

How ecological networks evolve

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Here be science yo.

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The extant structure and distribution of biodiversity is the outcome of macro-evolutionary processes, and the modelling of these processes stimulated a large variety of approaches^{1,2}. 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 isolated entities, in that even though they share ancestry, they are not involved in inter-specific interactions. This is problematic, as from an ecological³ and evolutionary^{4,5} standpoint, interactions serve as a *scaffold* for community persistence: plant require pollinators, predators require preys, etc.

Although modern macro-ecological models give an increasingly central role to interactions⁶, macro-evolution models are still unable to predict the structure of complex interactive communities⁷. Two key observations motivate the overcoming of this limitation. First, extant networks are non-random in their structure, and displays a strong macro-evolutionary signal⁵. Second, the structure of ecological networks is dynamic over evolutionary timescales⁸. This is strongly suggestive of ongoing action of macro-evolutionary processes. Models of macro-evolution with explicit consideration of species interactions will provide a theoretical understanding of how networks evolve, and how much of their extant structure originated through evolutionary processes.

Yet the relative lack of well-resolved long-term time series of species interactions rule out the comparison of temporal dynamics⁹ the (comparatively) extensive fossil and molecular record of species diversification allows. We addressed the question of network macro-evolution by confronting extent (bipartite) networks with the outcome of a birth-death simulation models, under the assumption that the best-fitting models will be a representation of the network's evolutionary history. We posit that the evolution of networks follows a series of simple rules. First, every network starts as two species with one interaction. Second, a speciation event happens at the top level with probability p , and at the bottom level with probability $1-p$. Any incipient

species start with all interaction of the ancestor. Third, interactions of the incipient species are lost with probability $\epsilon(\lambda, c, k)$ (see *Methods Summary*); this allows interactions to be lost either at a fixed rate λ , or as a function of the incipient species degree k . These three steps are repeated 10^4 times, for 10^5 random combinations of $\langle p, \lambda, c \rangle$. Whenever either level has more than 10^2 species, some are deleted at random.

The endpoint of these simulations are compared to 271 bipartite ecological networks (seed dispersal; herbivory; parasitism; bacteriophagy; pollination – see *Methods summary*) using Approximate Bayesian Simulation (ABC). ABC^{10,11} gives estimates of posterior distribution of parameters by comparing a measure of distance between empirical observations and a model, when no analytical expression of likelihood can be derived. We define the distance between a simulated (i) and empirical (j) network as $d(\mathbf{v}_i, \mathbf{v}_j)$, where \mathbf{v} is an array of network structural properties, including connectance, modularity¹², nestedness¹³, and the distribution of different network motifs¹⁴ (see *Methods summary*). All of these measures were ranged in $[0; 1]$. The posterior distribution of best-fitting parameters, for each network, is the parameters of the closest 500 simulated models.

1. parameters distribution
2. biplot
3. z-scores

Methods summary

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 networks), and host-parasite interactions (XX networks). Mutualistic and dispersers interactions come from the *WebOfLife* database. Phage-bacteria data are from¹⁵ Host-parasite data are from¹⁶. Plant-herbivore data are from¹⁷. 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 adjacency matrices in which all species have at least one interaction.

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.

Network measures

We measure the

- 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

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).

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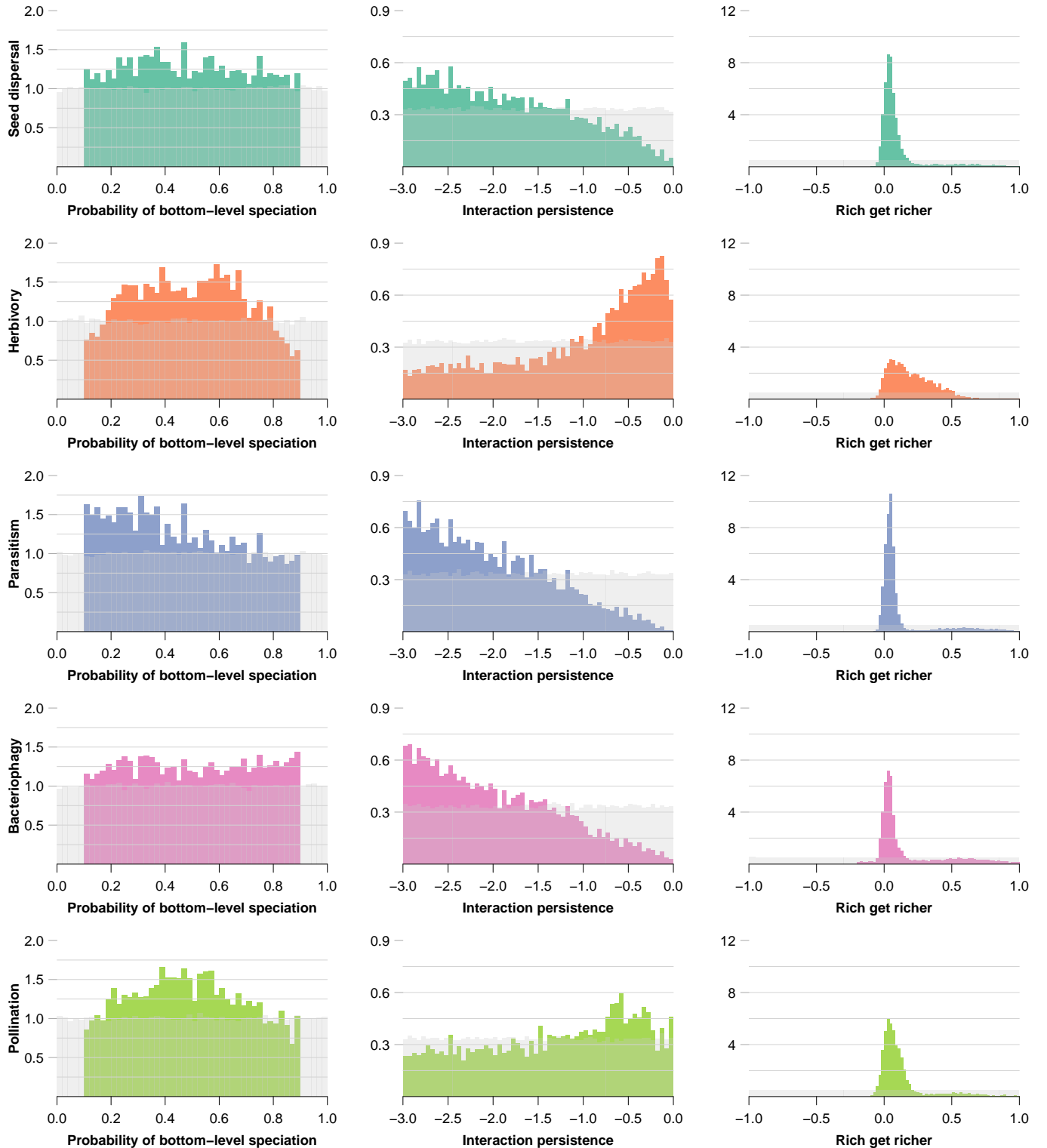


Figure 1: Posterior distributions of parameters p , $\log_{10}\lambda$ and $\log_{10}c$. The grey shaded area is a representation of the uniform prior distribution. Although there is no strong selection on the values of p , networks do differ strongly both from the prior, and from one another, on λ and c .

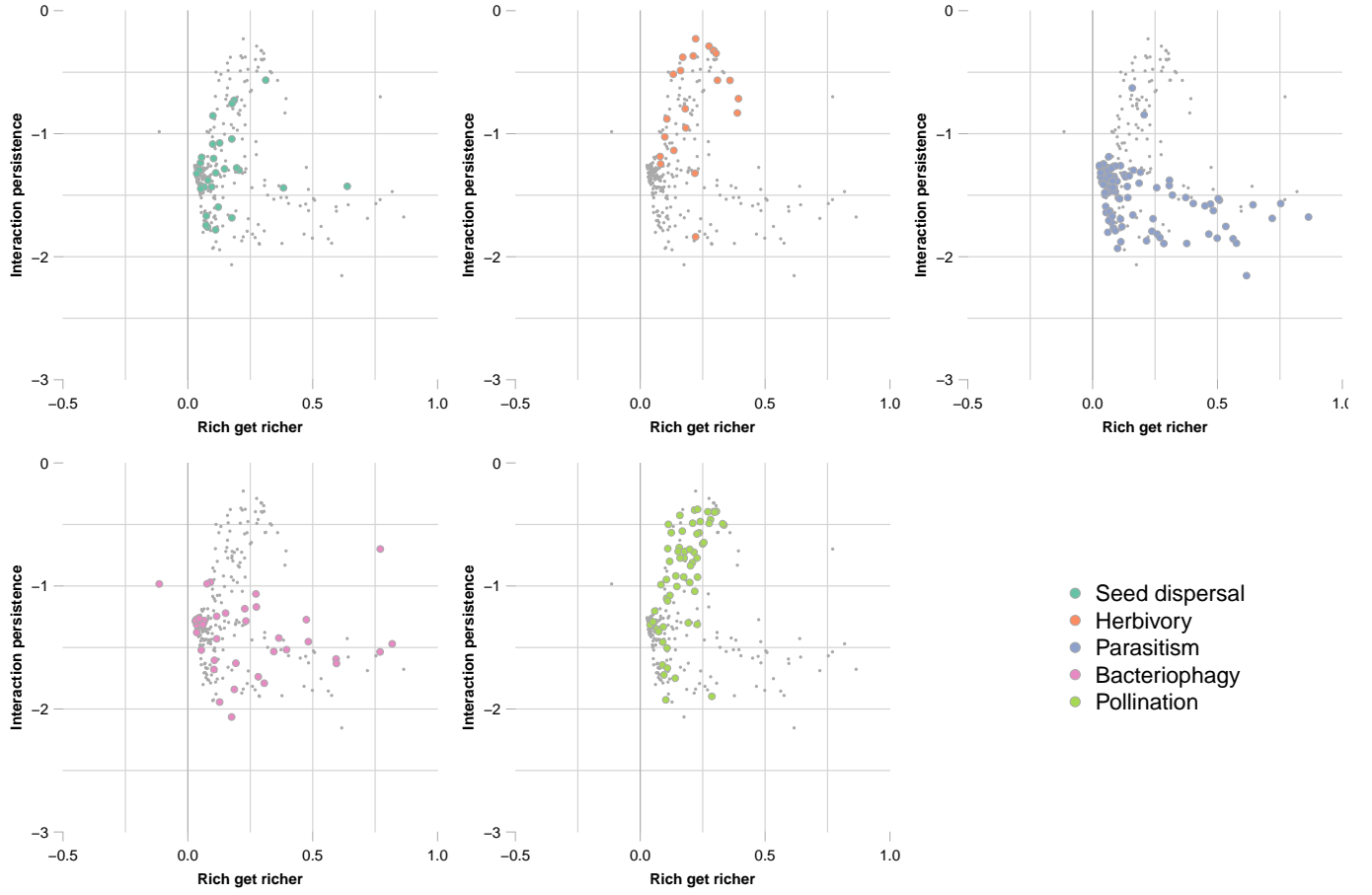


Figure 2: Relationships between parameters λ and c in the five different types of networks. The grey points indicate all networks in the dataset. Different types of ecological interactions occupy different positions along the λ - c continuum.