How ecological networks evolve

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1   Introduction

The extant structure and distribution of biodiversity is the outcome of macro-evolutionnary processes, and the modelling of these processes stimulated a large variety of approaches **???**. At their core, these approaches are birth-death processes, in that they model the rate of speciation and extinction to generate a prediction about both the temporal dynamics of species richness, and its predicted current state. Yet these models often consider species as being isolated entities, in that even though they share ancestry, they are not involved in inter-specific interactions. This is problematic, as from an ecological[1] and evolutionary **???** standpoint, interactions serve as a *scaffold* to build up increasingly diverse communities: plant require pollinators to persist, predators require preys, etc.

The addition of species interactions to models of macro-evolution is well motivated by two key observations. First, the structure of extant networks is non-random, and displays a strong evolutionary signal **???**. Second, there is a dynamics of the structure of ecological networks over evolutionary timescales **??? ???**, suggesting the ongoing action of macro-evolutionary processes. Models of macro-evolution with explicit consideration of species interactions are needed to develop a theoretical understanding of how networks evolve, and how much of their extant structure originated through evolutionary processes.

Despite the relative lack of well-resolved time series of the macroevolution of species interactions (ruling out modelling approches comparing temporal dynamics), the question of how networks evolve can still be adressed by confronting extent data with the outcome of network diversification scenarios. And although comparing two networks is a difficult task, comparing their structure, as represented by the distance between key summary statistics, is feasible. In this paper, we first present a stochastic model of network macro-evolution based on a speciation-extinction process. We then simulate this model under the complete range of meaningful parameter space, and compare its output to a large dataset of extent ecological interactions (mutualistic and antagonistic). Using Approximate Bayesian Computation (ABC), we show that (i) the structure of extent networks is

adequately described by our model; (ii) networks of different interaction types have different parameter values; (iii) networks of antagonistic interactions are, on average, more difficult to predict than networks of positive or mutualistic interactions.

2 Results and discussions

2.1 Model output

1. Model output

2.2 Posterior distribution of parameters

2. Parameters distributions for different types of networks

2.3 Accuracy of predictions

3. Z-scores

4. Use the method to *generate* realistic networks by sampling the relevant posteriors

3 Methods

3.1 Data selection

We used empirical data from mutualistic interactions (XX networks), plant-herbivore interactions (XX networks), phage-bacteria networks (XX interactions), plant-dispersers interactions (XX net-

works), and host-parasite interactions (XX networks). Mutualistic and dispersers interactions were taken from the *WebOfLife* database. Phage-bacteria data are from **???**. Host-parasite data are from **???**. Plant-herbivore data are from **???**. Each network was cleaned in the following way. First, species with no interactions (if any) were removed. Second, interactions strengths (if present) were removed. This yields adjancency matrices in which all species have at least one interaction.

3.2 Stochastic model

We model the diversification of bipartite networks. Bipartite networks are a useful way of representing several types of ecological interactions in which a group of species (*blue*) interacts with a second group of species (*red*; examples include pollination, frugivory, seed dispersal, parasitism, …). The starting point of every simulation is the simplest possible network: one blue and one red species, with a single interaction between them.

Our model is structurally close to speciation/extinction models – at each time step, there is a probability p that one of the blue species (taken at random) will undergo a speciation event (and conversely, a probability $1 - p$ that a red species will speciate). Upon speciation, the incipient species starts with *all* interactions of its ancestor; each of these interactions is lost with probability ϵ,

$$\epsilon = \epsilon_0 \times \text{whatever} \tag{1}$$

, where .

- parameters ranges (from preliminary simulations)

3.3   Simulations

We conducted the following two numerical experiments. First, we conducted a systematic exploration of the model's behavior using evenly spaced parameter values. Each combination of parameters was simulated 1000 times. Second, we sampled the parameter space uniformly, by drawing 10^5 parameters sets at random from within the aforementioned bounds. These outputs were used in the parameter selection experiment described below.

3.4   Network measures

We measure th

- connectance
- nestedness
- motifs (explain the correction)

The raw number of motifs was corrected to account for the number of species in each layer of the bipartite network. The maximum number of a motif with (e.g.) 2 species at the top and 2 species at the bottom is the product of the number of combinations of 2 species in the top layer, and of 2 species in the bottom layer (evaluated by their binomial coefficients). This gives a total number of sets of species that *could* be involved in a 2x2 motif; the raw number of this motif is divided by this maximum number. This yields values in the 0-1 range, representing the proportion of sets of species that *do* form a given motif out of the sets of species that *could*.

- modularity

3.5 Parameter selection

We used ABC (Approximate Bayesian Computation) to select the parameter values that yielded realistic networks, by assessing how closely each replicate of the second numerical experiment resembles empirical communities. For each empirical network, its array of ranged summary statistics was compared to each output of the stochastic model. The inverse of the Euclidean distance between the two arrays was recorded as the score of the parameter set. As every empirical network had different absolute values of scores, fixing a common threshold was not feasible. We selected the posterior distribution as the 500 parameters sets that gave the best scores (i.e. above the 95th percentile).

4 References

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