde{F}_{(0)}$  and  $\tilde{F}_{(1)}$  functions control the rate of change of the first two rows and columns of  $\tilde{\mathcal{A}}$ , we need conditions Eq. (27) and Eq. (28) to preserve the time invariants.

Appendix S2 shows how, from the addability criteria we just described, it follows that species 0 and 1 can be combined into a single one.

The case of addability in normalized systems is very similar. For details see Appendix S2.

## LITERATURE SURVEY

We surveyed the literature to find publications studying the BEF relation in ecological networks by theoretical means. Based on our previous experience in this field (e.g. Valdovinos *et al.*, 2010; Vázquez *et al.*, 2015; Miele *et al.*, 2019), we chose prominent models commonly used in the ecological literature to be analyzed by our methods. We included models that (1) used differential equations, and (2) their purpose was to study the effects of species diversity on community dynamics.

We summarize the results in Tables 1 and 2. One out of 10 models without adaptation and six (all game-theory based) out of 14 models with adaptation were scale-invariant. Lack of addability caused most of the test failures in models without adaptation, while equation mismatch did so in models with adaptation. Lack of interspecific competition was the prevalent source of scale-sensitivity in models without adaptation, but normalization was the most frequent source in models with adaptation. For details, see Appendix S5.

## DISCUSSION

The importance of biodiversity as a determinant of ecosystem functioning and the provision of services has been asserted before (Hooper *et al.*, 2005, 2012). Ecological tradition

suggest that both taxonomic diversity, usually measured through the raw number of species, and functional diversity, i.e. variety of functional features of species, play a role in shaping ecosystem responses to environmental changes. The raw number of species within communities is believed to foster ecosystem resilience through increasing ecological redundancy. Several functionally similar species would maintain ecosystem functions through the compensatory responses of species. Also, high redundancy protects ecosystem functioning against loss of species, via enabling alternative pathways of energy and mass flow (Lawton & Brown, 1994). However, the raw number of species is insufficient for generating such positive effects on ecosystem functioning. Strictly speaking, the compensatory effect requires response diversity among redundant species (Laliberte *et al.*, 2010; Naeem & Wright, 2003; Yachi & Loreau, 1999). Following (Laliberte *et al.*, 2010), we consider response diversity as a component of functional diversity. Besides, in a limiting scenario of a community composed of truly identical species, there should not be a distinction between eliminating a species versus eliminating fractions of other species, assuming the total amount of biomass or individuals removed are the same in both cases. In short, changing the species diversity while preserving functional diversity should not affect the ecosystem functioning (Cadotte *et al.*, 2011). Ecological redundancy requires functional variability among species to have an effect on the system dynamics. Therefore, whenever evaluating the BEF relation through mathematical models, one should be wary about artifacts that may be introduced when adding species to the network. In particular, for most BEF studies, we should use scale-invariant models, i.e. those that preserve system dynamics when introducing functionally identical species (Arditi & Michalski, 1996; Kuang, 2002). The key point is that even when no identical species are added, the artifacts may be still present. To understand the reason behind this, assume that, using a scale-sensitive model, we observe alterations in the system dynamics after changing the number of functionally different species. The problem is that from this result we could

not establish a causal relationship between functional diversity and system dynamics, because the artifactual effect of changing the raw number of species is not controlled for. Regarding BEF, when a scale-sensitive model is used, it is hard to discriminate between a significant BEF relation, attributable to biodiversity effects, and a spurious relation arisen from scale-sensitivity. Thus, a necessary condition for any model used for evaluating the consequences of biodiversity shifts is that its dynamics must not be altered by the addition of identical species or, equivalently, to artificially split a species.

Hence we present a test to verify scale-invariance of ecological network models. We provide an operational definition of the test that complements Arditi and Michalski's conceptual approach to logical consistency. The usefulness of our test extends to many fields of ecological research, particularly when modeling networks of varying size. However, we focused on BEF studies, where the procedure of growing networks is central. As a key contribution of our study, we also present a generalized version of the test that can be applied to eco-evolutionary models, i.e., those that include trait adaptation. This feature tends to increase stability in ecological networks (Valdovinos *et al.*, 2010). To the best of our knowledge, the issue of scale-invariance in systems with adaptive trait dynamics has not been addressed before. In our generalization, we considered systems in which trait values are either normalized or non-normalized. Testing for addability of species is more complicated in the case of normalized models due to the need for preserving the normalization of trait values. We described a test that works for the renormalization rule defined in Eq. (S2.26). This rule is reasonable but somewhat arbitrary. However, the same procedure we used to derive the differential equations for the trait values, i.e., Eq. (S2.34) through Eq. (S2.39) can be used for other rules. Our scale-invariance test can be extended to similar models, such as Eq. (S4.15), that can include age or spatial structure. The latter has been partially explored by Kuang (2002). To assess scale-invariance of an ecological network model, we need unambiguous definitions for the rule

to translate networks into ODEs, and for the rule to grow a network by splitting a species into two identical ones. While surveying articles we noted that the form of the equations, and the rule to write them for a network were clear. Yet, the operation for duplicating species was difficult to infer. Nonetheless, the test is robust against erroneous detection of scale-sensitive models, in the following sense. For scale-sensitive models, completing the proof does not require guessing the entire duplication rule. Very weak assumptions are sufficient. By contrast, to prove a model is scale-invariant we need a detailed definition of the duplication rule. Thus, if we want to rule out the possibility of scale induced artifacts in BEF studies, the model specification should leave no doubts about how to add species to an existing network. This issue should be dealt with whenever presenting a model for studies aimed at determining the effects of biodiversity shifts.

Our survey of the literature showed a pervasive ambiguity in the rule to grow networks. We then had to rely on reasonable assumptions to apply our test. Under these assumptions, most surveyed systems are scale-sensitive. This is striking since many of these systems form the foundation of the current BEF theory. Remarkable exceptions are in Bastolla *et al.* (2009), and Drossel *et al.* (2001) and variants (Drossel *et al.*, 2004; McKane, 2004; Quince *et al.*, 2005a,b; Powell & McKane, 2008). The preponderance of scale-sensitive models undermines the development of biodiversity theory. This may hamper the much-needed application of this theory to environmental policymaking, ecosystem management, and conservation efforts. It is worthwhile to note that the venerable Lotka–Volterra model is scale-invariant, as we showed in section *Example applications of the test*. This formulation has been used as a starting point to create more sophisticated developments for studying biodiversity effects. Unfortunately, many of these extensions had features that corrupted the scale-invariance.

The most frequent model components that cause scale-sensitivity are the lack of direct interspecific competition in the presence of intraspecific one, using a Hill exponent other

than one, and the unsuitable use of normalized trait values in eco-evolutionary models. Normalization does not immediately implies scale-sensitivity. The way in which the normalized trait values appear in the differential equations is what causes scale-sensitivity. Scale-invariant models with normalized trait values do exist, as the one by Drossel *et al.* (2001). Although the form of their equations fall outside the scope of this article, the resulting dynamics can be shown to be scale-invariant.

Our findings suggest the need to revisit a number of classic results in the area. For example, our simulations based on the original model by Thébault & Fontaine (2010) and our slightly modified scale-invariant version, displayed qualitative differences in the relationship between species diversity and both stability and biomass. Our analysis serves to identify the causes of scale-sensitivity, and it also helps to find solutions for it. Since there are three main sources of scale-sensitivity in published models, it is usually straightforward to produce scale-invariant versions of them. Our approach is useful because it provides an operational test that can be directly applied to a wide variety of ODE based models, with or without trait dynamics. However, these do not cover every possible formulation found in the ecological literature. For example, models found in Drossel *et al.* (2001) follow a game-theoretical approach that does not use differential equations to describe the time evolution of trait values. Instead, they adjust the foraging efforts instantaneously, so they achieve an evolutionary stable equilibrium, after fixing the values of all state variables. This equilibrium has to be computed by solving an algebraic set of equations. This is conceptually similar to having an infinite rate of adaptation when using differential equations. For example, we could assign very large values to the adaptations rates in the replicator equation. This suggests that our test could be extended to a game-theoretical adaptation model.

Promising research avenues include extensions of the test in several directions. One of them is spatial heterogeneity that affects trait and population dynamics. This problem

can be addressed assuming continuous or discrete space structures, such as the growth of biofilms or metacommunity dynamics. Another extension useful in the context of studying the BEF would be the inclusion of age or stage structure. Again, these can be discrete, continuous, or even a combination of both (Valdovinos *et al.*, 2013, 2016; Ramos-Jiliberto *et al.*, 2018). For continuous space or age structure, the preferred approach is to rely on partial differential equations, which would require to develop a more general scale-invariance test. Another interesting aspect is considering network dynamics (Ramos-Jiliberto *et al.*, 2012). This topic is capturing the attention of ecologists since recent empirical long-term records of ecological networks indicate a high interaction turnover (Petanidou *et al.*, 2008; CaraDonna *et al.*, 2017; Chacoff *et al.*, 2018). In models considering additions/deletions of species and links, this could determine discontinuous changes on the value of state variables, such as populations abundances or trait values. In such discrete events, scale-invariance should also be preserved.

A theoretical challenge is finding criteria for developing proper models that include the interplay among space heterogeneity, age/stage population structure, and network dynamics. These issues are of paramount importance in epidemiological dynamics in the framework of biodiversity-driven dilution/amplification effects on disease propagation (Civitello *et al.*, 2015; Luis *et al.*, 2018). This topic has been studied using essentially the same models and techniques as we described here but without addressing scale-invariance (Duffy & Collins, 2019). These advances could be an important step toward a deeper understanding of the role of biodiversity in the stability and functioning of ecosystems and social-ecological systems. If we intend to achieve robust predictions about ecosystems and we admit the importance of mathematical modeling to achieve this goal (Valdovinos, 2019), then ecologists must be especially careful when formulating new models, and when interpreting model outcomes.

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**Table 1.** Summary of reviewed models that do not include trait adaptation. It is indicated whether or not they pass our scale-invariance test and, if they do not, which test criteria failed (species addability or equation matching, according to Fig. 2), and which component of the model is responsible for that: direct interspecific competition (ISC), Hill exponent or normalization of preferences (Norm.)

Reference	Scale-invariant	Test criteria failed	Equation component impeding scale-invariance
Williams & Martinez (2004)	No	Addability	ISC
		Addability	Hill exp.
		Matching	Norm.
Brose <i>et al.</i> (2006)	No	Addability	ISC
		Addability	Hill exp.
		Matching	Norm.
Berlow <i>et al.</i> (2009)	No	Addability	ISC
		Addability	Hill exp.
		Matching	Norm.
Bascompte <i>et al.</i> (2006)	No	Addability	ISC
Okuyama & Holland (2008)	No	Addability	ISC
Thébault & Fontaine (2010)	No	Addability	ISC
Mougi & Kondoh (2012)	No	Addability	ISC
		Matching	Norm.
Bastolla <i>et al.</i> (2009)	Yes	-	-
Kondoh (2003)	No	Addability	ISC
		Matching	Norm.
Uchida <i>et al.</i> (2007)	No	Addability	ISC

**Table 2.** Same as Table 1, but for reviewed models that include trait adaptation. † These models do not conform the equations we address in this study. Thus, we do not conducted our test on them. Authors’ claims about logical consistency indicate that their models are scale-invariant.

Reference	Scale-invariant	Test criteria failed	Equation component impeding scale-invariance
Kondoh <i>et al.</i> (2005)	No	Addability Matching	ISC Norm.
Garcia-Domingo & Saldana (2007)	No	Addability Matching	ISC Norm.
Garcia-Domingo & Saldana (2008)	No	Addability Matching	ISC Norm.
Guill & Drossel (2008)	No	Matching	Norm.
Kondoh (2007)	No	Addability Matching	ISC Norm.
Uchida & Drossel (2007)	No	Addability Matching	ISC Norm.
Uchida <i>et al.</i> (2007)	No	Addability Matching	ISC Norm.
Drossel <i>et al.</i> (2001)	Yes†	-	-
Drossel <i>et al.</i> (2004)	Yes†	-	-
McKane (2004)	Yes†	-	-
Quince <i>et al.</i> (2005a)	Yes†	-	-
Quince <i>et al.</i> (2005b)	Yes†	-	-
Powell & McKane (2008)	Yes†	-	-
Calcagno <i>et al.</i> (2017)	No	Matching	Trait dynamics



**Figure 1** The concept of scale-invariance. **(A)** The consumers (snails) are represented by a single population of size  $x$  that feeds on a resource (plant) of population size  $y$ . **(B)** The consumer population is artificially split into two separate variables,  $x_1$  and  $x_2$ . Bottom plots illustrate example trajectories of the resource and consumer populations. In the plot of panel **(B)**, the sum of variables  $x_1$  and  $x_2$  must equal the value of variable  $x$  of panel **(A)**, at every time.

**Figure 2** Test for scale-invariance in ecological networks. Sequence of steps for conducting our scale-invariance test.

**Figure 3** Sample simulations based on Eq. (19). **(A)** Original equations. **(B)** Eq. (19) with added direct interspecific competition. Black lines with green/red error areas show plant/herbivore persistences. Green/red lines with grey error areas show plant/herbivore biomasses. Mean  $\pm$  95% confidence intervals are shown.

Figure 1

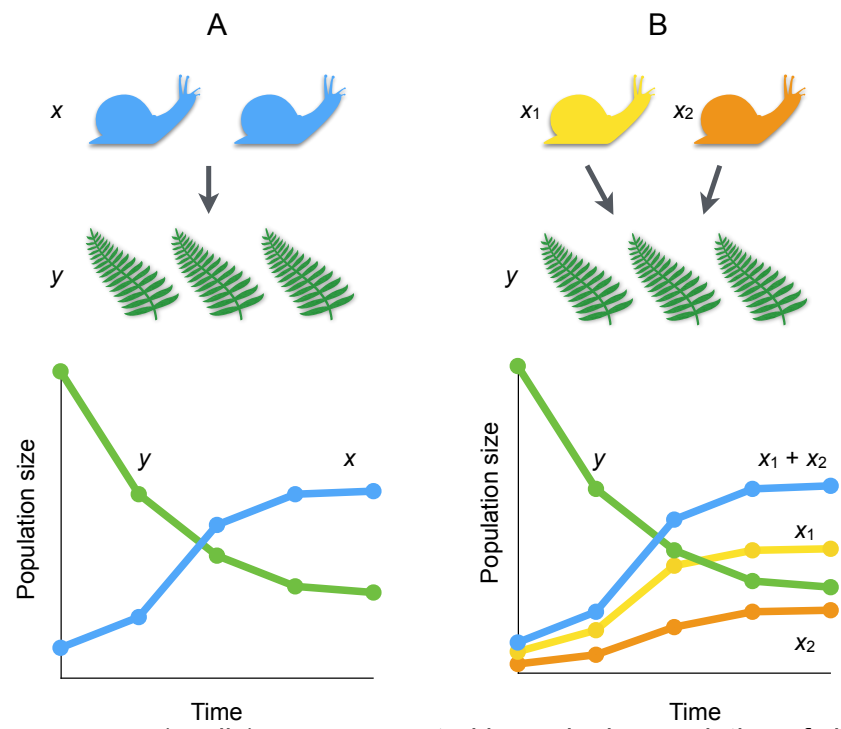


Fig. 1

Figure 2

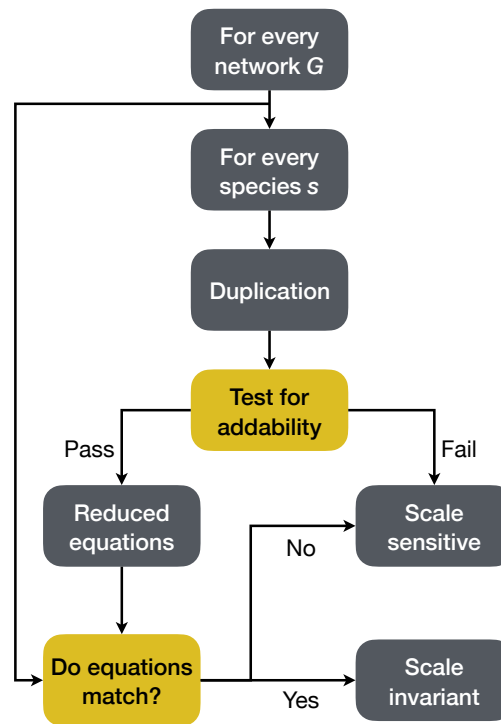
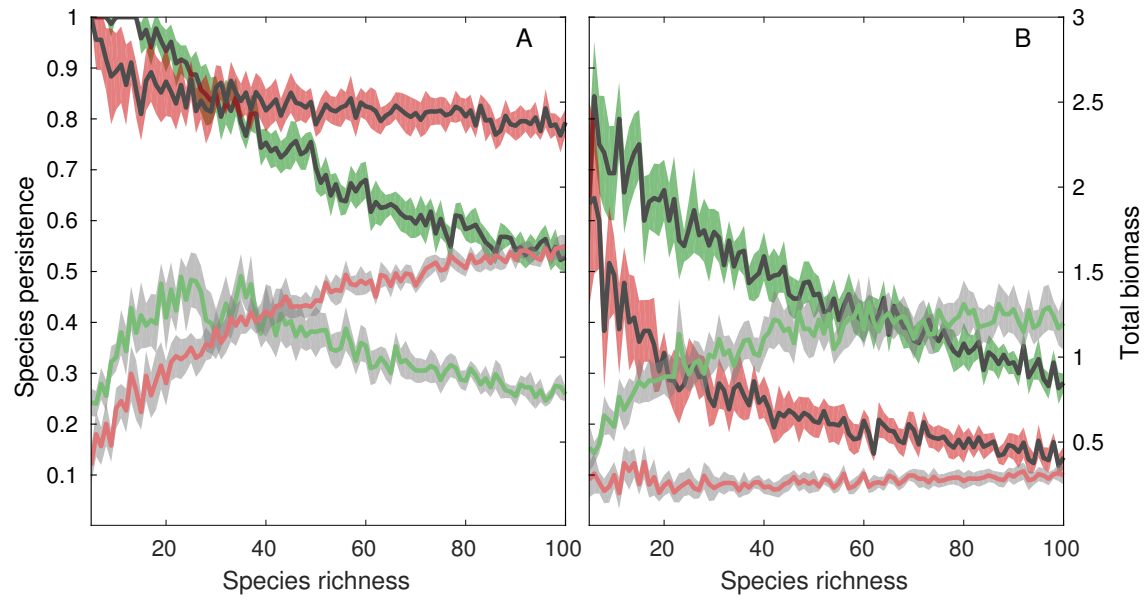


Fig. 2

Figure 3



**Fig. 3**