

Evolutionary Food Web Modelling

Evolution 2017,
Portland

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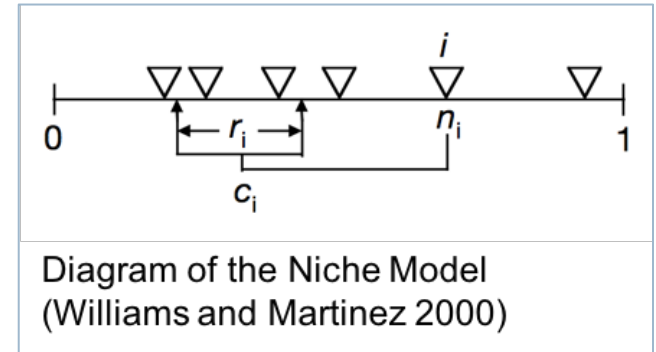
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Food Web Modelling Approaches

▶ Static, Statistical Models:

- ▶ Cascade (Cohen 1985)
- ▶ Niche (Williams and Martinez 2000)
 - ▶ Assigns species a one-dimensional niche (n_i), a feeding midpoint (c_i) beneath its niche value, and a feeding range (r_i).
- ▶ Nested-Hierarchy (Cattin et al 2004)



▶ Community Assembly

- ▶ Includes population dynamics (typically Lotka-Volterra).
- ▶ Species are added to the model over time from a limited, fixed pool of species, with pre-defined trophic position.
- ▶ E.g. Newman et al 1996, Morton and Law 1997, Drake 1990, Law 1999.

▶ Eco-Evolutionary Models

- ▶ Evolutionary Niche Model (Guill and Drossel 2007)
- ▶ Matching model (Rossberg 2006, 2008)
- ▶ Yoshida 2003
- ▶ Ito and Ikegami 2006

Eco-evolutionary Models with one continuous species characteristic: Body-Size

- ▶ Loeuille-Loreau (Loeuille and Loreau 2005):

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

- ▶ A single continuous trait, body mass, characterises a species and imposes a feeding hierarchy.
 - ▶ Mass-specific production efficiency f , mortality rate m , decrease with body size.
 - ▶ 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: the child has body size drawn within 20% of that of its parent.
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- ▶ Allhoff et al 2015
 - ▶ Three separately-evolving traits: body mass, preferred body mass of prey, and feeding range.
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Webworld Model

(Drossel et al 2001)

Start with a resource and one phenotype.

Species reproduce according to the balance equations:

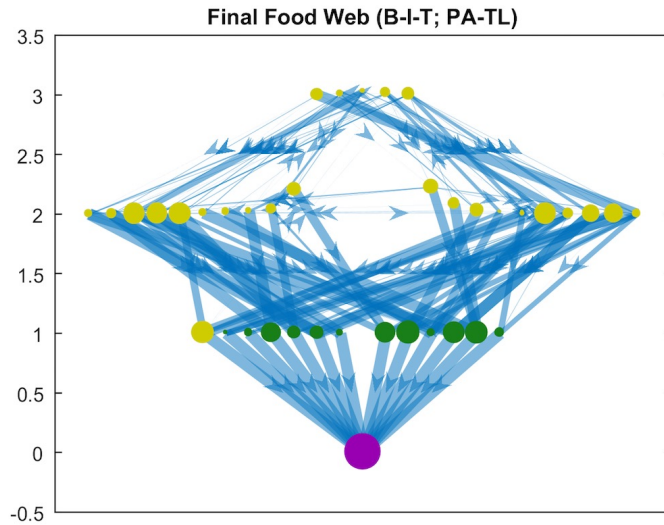
$$\frac{dN_i}{dt} = -N_i + \lambda \sum_{j=0}^n N_i g_{i,j}(t) - \sum_{k=1}^n N_k g_{k,i}(t)$$

► Features:

- Each species is defined by the 10 (out of 500 possible) binary traits that it possesses.
- Uniform mortality and ecological efficiency λ .
- Their binary trait strings 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 retains 9 of its parent's 10 traits, with the other randomly exchanged.

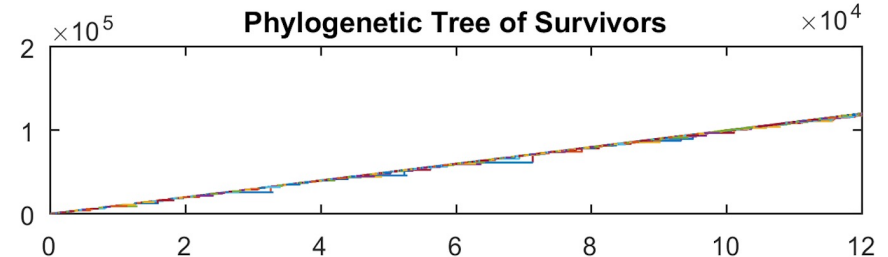
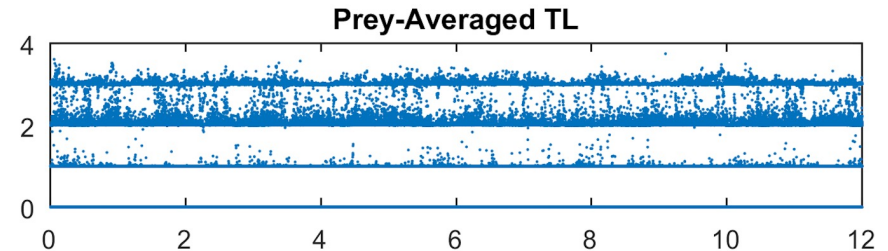
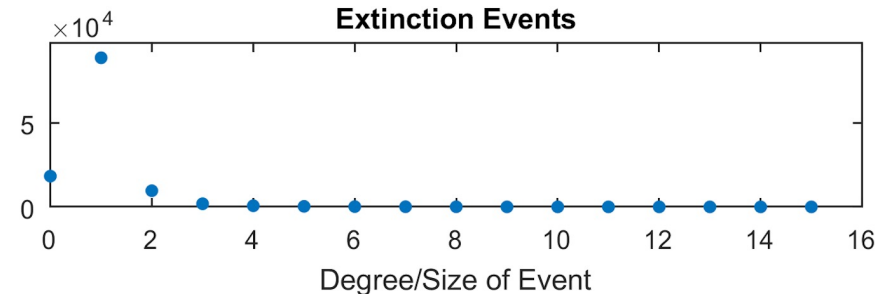


Webworld Model: Reproduction of original results



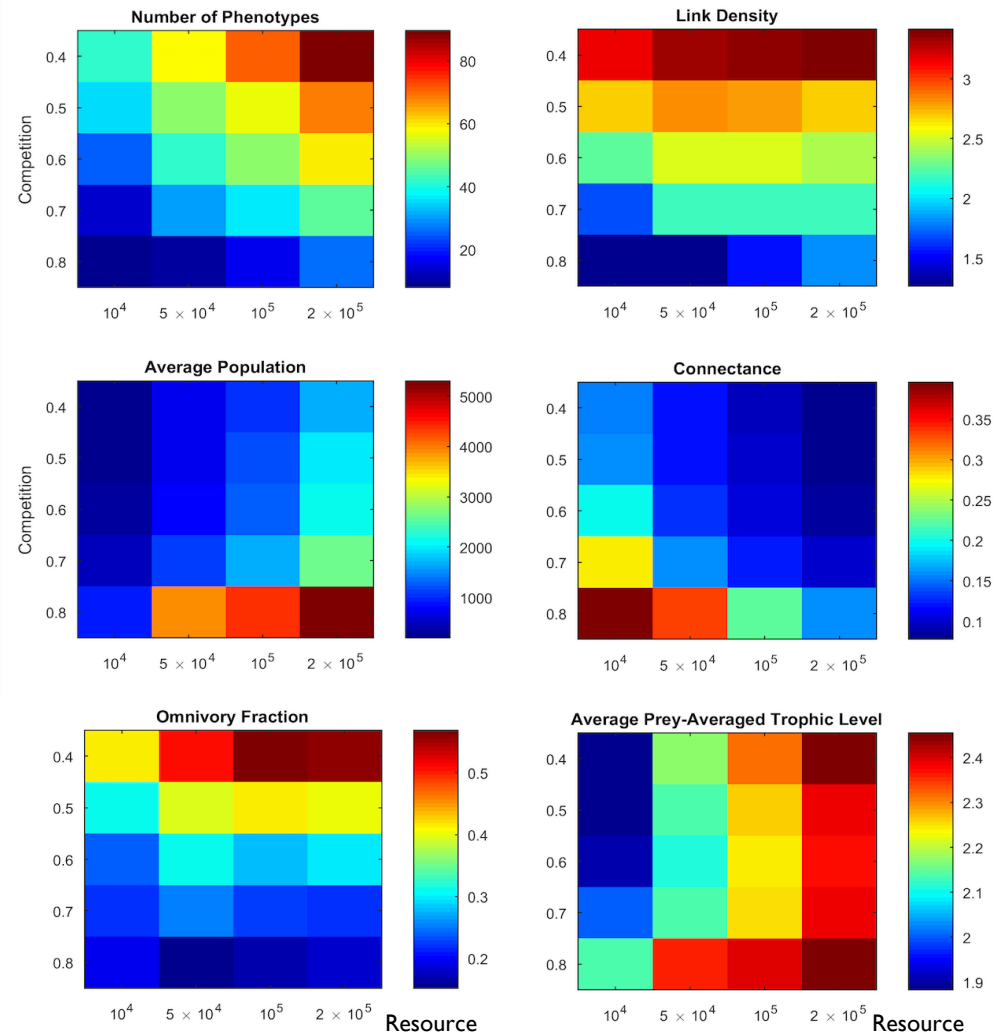
► Per-simulation data:

- Phylogenetic tree of survivors shows turnover.
- Frequency of extinction events.
- Degree distribution.
- All prey-averaged trophic levels occupied over time.
- Variation of B-I-T ratios, L/S, C, trophic levels, and omnivory.



Webworld Model: Reproduction of original results

- ▶ We collect data averaged over the last 10,000 evolutionary iterations of 30 simulations for:
 - ▶ 4 values of resource input size.
 - ▶ 5 values of competition strength.
 - ▶ Both Taxonomic and Trophic webs.
- ▶ 42 properties in total, with standard deviations.

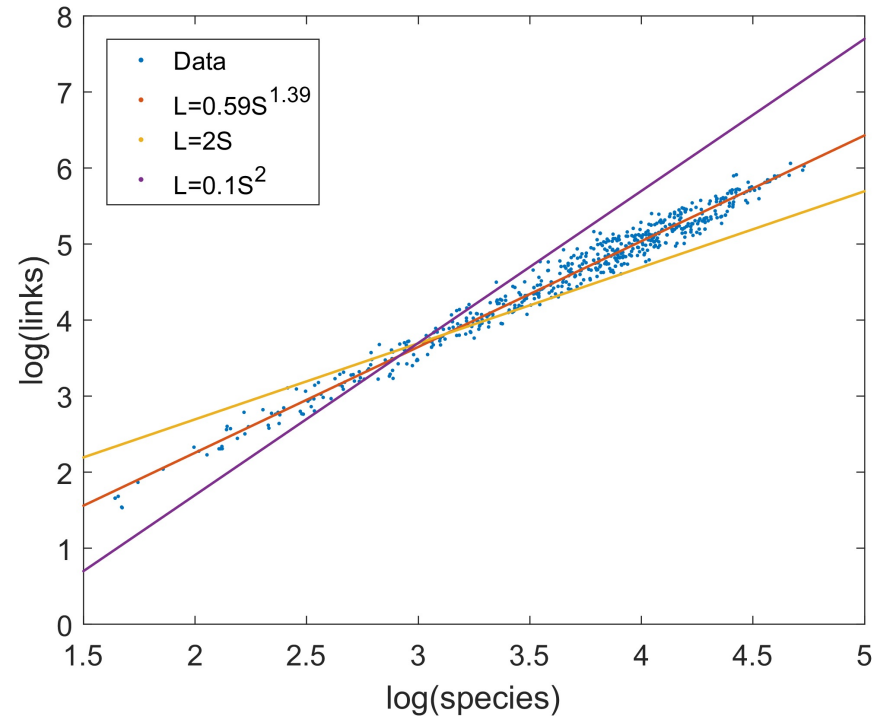


Webworld Model: The Link-Species Relationship

- ▶ Consider the link-species relationship $L \sim S^m$
- ▶ Data over all 600 simulations supports neither the constant connectance hypothesis, nor the link-species scaling law. Excluding small networks ($S < 20$) does *not* improve the fit, supporting exponent $m = 1.37$.
- ▶ Matlab's linear fit functions return a best fit of the form:

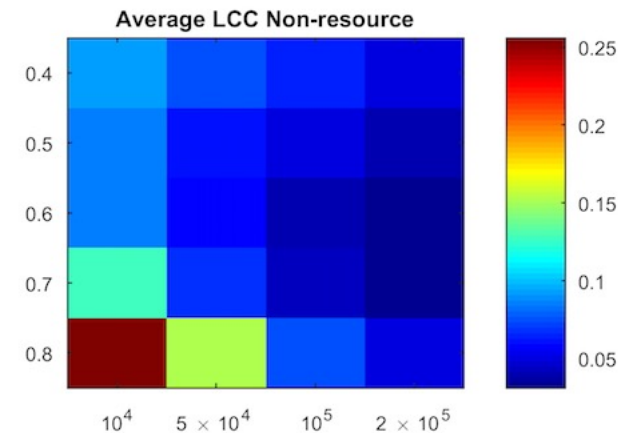
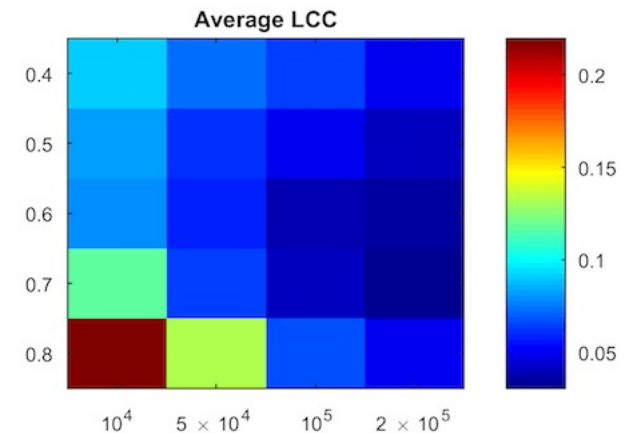
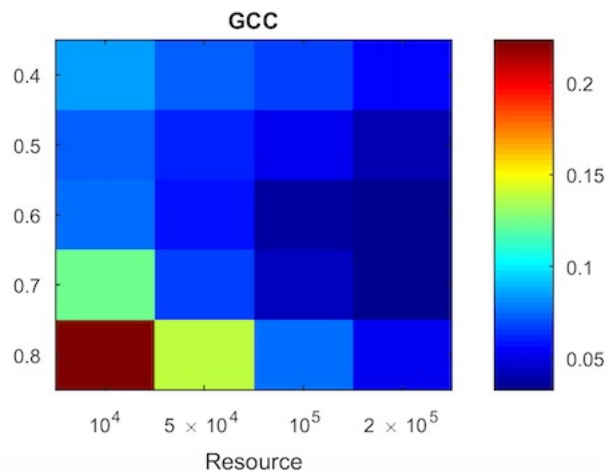
$$L = 0.59S^{1.39}$$

- ▶ Exponent $m = 1.39$ with $R^2 = 0.978$.
- ▶ Coherent with empirical data exponent $m = 1.5$ (Dunne 2006).



Webworld Model – New Results: Clustering Coefficients

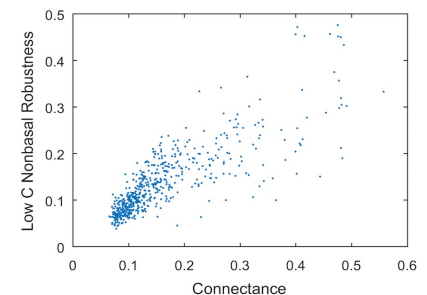
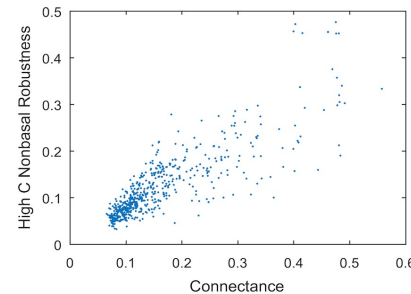
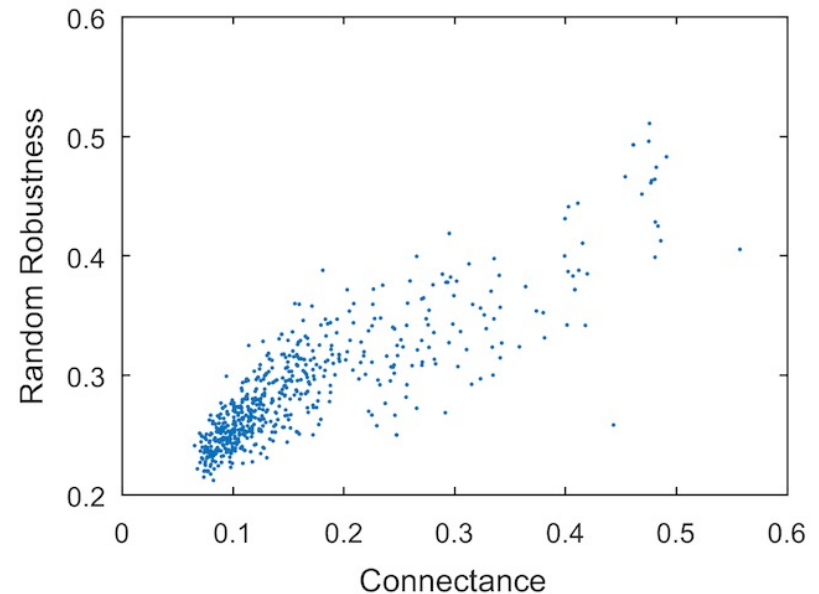
- ▶ **Local Clustering Coefficient:** average (per node) probability that two neighbours of the node are also connected directly.
- ▶ **Global Clustering Coefficient:** probability that paths of length 2 are closed.
- ▶ For both, we find an average ~ 0.07 for large webs.



Webworld Model – New Results:

Correlation of Connectance and Robustness

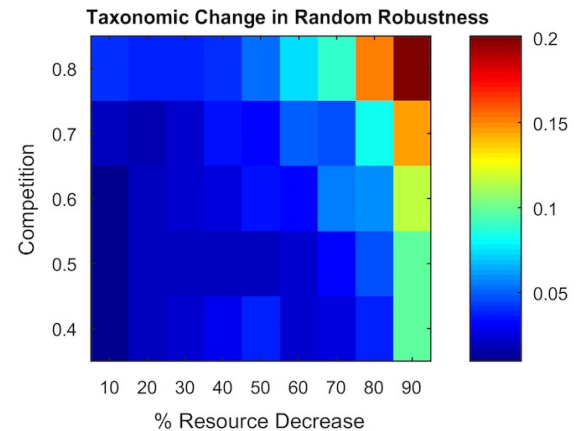
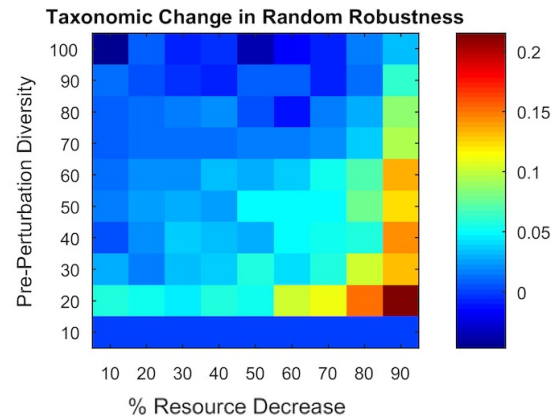
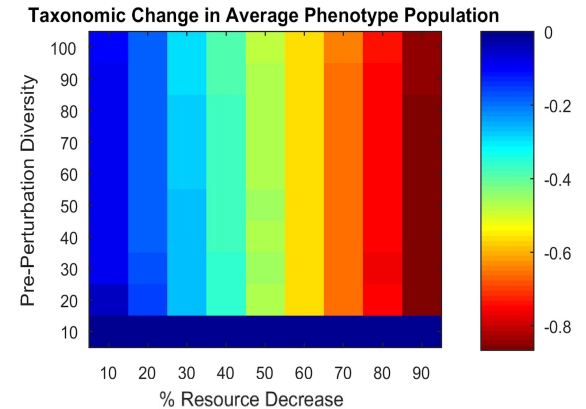
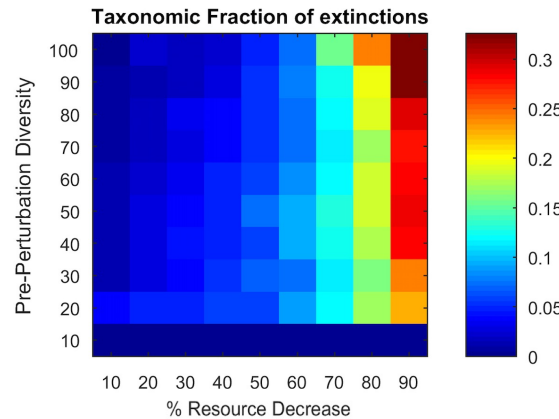
- ▶ **Robustness** to species deletion in random, most-, least-connected order.
- ▶ Robustness of taxonomic web to random species deletions positively correlated with *connectance*.
 - ▶ Coefficient 0.855.
- ▶ Coherent with findings from empirical data (Dunne et al 2002, Dunne et al 2004), and the Cascade, Generalised Cascade, Niche and Nested-Hierarchy Models (Dunne and Williams, 2009).
- ▶ Robustness to deletions in order of most- or least-connected do not have a strong correlation. However, the correlation becomes strong (0.799 and 0.819 res.) if basal species excluded.



Webworld Model – New Results:

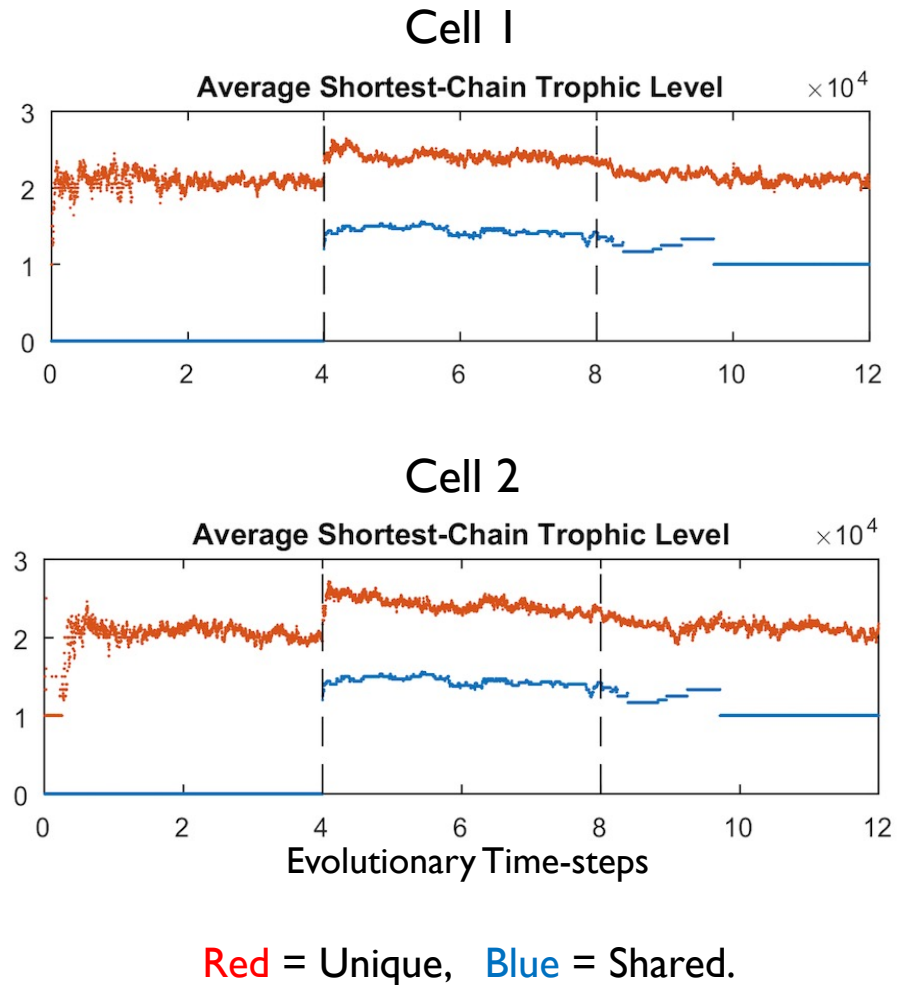
Response to Perturbation of the Resource

- ▶ We allow the web to develop for 100,000 time steps, before dropping the amount/biomass of the resource.
 - ▶ Average populations decrease with the resource.
 - ▶ The number of species extinctions is correlated with high species numbers and low competition (low c networks had higher species counts prior to perturbation).
 - ▶ Robustness increases – perhaps as ‘loose’ species are dislodged.
 - ▶ The fewer species (higher c) and greater the perturbation, the larger the robustness increase.



Webworld Model – New Results: Metacommunity Variant

- ▶ Consider a spatial variant with two cells and diffusion migration following feeding between evolutionary timesteps 40,000 and 80,000:
 - ▶ No obvious effect on S , L/S , C , Robustness, or trophic levels averaged over all species in each cell.
- ▶ Then average properties separately over *shared* and *unique* (to that cell) species:
 - ▶ Shared species occupy lower trophic levels than unique species, due to larger populations facilitating diffusion migration.



Acknowledgements

- ▶ Supervisors: Dr Mark McCartney, Dr David Glass
 - ▶ School of Computing and Mathematics; Artificial Intelligence Research Group; Centre for Computer Science; Faculty of Computing, Engineering, and the Built Environment.
 - ▶ Ulster University
- ▶ PhD funding by Department of Employment and Learning (DEL), Northern Ireland, UK

Future work

- ▶ Spatial version of the Webworld model
 - ▶ 3x1 with spatial and temporal resource variation.
 - ▶ 2x1 with a different *resource* and initial species in each cell.
 - ▶ Create a hybrid model by adding a loose feeding hierarchy, variable mortality and feeding efficiency determined by a body-size trait as in Loeuille-Loreau.
 - ▶ Migration rate determined by body size.



References

- ▶ **Historical review of Food Web Modelling:**
 - ▶ Brannstrom et al, “Modelling the ecology and evolution of communities: a review of past achievements, current efforts, and future promises.” *Evolutionary Ecology Research*, 2012.
 - ▶ Dunne and Pascual (Editors) “Ecological Networks: Linking Structure to Dynamics in Food Webs.” OUP, 2006

- ▶ **Webworld Model**
 - ▶ Drossel et al, “The influence of predator-prey population dynamics on the long-term evolution of food web structure.” *Journal of Theoretical Biology*, 2001.

- ▶ **Loeuille-Loreau Model**
 - ▶ Loeuille and Loreau, “Evolutionary emergence of size-structured food webs.” *PNAS*, 2005.

- ▶ **State of the art in spatial evolutionary food web modelling:**
 - ▶ Bolchoun et al, “Spatial topologies affect local food web structure and diversity in evolutionary metacommunities.” *Scientific Reports*, 2017.

