

Evolutionary Food Web Modelling

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Overview

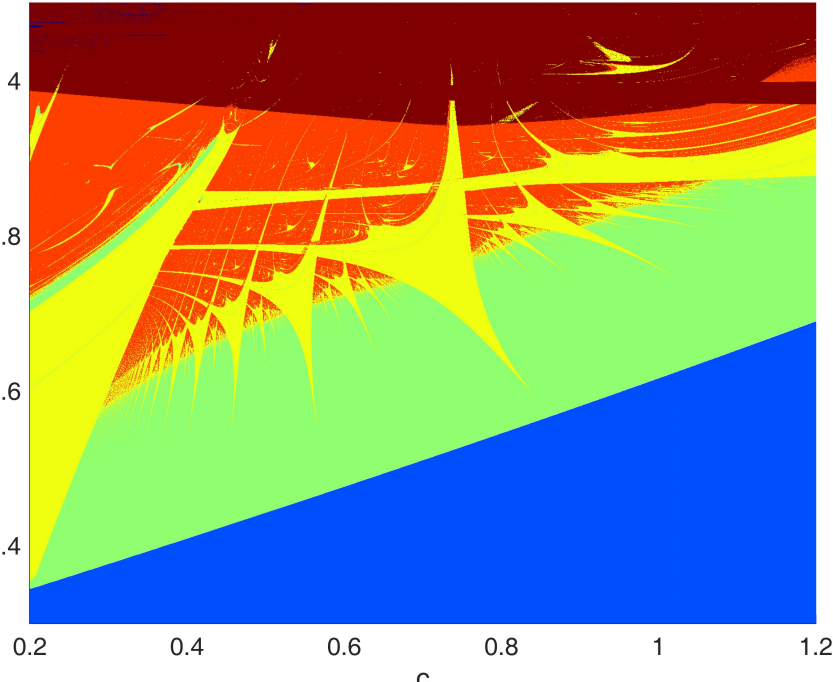
This work is concerned with a variety of approaches to modelling trophic interactions and their evolutionary change in an ecological network, that is, food webs and their temporal evolution.

This is important for conservation and maintenance of biodiversity in response to climate change and habitat destruction. Complex network theory implies that the simplest and most intuitive hypotheses of consequences are not always correct. For example, some predatory relationships have a positive effect on the prey population due to other indirect effects.^[1]

We illustrate three approaches, increasing in scope and complexity, and transitioning from a mathematical dynamical systems analysis that conceptually explores the rise of a two-species ecosystem, to a fully computational numerical simulation-based approach that allows for arbitrarily-many species to be added to the network via mutation. These final models are “eco-evolutionary” – they consider the interplay of ecological interactions *within* the network and evolutionary processes that *change* the network.

1. Low-Dimensional Systems with Mutation and Predation^[2,3]

We consider three variants of a model with one species x_n which reproduces according to the logistic map, and produces a daughter species y_n by mutation. The second species is able to predate upon the first.



Model 3 parameter space with $p=0.001$ and initial conditions $x_0 = 0.1$ and $y_0 = 0.0$.

Blue = Coexistence Period-1, Red = y-only Period 1, Green = 2D Quasiperiodicity, Yellow = 2D Periodicity, Orange = 2D Chaos.

Model 1.

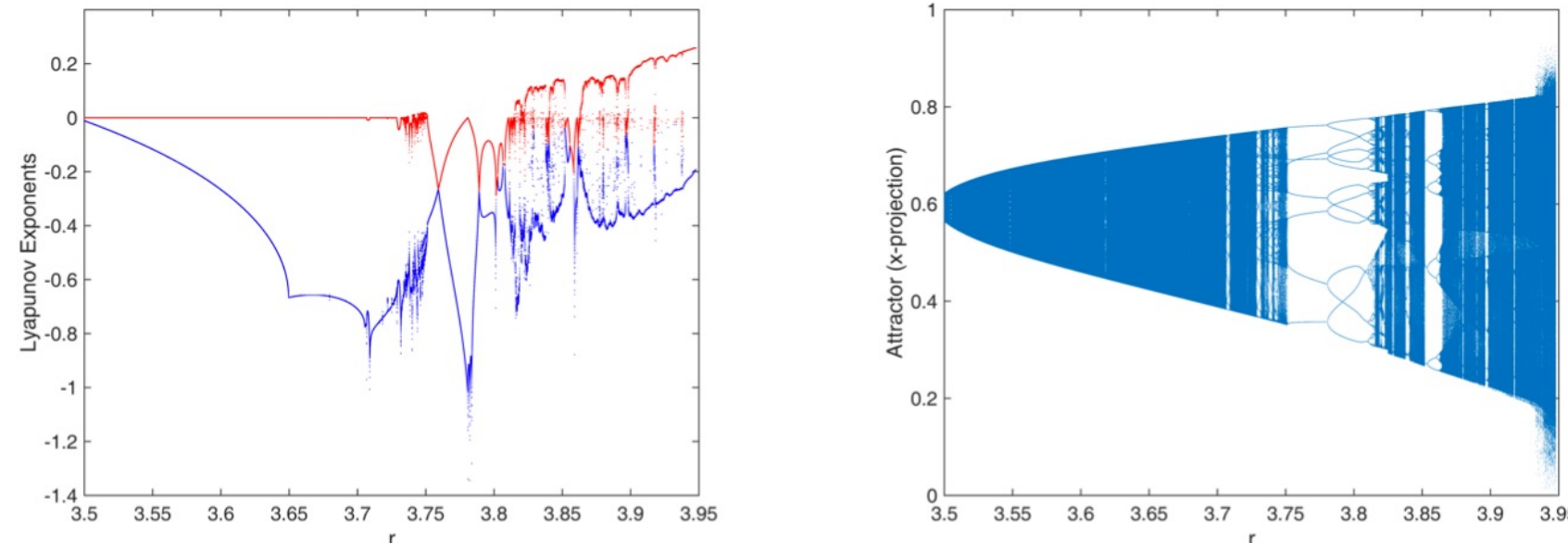
$$\begin{aligned}x_{n+1} &= \max((1-p)rx_n(1-x_n-y_n)-cx_ny_n, 0) \\ y_{n+1} &= \max(prx_n(1-x_n-y_n)+rx_ny_n, 0)\end{aligned}$$

Model 2.

$$\begin{aligned}x_{n+1} &= \max((1-p)rx_n(1-x_n-y_n)-cx_ny_n, 0) \\ y_{n+1} &= \max(prx_n(1-x_n-y_n)+\frac{2r}{3}(1+x_n)y_n(1-x_n-y_n), 0)\end{aligned}$$

Model 3.

$$\begin{aligned}x_{n+1} &= \max((1-p)rx_n(1-x_n)-cx_ny_n, 0) \\ y_{n+1} &= \max(prx_n(1-x_n)+\frac{r}{2}(1+x_n)y_n(1-y_n), 0)\end{aligned}$$



Lyapunov exponents and dynamic behaviour of Model 3 at $c = 0.65$

Issues in Food Web Modelling

In the 1980's, Cohen's Cascade Model and analysis of many small documented food webs gave rise to the constant L/S hypothesis – the linkage density is invariant to the size (diversity) of the food web. However, in the 1990's, the prior data was questioned, and largely replaced with 16 large, reliable food webs. Fresh analysis gave rise to the constant connectance hypothesis, supported by the more sophisticated Niche Model^[4] and its variants.

The Stability-Complexity debate – are larger food webs less stable?

- Began when Robert May's analysis seemed to show that stability decreased with size and complexity.^[5]
- Proposed mechanisms of stability in real webs include non-random interaction strengths, relatively many weak links, adaptive foraging, realistic functional responses, redundancy, and simply by considering more appropriate dynamic forms of stability that emphasise species persistence rather than constant populations.

Types of food web stability:

- Linear stability – considers the tendency to return to a fixed point under small perturbation.
- Robustness – the fraction of species that must be artificially deleted in order to result in 50% total extinctions.
- Species deletion stability – the fraction of species that can alone be deleted without incurring further secondary extinctions.

Modelling the functional response (number of prey eaten per predator):

- Linear/Lotka-Volterra (i) is simple but unrealistic.
- Holling Type-II (ii) saturates with prey numbers.
- Beddington-deAngelis (iii) and Ratio-dependent (iv) introduce a further dependence on predator population.

$$\begin{aligned}i. & g(N) = \alpha N \\ ii. & g(N) = \frac{mN}{1+bN} \\ iii. & g(N, P) = \frac{mN}{1+bN+cP} \\ iv. & g(N, P) = \frac{mN}{bN+cP} = \frac{m(N/P)}{b(N/P)+c}\end{aligned}$$

2. 10-Predator, 10-Prey Lattice^[6,7,8,9]

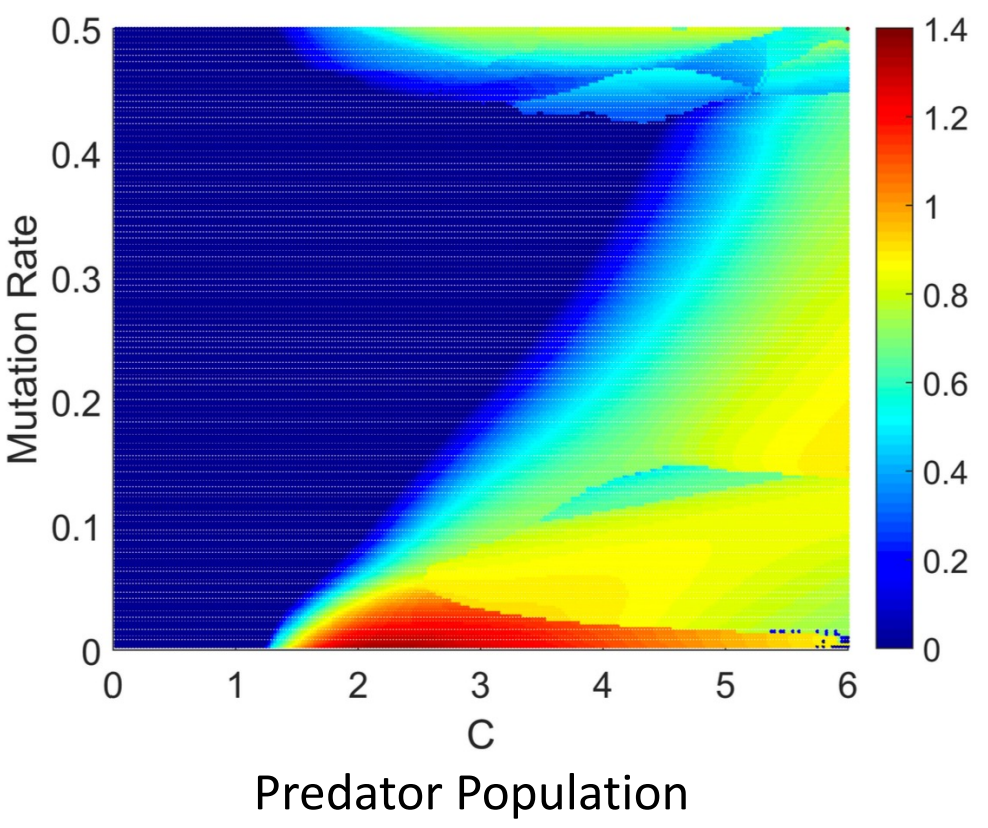
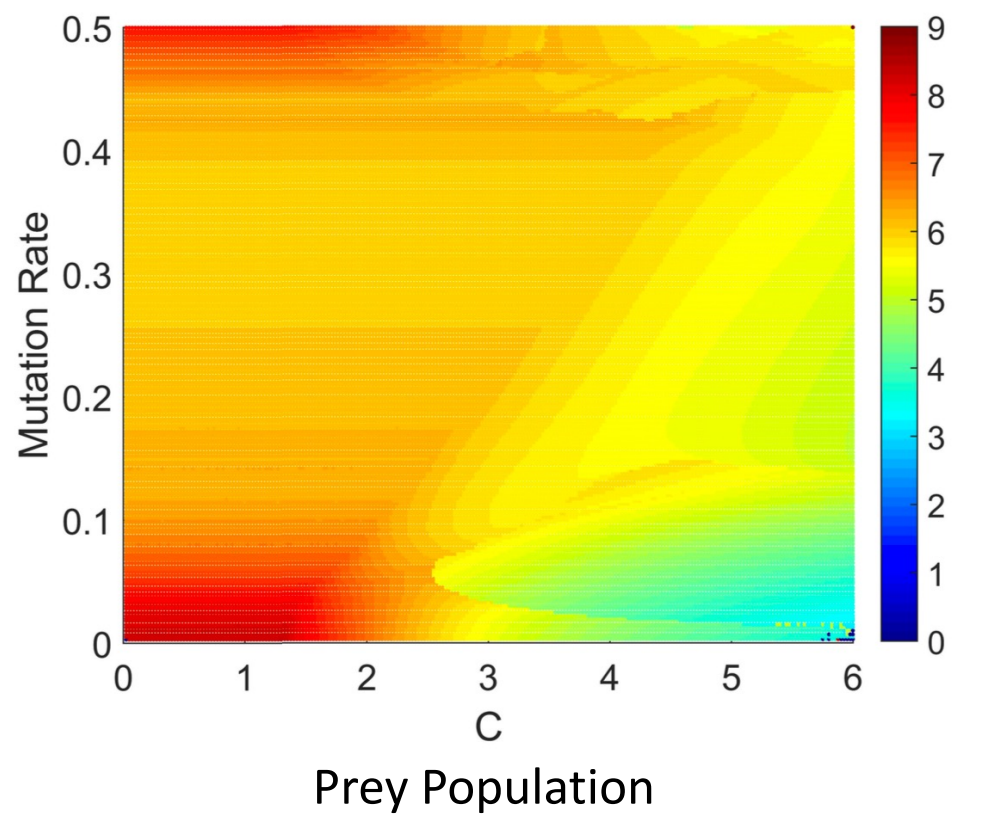
We construct a system of $n = 10$ mutating prey N_t and $m = 10$ mutating predators P_t . Prey vary by reproductive parameter r and predators by the degree to which they focus on the most populous prey phenotype. We vary the mutation rate p , the feeding parameter c and the relative weighting of inter and intraspecific prey competition.

$$\begin{aligned}N_{t+1}^j &= \sum_{l=1}^n p_{l,j} r_l N_t^l (1 - b N_t^{l-1} - a N_t^l - b N_t^{l+1}) (1 - \Phi_t(l)) \\ P_{t+1}^i &= \sum_{l=1}^m p_{l,i} (P_t^l)^2 \sum_{j=1}^n \frac{1}{\phi_t(j)} (f_{t,j}^l)^2 c N_t^j (1 - c f_{t,j}^l P_t^l)\end{aligned}$$

Findings:

- For a single predator phenotype with fixed strategy, adaptive foraging linearly proportional to the prey phenotype population size ($\alpha = 1$) is the optimal strategy.
- When predators can change their strategy, no adaptive foraging is best when the kill rate c is high, and exclusive adaptive foraging may be the best chance of survival when the rate is low.
- Total prey populations increase with a greater degree of interspecific competition
- The system exhibits qualitative changes as the case where intraspecific and interspecific competition are equal in strength is approached.

One Mutating Predator, $a = b = 1/3$



3A. Reproduction of the Webworld Model^[10,11]

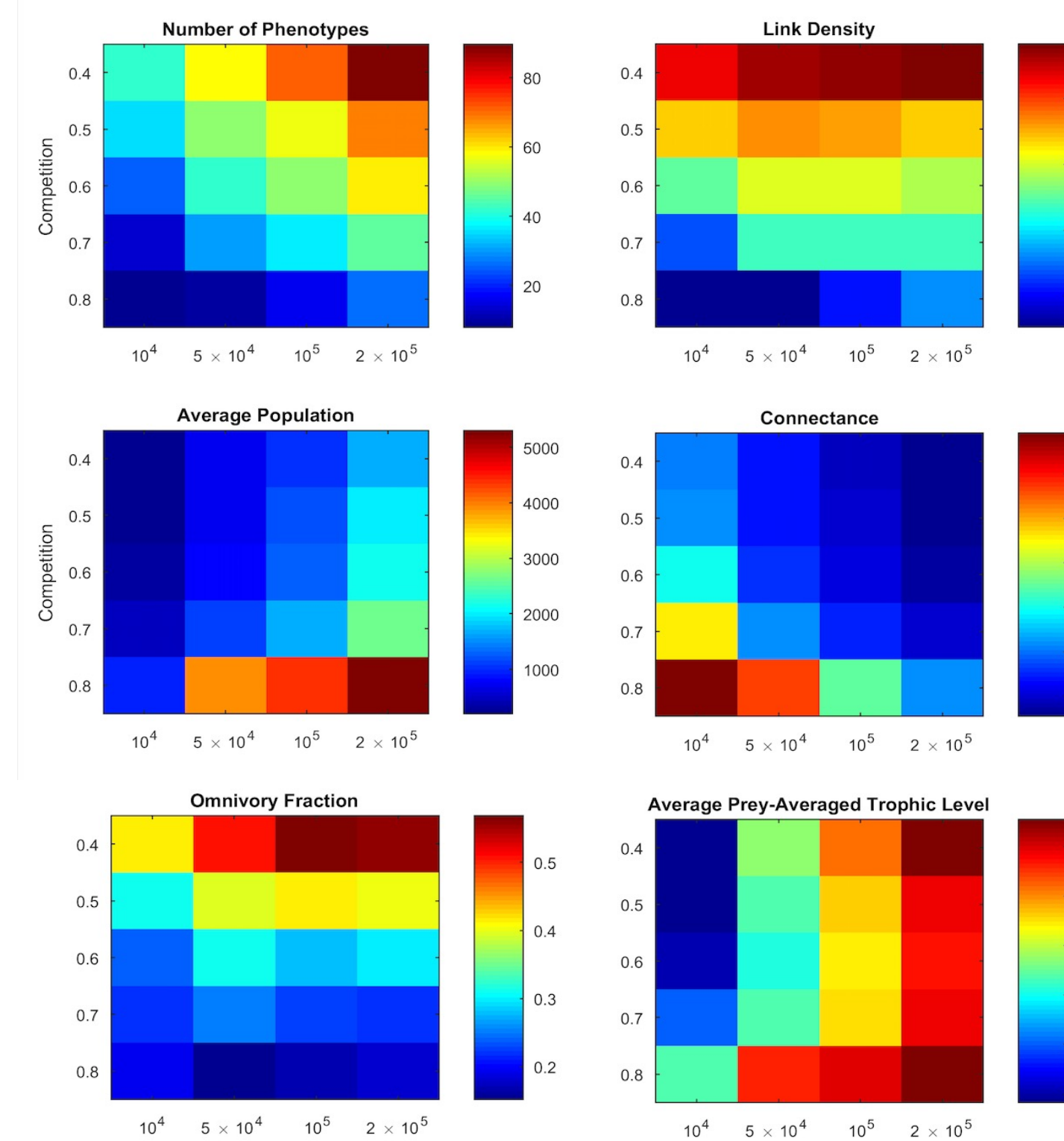
This is an eco-evolutionary model. We start with a resource and one phenotype. Species reproduce according to the balance equations:

$$\frac{dN_i}{dt} = -N_i + \lambda \sum_{j=0}^n N_j g_{i,j}(t) - \sum_{k=1}^n N_k g_{k,i}(t)$$

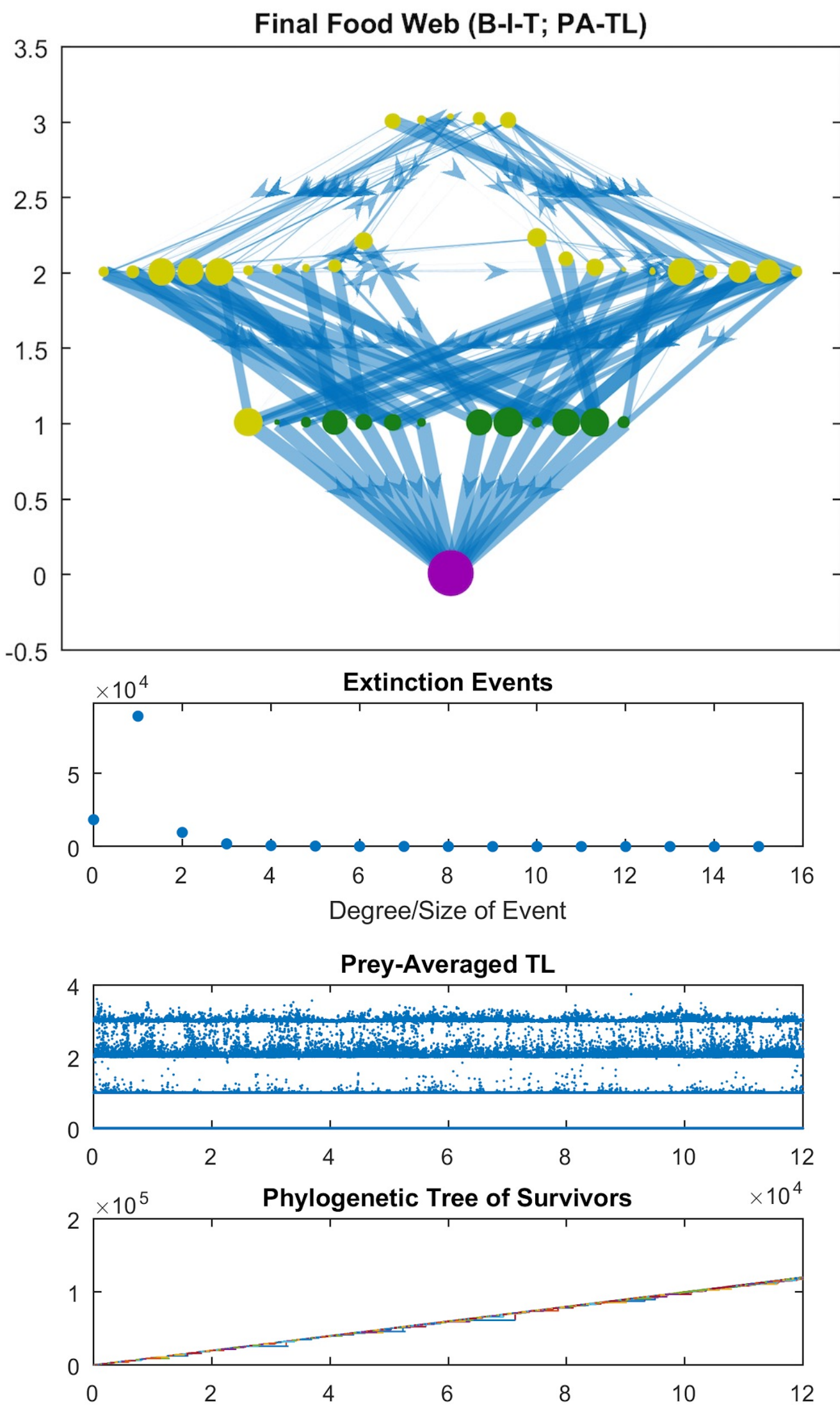
Features:

- Each species is defined by the 10 (out of 500 possible) binary traits that it possesses.
- Uniform mortality and ecological efficiency λ .
- The traits determine the existence and strength of predator-prey interactions between species.
- Ratio-dependent functional response g and adaptive foraging strategy with which it is consistent.
- Speciation mechanism: the mutant child has 9 of its parent's 10 traits, with the other randomly exchanged.

Our reproduction of the average results:

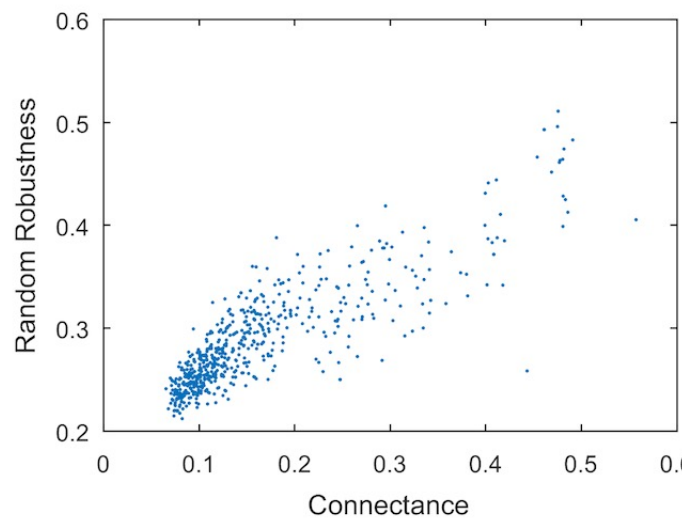


Results from one simulation:



New result:

Average robustness of the taxonomic web to random species deletions positively correlated with connectance (coefficient 0.8548). Coherent with empirical^[12], Niche and Cascade Model^[13] findings.



3B. Reproduction of the Loeuille-Loreau Model^[14]

Start with resource

and one species,

and use the

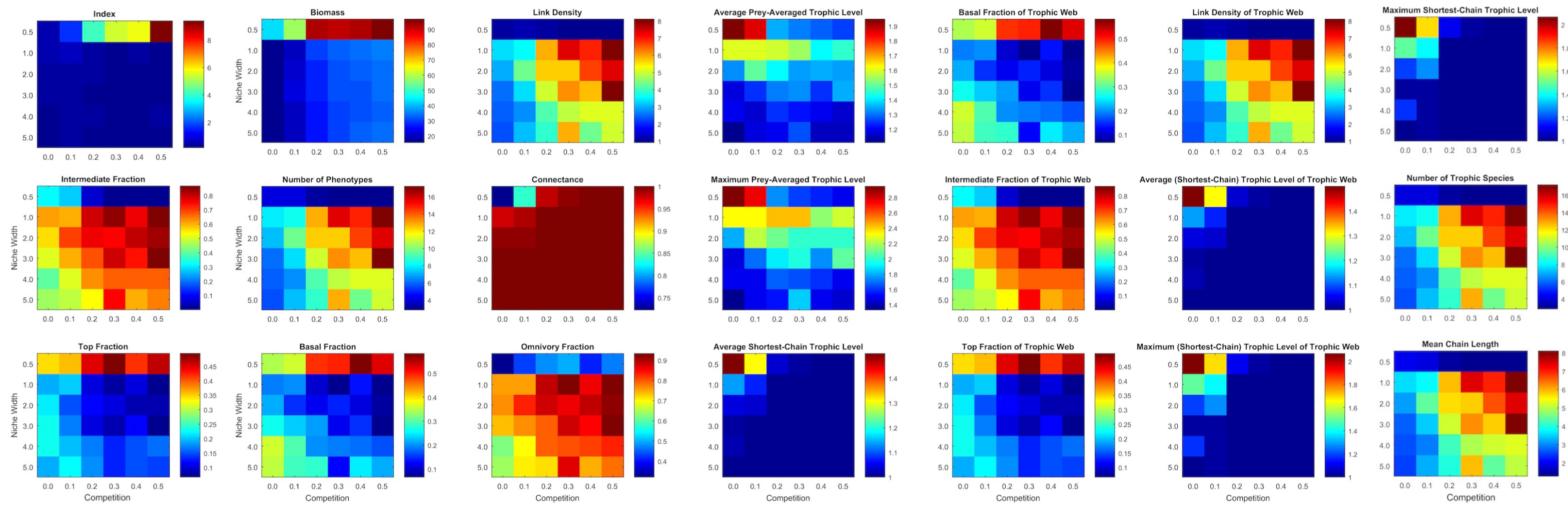
ecological equation:

$$\frac{dN_i}{dt} = N_i \left(-m(x_i) + f(x_i) \sum_{j=0}^{i-1} \gamma(x_i - x_j) N_j - \sum_{k=i+1}^n \gamma(x_k - x_i) N_k - \sum_{l=1}^n \alpha(|x_i - x_l|) N_l \right)$$

Features:

- A single continuous trait, body mass, characterises a species.
- Mass-specific production efficiency f and mortality rate m decrease as body size increases (“allometric scaling”).
- Linear functional response γ centred on prey a set distance ‘below’ the predator on the body-mass spectrum.
- Interference competition α occurs between species of a similar size.
- Speciation mechanism: the mutant child has body size randomly drawn within 20% of that of its parent.

Our reproduction of the results, with Beddington-deAngelis functional response:



Future Research Goals

- Study the response of the Webworld and Loeuille-Loreau models to perturbation (resource variation, species deletion).
- Develop a hybrid eco-evolutionary model:
 - Using the structure of Webworld, with added body size as a single continuous trait, on which mortality and ecological efficiency depend.
- Develop a spatial variant of the Webworld model:
 - 2x1 with uniform resource.
 - 3x1 with non-uniform resource.
 - 2x2 with both spatial and temporal variation in resource.
 - 2x1 with two different immobile resources and initial non-resource species, one pair in each cell.

References

[1] Montoya JM, Woodward G, Emmerson MC, Solé RV. “Press Perturbations and Indirect Effects in Real Food Webs.” *Ecology* 2009; 90(9):2426-2433

[2] Abernethy GM, McCartney M. “Analysis of a Class of Low-Dimensional Models of Mutation and Predation.” *Int. J. Bifurcat Chaos* 2016; 26.11: 1630029.

[3] Abernethy GM, McCartney M. “Cannibalism and chaos in the classroom.” *Int J Math Educ Sci Tech* 2017;48.1:117-129.

[4] Williams RJ, Martinez ND. “Simple Rules Yield Complex Food Webs.” *Nature* 2000;404:180-183.

[5] May R. “Will a Large Complex System be Stable?” *Nature* 1972; 238:413-414.

[6] Mullan R, Glass DH, McCartney M. “Modelling Prey in Discrete Time Predator-Prey Systems.” In: *Systems, Man, and Cybernetics (SMC), 2013 IEEE International Conference on*; 2013. p. 2617–2622.

[7] Mullan R, Glass DH, McCartney M. “Species diversity and predation strategies in a multiple species predator–prey model.” *Commun Nonlinear Sci Numer Simul.* 2015;25(1–3):118 – 135.

[8] Mullan R, Abernethy GM, Glass DH, McCartney M. “A Single Predator Multiple Prey Model with Prey Mutation.” *Commun Nonlinear Sci Numer Simul.* 2016;40:51–70.

[9] Mullan R, Abernethy GM, Glass DH, McCartney M. “A Multiple Phenotype Predator-Prey Model with Mutation.” *Physica A.* 2017;465:762–774.

[10] Caldarelli G, Higgs PG, McKane AJ. “Modelling Coevolution in Multispecies Communities.” *J Theor Biol.* 1998;193(2):345 – 358.

[11] Drossel B, Higgs PG, McKane AJ. “The Influence of Predator-Prey Population Dynamics on the Long-term Evolution of Food Web Structure.” *J Theor Biol.* 2001;208(1):91 – 107.

[12] Dunne JA, Williams RJ, Martinez ND. “Network Structure and Biodiversity Loss: Robustness increases with Connectance.” *Ecol Lett.* 2002;5:558-567.

[13] Dunne JA, Williams RJ, Martinez ND. “Network Structure and Robustness of Marine Food Webs.” *Mar Ecol-Prog Ser.* 2004;273:291-302

[14] Loeuille N, Loreau M. “Evolutionary emergence of size-structured food webs.” *Proc Natl Acad Sci.* 2005;102(16):5761–5766.