The dynamics of neutral and trait-based multi-trophic interactions

Timothée Poisot[1,2] and Dominique Gravel[1,2]

[1]Université du Québec à Rimouski, Rimouski, Canada.
[2]Quebec Centre for Biodiversity Science, McGill University, Montréal, Canada.
*email: timothee_poisot@uqar.ca

Abstract

We describe *manna*, a simple modeling framework of individuals establishing trophic interactions under neutral or trait-based rules. We use this model to show that neutral and trait-based interactions differ in their temporal dynamics, and discuss how our results contribute to highlighting the need to understand spatial and temporal dynamics of species interaction networks.

1   Introduction

Over the last years, there has been the emergence of two bodies of theory regarding the structure of ecological networks. On one hand, proponents of the "niche" approach emphasized the importance of trait matching between species [3]. To simplify, two species can interact assuming that their traits allow it, e.g. the jaw morphometry of the predator allows it to bite, and eventually eat, its chosen prey. Arguably, this has been the dominant view in the field of network studies, and it inspired many methodological tools which peformed well at reproducing the structure of food webs [6]. On the other hand, several authors adopted a "neutral" perspective, putting more emphasis on the fact that interactions rely on density-dependent processes, most notably the probability that individuals from the prey and predator species will meet. Although this perspective was originally develloped in plant–mutualistic interactions [1], where it showed a great predictive power, recent work expanded it to food webs with equal success [2]. Much like in other fields of community ecology, there is a need to integrate these two perspectives so as to derive more accurate predictions about the structure of networks, and their variability through space and time.

Indeed, the basic "ingredients" of both the neutral (population sizes) and trait-based (trait values carried by populations or individuals) are expected to vary through space and time. Not only will they vary because of extrinsic constraints (e.g. organisms with different body sizes are differently affected by environmental disturbances), but they will also vary because the populations are interacting. Ecological dynamics results in covariances in the population sizes of preys and predators, and coevolutionary feedbacks will select different traits values. For this reason, accounting for both the neutral and trait-based effects will have two advantages. First, it will somehow reconcile the two perspectives on network structure, and allow a conceptual unification of the two most important families of explanations of network structure. Second, it will integrate the basal processes involved in these perspectives, and thus increase the accuracy of our expectations regarding network structure and dynamics. Because networks are notoriously difficult to adequately sample, and replicating them over time and space is not easily done, there is value in exploring the behavior of simple, highly phenomenological models.

In this manuscript, we present such a model, whose goal it is to account for both trait-based and neutral processes in the assembly, structure, and variation of multi-trophic networks. We add a layer of individual based population dynamics on top of the well-known "niche model", and use this to derive predictions about (1) the structure of multi-trophic communities under different scenarios, and (2) the variation of network structure over time. We show that although there is a clear effect of switching from neutral to trait-based rules, the entirely neutral situation cannot be differenciated from a trait-based networks in which predators have a large feeding range. We discuss the implications of these findings, and how they can help refine future research questions pertaining to the relationships between neutral and trait-based processes.

2   The model

We define a time-discrete, individual based model of multi-trophic interactions in a single patch. Species are defined by a vector of functional traits, them being their niche position ($\mathbf{n}_i$), the centroid of their feeding range ($\mathbf{c}_i$), the breadth of their range ($\mathbf{r}_i$), and their maximal population size ($\mathbf{K}_i$).

2.1   Generation of the species pool

The species pool is generated so as to obtain a number of species S, with an expected connectance value of Co. To generate the species pool, we draw at random in an uniform distribution ranging from 0 to 1, S values forming the vector $\mathbf{n}$. The vectors $\mathbf{c}$ and $\mathbf{r}$ are generated following the method

described by Williams and Martinez [6]. The number of individuals in each species is $\mathbf{p}_i$, and is drawn at random according to the following procedure.

First, the values of $\mathbf{K}_i$ are drawn at random from the uniform distribution between 0 and $K_{\max}(i)$, where $K_{\max}(i)$ is simply $10^3 \times (1 - \mathbf{n}_i) + 100$. This way, species with the large $\mathbf{n}_i$ have lower carrying capacity, and species with low $\mathbf{n}_i$ have high carrying capacity. This accounts for the well known negative relationship between trophic rank and population size, and give a structure to the community. To initialize the simulation, a number of individuals $\mathbf{p}_i$ is drawn from the uniform distribution from 10 to $\mathbf{K}_i$.

2.2 Simulation

Before the interactions happen and the demographic changes are calculated, there is a (possible) immigration step, to implicitely simulate some spatial context and maintain species richness. The identity of the species receiving each migrant is drawn at random from within the regional species pool. This makes it so that locally extinct species can be rescued through immigration. After the immigration is over, the probability that each individual will reproduce or die is calculated given the following set of rules. The mortality probability of individual i is

$$m_i = \mu + s_i c_\mu \tag{1}$$

, while its natality probability is

$$b_i = \nu - s_i c_\nu \tag{2}$$

, and s_i is a scaling factor related to the niche position, wherein

$$1 - (1 - \mathbf{n}_i)^k \tag{3}$$

. The exponent k regulates the strength of the scaling. The population size of species i at time $t + 1$ is calculated as

$$\min(\mathbf{K}_i, \mathbf{p}_i - \mathcal{B}(m_i, \mathbf{p}_i) + \mathcal{B}(b_i, \mathbf{p}_i)) \tag{4}$$

, where $\mathcal{B}(p, n)$ is the number of successes of a Bernoulli process with probability of success of p and n trials.

After the demographic changes are done, we pick at random 15% of the individuals, which will be seeking a prey at this timestep (decreasing or increasing this fraction will, respectively, simulates an increase or decrease in the prey handling time). Each indiviual has an equal probability of being picked, so that species with high abundances will be over-represented among the pools of predators (in this regard, our model assumes that the search for preys is an active task, which is a fairly common situation in nature). The identity of preys items is detailed in the next two sub-sections. The interactions are done on an individual basis, meaning that we pick a predator, then its prey, and reproduce this routine once we have reached enough predators.
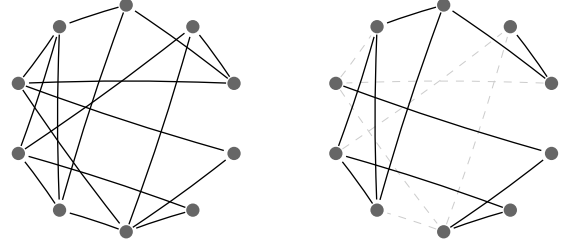

Figure 1: Comparison of the structure of networks under the neutral (left) and trait-based (right) approaches. When the only rule for the existence of an interaction is that the two populations are large enough to interact (neutral rules), we expect more interactions than when traits are used to delineate a feeding range (trait-based rules). These trait-forbidden links are dashed in the right network. Switching from one situation to the other can lead to complex effects, both on networks dyamics and community composition.

2.3 Neutral interactions

In the neutral scenario, the only factor regulating the identity of the prey is its abundance, i.e. none of the traits are looked at when deciding if the predator can consume the prey. Once the predating individual is selected, we pick at random one individual from any species (including the possibility of cannibalism) in the pool. The predated individual is then removed. In this scenario, it is possible that a small species will eat a much larger species, though it should be kept in mind that because of allometric scaling between the body size traits and demographic parameters, we expect the interactions to still retain some size structure. Because of this feature, our model departs from the purely neutral assumption made by Canard et al. [2].

2.4 Trait-based interactions

In the trait-based scenario, preys are selected only among the species that can be fed upon, as in the *niche* model of Williams and Martinez [6]. Preys are still selected on the basis of their abundances, although this time we consider the relative abundance among all preys falling within the predator feeding range.

2.5 Implementation and availability

A C99 implementation of the model, using the Gnu Scientific Library, is available at https://github.com/tpoisot/ms_pop_networks/, under the conditions of the GNU GPL licence. We would appreciate that a reference to this preprint is made when the program is used. A R script to reproduce the results showed in this paper is also made available.

3 Methods

3.1 Simulations

We used the model to generate species pools of size $S = 50$, with connectance varying from 0.01 to 0.5 by varying increments choosen to represent the changes induced by connectance. 5 individuals of any random species migrated into the system at each timestep. Each community is simulated under the neutral and trait based assumptions, and replicated 20 times (20 times for the neutral scenario, and 20 times for each value of connectance under the trait-based scenario). Simulations are done over 5×10^3 timesteps, as preliminary analyses showed it was long enough to reach an equilibrium in number of persisting species, number of persisting links, and overtime dissimilarity.

3.2 Analyses

Networks were aggregated in bins of 10 timesteps for the analysis (exploratory work showed that the bin size made no quantitative difference on the results, though it did considerably speed up the calculations). Within each bin, we measure the number of species in the network ($\mathcal{S}$), the number of links ($\mathcal{L}$), the effective connectance ($\mathcal{C}$, expressed as $\mathcal{L}/\mathcal{S}^2$).

Within each run of the simulation, we measure components of network dissimilarity through time, using the method described in Poisot et al. [4]. We measure turnover of interactions and community structure between the network at time t and the network at time $t + 1$. We report the overal network dissimilarity (β_{WN}), the dissimilarity of links across shared species (β_{OS}), the species turnover (β_S), and its contribution to network turnover (β_{contrib}). In addition, we report the turnover of predators (β_U) and preys (β_L) species through time.

4 Results

4.1 Community dynamics

Regardless of the rules or connectance, all simulation conditions yield a common pattern: a rapid decrease is the number of species (*i.e.* sorting) and links (Fig. 2). This results in changes in connectance, with all the simulations eventually stabilizing around a value of $\mathcal{C} \approx 0.05$. The number of species maintained is higher in the neutral conditions. When connectance increases, the number of persisting species increasing as well. For a connectance of Co = 0.5, there are almost no differences in species richness between the neutral and trait-based situations. The same is true of the number of interactions. The equal connectance across the different rules is easily explained by the fact that, with increased restrictions on trait matching (i.e. switching from neutral to trait-based, or from high connectance to lower connectance

within trait-based rules), both the number of species and the number of interactions decreased. However, the dynamics of connectance through time were different. Neutral systems started with high realized connectance (on average 0.3, close to the values reported by Canard et al. [2] for the purely neutral scenario), and the sharply decreased. On the other hand, trait-based systems generated with a low connectance remained at this level through time.

4.2 Networks dynamics

5 Discussion

One interesting outcome of the simulations presented here is that neutral and trait-based systems differed on some, but not all, of the features of the networks they generated. Increased restrictions on the range of preys that can be consumed (through the generation of networks with decreasing expected connectances) resultes in less species and less interactions being maintained at equilibrium. However, because the loss of species and interactions happenned at a similar rythm with regard to changes in expected connectances, the networks showed the same realized connectance at equilibrium. In our system at least, there is no signature of neutrality or traits on network connectance. Looking at the dynamics of network turnover, however, is far more telling about which mechanisms may be acting in a particular system. Increasingly neutral networks had a lot more temporal turnover, both in terms of their overall structure, or the interactions between shared species, than did trait-based networks with low expected connectance. The temporal dynamics of species dissimilarity is less obvious, though networks with intermediate expected connectances tended to have more species turnover. The more revealing difference, however, is in the impact of species turnover on network turnover. While it is almost null in neutral networks, or in networks with high expected connectance, it moves closer to unity when expected connectance decreases. This results makes sense, in that when the expected connectance is low, species have a low generality [5], and there is very low functional redundancy across species.

These results highlight that determining wether network structure is driven by neutral or trait-based dynamics may require a more dynamic approach than what is currently done. Although previous studies focused on stastitical analyses to detect whether relative abundances, or traits combinations, allowed predicting the existence of interactions, we show that these two factors can interact in complex ways. Notably, we report no impact on network connectance, with highly-connected systems being impossible to distinguish from neutral systems on the measures we followed. However, by following network dynamics, one can paint a sharper picture of the different facets of network turnover, all of which respond strongly to the relative importance of neutral and trait-based processes. Based on this information, we suggest that follwoing the dynamics of networks, however hard

it may be to achieve in nature, can be an invaluable information in order to pinpoint which mechanisms are driving the structure of this network.

3. role of connectance

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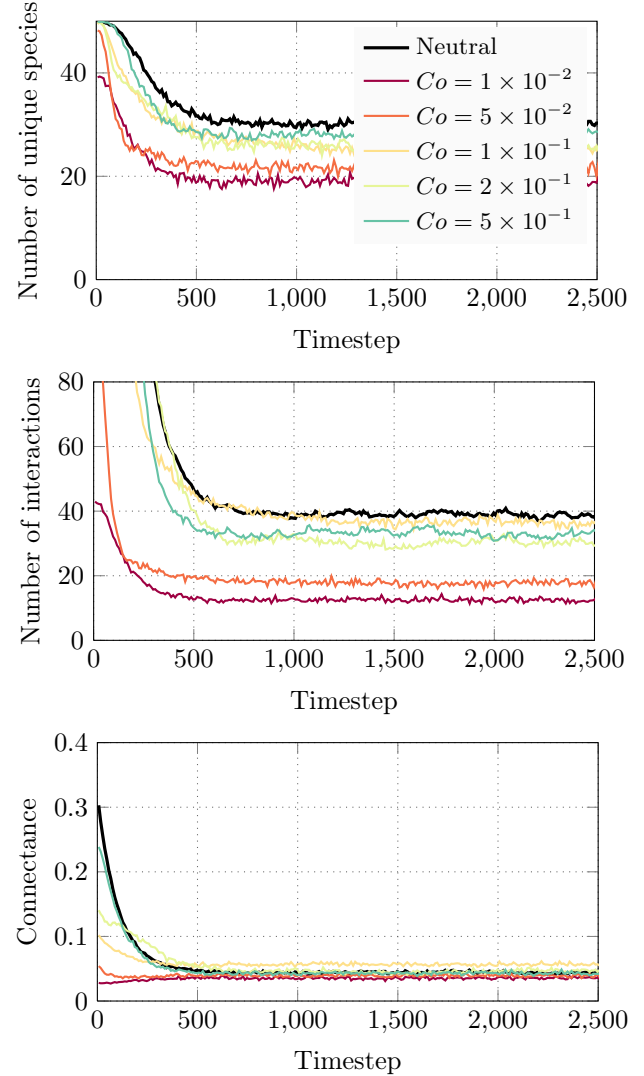[6] RJ Williams and ND Martinez. "Simple rules yield complex food webs". In: *Nature* 404.March (2000), 180–183.

Figure 2: Temporal dynamics of network structure, as a function of wether the system behaves neutrally (black lines) or under trait-based rules (colored lines). The first 2500 timesteps are shown, all simulations reached equilibrium at approx. $t = 1000$. **A.** Number of unique species ($\mathcal{S}$). **B.** Number of unique interactions ($\mathcal{L}$) **C.** Connectance of the network ($\mathcal{C}$).
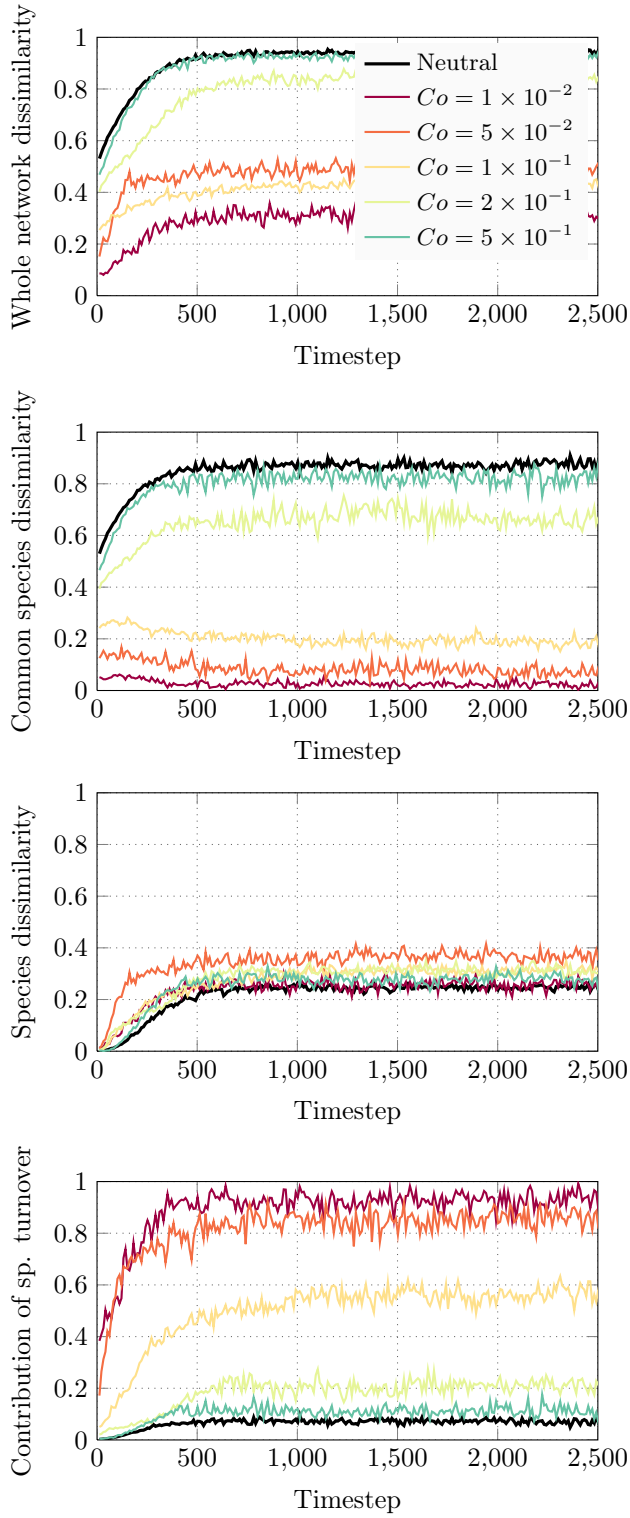
Figure 3: Temporal dynamics of network turnover, as a function of wether the system behaves neutrally (black lines) or under trait-based rules (colored lines). The first 2500 timesteps are shown, all simulations reached equilibrium at approx. $t = 1000$. **A.** Whole-network dissimilarity (β_{WN}) remains high under the neutral scenario. **B.** The same is true of interaction turnover across shared species, β_{OS}. **C.** Species turnover displays a hump-shaped pattern with connectance (see also FIGURE XXX). **D.** The impact of species turnover on interactions turnover is low is the neutral model, but increasingly higher when trait-based rules are used and connectance decreases.