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The Robustness, Link-species Relationship and Network Properties of Model Food Webs

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Abstract

New results are collected using the Webworld model which simulates evolutionary food web construction with population dynamics [1]. We show that it supports a link-species relationship of neither constant link-density nor constant connectance, and new properties for the food webs are calculated including clustering coefficients and stability in the sense of community robustness to species deletion. Time-series for more than 40 properties of the taxonomic and trophic webs are determined over the course of individual simulations. Robustness is found to be positively correlated with connectance, but negatively with diversity, and we study the long-term development of model webs including the distribution of extinction events in a simulation with 10^8 speciation events.

1. Introduction

Predicting the impact of challenges such as climate change on the earth's ecosystems requires models that can simulate the ecological and evolutionary responses to perturbations of complex ecological networks. Simulated ecosystems should possess realistic network structure that not only could exist, but could have been reached by evolution from a first species. Eco-evolutionary models accomplish this by periodically adding species through stochastic mutation events which are then subject to predator-prey dynamics. The researcher specifies the evolutionary and ecological rules of the system, and then allows it to select the number, type and relationships of the surviving species as emergent properties.

Previous efforts at ecological modelling took several approaches. Classic population dynamics based on the work of Lotka and Volterra [2] performed detailed mathematical studies of small systems of two or three species with fixed functional responses and predatory relationships. Static models such as the Cascade Model [3] and the Niche Model [4] used statistical rules to try to approximate the network properties of empirical food webs. Community Assembly models [5, 6, 7, 8, 9] incorporated population dynamics with larger species networks by modelling periodic invasions of species with predetermined trophic properties. In recent years, advancements in computing power have enabled efforts to be made to combine the strengths of all of these methodologies. Eco-evolutionary models include complicated population dynamics on large-scale networks, and allow ecological and evolutionary processes to feedback to each other, so that the model's rules dynamically determine which species flourish and what trophic level they currently occupy in the present network.

Some eco-evolutionary models include that of Loeuille and Loreau [10] which features a single continuous body-size trait to distinguish species and determine predatory and competitive interactions. A related, improved model with three evolving traits (body size, feeding range, and feeding window) was developed by Drossel and Allhoff [11], and extended to a spatially-explicit variant [12]. Guill and Drossel [13] studied an evolutionary version of the static Niche Model, with added population dynamics. Bastolla and Lässig's model [14, 15] arranges species into a hierarchy with each group able to consume members of the one below, and new species are obtained by randomly altering the interaction coefficients between species. Rossberg's Matching Model [16, 17] assigns each species traits from two spaces: a space of hunting traits, and a space of vulnerability traits. A species is able to predate upon another if its hunting traits correspond to the prey's vulnerability traits. A model proposed by Ito and Ikegami in 2006 [18, 19] employs a two-dimensional phenotype space, with the two continuous traits describing a species' role as a predator and as a prey. The simulation begins with a single concentration of biomass at one point in the space (in other words, a single initial species) and mutation is then modelled by continuous diffusion across this trait space, demonstrating evolutionary branching as the cluster breaks apart into multiple separated groups.

All of the models discussed so far have focused entirely upon one type of ecological interaction: the trophic interaction between one predator and one prey species, the former benefitting from the interaction and the latter suffering. However, some

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models [20, 21] have taken into account mutualistic relationships where both parties benefit from the existence of the other.

The Webworld model was originally proposed in 1998 [22] and then further refined with a more sophisticated ratio-dependent functional response, amongst other improvements, in what is now the canonical 2001 version [1]. In this approach, species are each assigned a number of integers, which represents the presence of an abstract morphological or behavioural trait, the combination of which determines that species' relationship with every other species. In particular, each trait is randomly assigned a score against every other one, and the direction and strength of a predatory link between two species is calculated from the sum of their traits' scores. A bioenergetic resource model of population dynamics, in the form of balance equations, is superimposed on this food web structure. This form of dynamics, based on the influential work of Yodzis and Innes [23], has become a popular paradigm, with researchers implementing it on a variety of other food web models (e.g. [24, 13, 25, 26, 27]). The system is iterated repeatedly using the Euler method to calculate the resulting population densities. After a steady state is reached or a sufficiently large number of iterations have passed, one "evolutionary time-step" is deemed to have occurred and a surviving species is selected to undergo speciation. In this process, a child species is created that inherits all but one of its parent's traits, and the population dynamics then decide if the mutant child perishes or if it successfully invades and establishes itself as a viable member of the ecosystem. A food web is generated from one initial species through a series of these events.

In this article, we use the Webworld model to verify results of ecological interest, and give attention to aspects of the networks generated by the model which have not yet been studied. We investigate the stability of the networks in the form of community robustness (and how this correlates with other food web properties), the relationship between the number of links and the number of species which has been of interest to theoretical ecologists for several decades, and we consider the behaviour of the model over very long timeframes as well as its response to perturbation of the resource. In the following section, we summarise the body of work that has been previously conducted using this model.

1.1. History of the Webworld model

The original paper [22] presented a version with a simple functional response. The authors studied the properties of the web with different parameter sets, the distribution of species across trophic levels, and the growth of the web over time. In this version, the webs eventually converge to a stable configuration that cannot be further invaded by any phenotypically-similar species. This property is not present in the updated 2001 model [1], where the changes to the functional response reduces predation on new species with low populations, increasing the possibility that they can successfully invade. This results in a continual change in the exact arrangement of species in the ecosystem. However, simulations which were restricted to only permit basal species are still found to become uninvadable. They then tested the effect of the competition and resource parameters on the size and other properties of the web, and the size distribution of extinction events which they find supports an exponential decay rather than a power law - making large extinction events very improbable.

The significance of this change in the functional response was further investigated in 2004 [28]. This study tested various other types of functional response, including Lotka-Volterra, Holling, and Beddington-deAngelis. The results showed that an essential feature for the construction and persistence of large, complex webs is the ability of predators to focus their efforts on their most efficient prey. This verifies the central reason for developing eco-evolutionary models in the first place - namely that the population dynamics has an important effect on the long-term evolutionary network dynamics (and vice-versa, although this is more obvious).

An in-depth study of the response of the networks to perturbation by conducting tests using Species Deletion Stability (artificially forcing the deletion of a species) was conducted [29]. Competitors are less likely to go extinct as a result of the deletion than an average species, prey are somewhat more likely, and predators are much more likely - with the probability of extinction increasing with the fraction of their diet devoted to the deleted species. They also considered how the trophic position of the deleted species affects the impact of its deletion, and in particular the likelihood of secondary extinctions on each trophic level. They found that deletions are most to least impactful in the order 1-4-2-3 by trophic level, and show a transition from bottom-up to weaker top-down effects as one goes up the web: deleting low-level and, in particular, basal species is very likely to cause secondary extinctions of their specialised predators, while deleting very high-level species (which are more generalist predators) can cause extinction of prey. This is due to "predator-mediated coexistence", where the pressure from a predator allows a poorly adapted prey to coexist alongside a better one. If the predator is removed, the more efficient prey species can then force the extinction of its less-effective competitor. Furthermore, deleting more-connected species results in more secondary extinctions. Redundancy (the fraction of species who possess the same set of prey and predators as another species) and link density are positively correlated with species deletion stability of the whole web, while omnivory and diversity are negatively correlated with it, so no statement on the general impact of "complexity" on stability can be made.

Quince et al [30] studied the mechanism and effects of speciation events in detail. 89% of invasions result in the mutant child going extinct immediately and no other change in the network. Parents, other competitors, and prey of the mutant child are more likely than average to go extinct as a result of the invasion, while predators of the mutant are less likely. Since non-parental competitors are more likely to go extinct than a random species, competition is a significant factor in facilitating

successful invasions. Because of this, and the similar trophic roles between parents and children, children of species on trophic levels 2 or 3 are more likely to successfully invade than those on trophic levels 1, or on 4 though this is more likely due to the lack of available prey.

Next there is a very in-depth study of how varying the parameter values impacts the structure of the constructed food webs [31]. This research highlights the relationship between the population dynamics (to which the parameters pertain) and the network structure. They find that for most species trophic height (referred to in this paper as prey-averaged trophic level or PATL) and trophic level (shortest-chain trophic level or SCTL) are very similar, that both the competition and predator saturation parameters have critical thresholds beyond which diversity is kept very small, and that diversity and average trophic levels increase with the amount of resource. They further develop the specialist-to-generalist principle of the food webs that other papers have discussed. Rising up the food chain, the species transition from specialised (higher scores and well-adapted to exploit a small number of species) to more generalised predation that is instead limited by available prey populations. Increasing the amount of resource pushes this effect further up the chain so that on each trophic level prey numbers decrease and predator numbers increase with the resource. Furthermore, linear stability analysis of the populations at equilibrium confirm that at lower trophic levels, predators and competition control the population sizes, while at higher trophic levels the effects of prey on predator populations becomes stronger whilst that of predators on prey weakens. This paper also studies the distribution of link strengths, finding that the model supports the popular hypothesis that complex food webs possess many weak links, whether by considering the efforts or diets of the species (most of which are close to either 0 or 1), or by considering the direct effect of each species' population on each other at equilibrium. They find that this latter measure also skews towards weak interactions, and shows some mutualistic relationships between prey and predators. However, it is noted that the Webworld model typically has lower link density than the most reliable empirical food webs, although this property could vary depending on how and what strength of links are counted.

A study by Lugo and McKane [32] focused on the nature of species definition in the model, considering the effect of changing how species are defined in a number of ways: firstly by occasionally adding additional traits rather than always replacing them at mutation (this produces complex webs provided complexification is less likely than mutation, although there is the possibility of a dominant species that increases in complexity and prevents significantly different species from invading). Second, they remove the explicit use of traits and instead use a dichotomous form of competition (unifying all interspecific competition) and then assign feeding scores against other species which are subject to random mutation. This also produces similar webs to the standard model, although they grow faster and stabilise with lower species numbers and lower maximum trophic levels. However, the main result here is that the model can be successfully simplified in this manner, which would facilitate comparison to other evolving food web models that use interaction scores instead of explicit traits [20, 21].

A second study by the same authors [33] varies the values of the properties which define species and how this definition determines the feeding relationships: the number of traits per species and in the trait space, the stochastic distribution from which the trait scores are chosen (including Gaussian, discrete, and uniform distributions), initial species populations, and population thresholds. Most of the possible changes do not prevent the model from successfully constructing realitic food webs, although if the number of traits that define a species is greatly increased, the transient stage of web development is longer as diversification requires more mutations, since a smaller fraction of the features of a species are substituted at each speciation event.

Finally the Webworld model has been described in several other publications [34, 35, 36] including a general summary of the model by McKane [37], where he also provides a comparison to other models and an overview of the recent history and context of food web research. Of particular interest in this article is the size and structure of the web as a function of resource input.

2. Description of the Model

We describe the model here in detail. For full justification of each step, refer to the original paper by Drossel et al [1].

2.1. Model Initialisation

1) Draw trait scores for a 500x500 array. The default is an antisymmetric array, β, with zeros on the diagonal and all other scores drawn from a Gaussian distribution with mean 0 and variance equal to 1, however for one comparative experiment in Section 8 we will employ a different form for the trait score matrix.

2) Draw ten distinct traits for the resource, and a further ten to define the initial non-resource species. If the first species is unable to feed on the resource, we discard it and draw a new set of traits.

3) The resource begins with a population equal to its parameter R/λ, where R is a parameter of the simulation and usually on the order of 10^4 or 10^5, and λ is the ecological efficiency (that is, the fraction of the biomass of a slain individual that is successfully converted to biomass of the consumer) and is taken to be 0.1 in accordance with empirical estimates [38]. The first species begins with population (equivalently, biomass, as all species are assumed to have density equal to unity) equal to 1.0, which is the minimum permitted population size. If a non-resource species falls beneath this threshold during any point in the

ecological dynamics, it is considered extinct.
4) Enter the evolutionary timestep loop. This usually consists of 120,000 evolutionary timesteps.

2.2. Iteration of the model

Each evolutionary timestep consists of iterating the ecological loop, described below, until either a maximum of 100,000 ecological timesteps are carried out or for each species a steady state (fixed point or cycle up to period 10) is detected with tolerance equal to 1.0 (i.e the population changes by no more than 1.0 between ecological timesteps). Then, a speciation event occurs. This involves selecting a species with probability proportional to its population or biomass, so that in disconnected spatial scenarios (which we shall examine in a subsequent paper that is currently in preparation) we can prevent a situation whereby one cell's species diversity grows increasingly while the other is left with a small number of species who are consistently not chosen as a parent. Then we introduce a child species with population 1.0, and the parent population is reduced by 1.0. The child species retains 9 of the parents' 10 traits, with one randomly selected and exchanged. We ensure that the new trait is not a repeat of one of the species' existing traits, however if the new trait set matches another species then we allow that and 1.0 population simply migrates between the two existing species.

An ecological timestep consists of the following:
1) Alternately iterate the "foraging timestep" between the following two forms, until either a fixed point is reached with tolerance 0.1 or a maximum of 100,000 foraging timesteps have expired.
    a) For each predator i, distribute the foraging efforts (if it is the first timestep, they are distributed equally amongst possible prey), according to the equation $f_{i,j} = g_{i,j}/\sum_{k \in Prey} g_{i,k}$.
    b) For each predator i, update their ratio-dependent functional responses g according to the equation:

$$g_{i,j} = \frac{S_{i,j} f_{i,j} N_j}{b N_j + \sum_{k \in P_j} \alpha_{i,k} S_{k,j} f_{k,j} N_k}, \tag{1}$$

where:
b is a saturation parameter, which effectively scales all feeding scores in the simulation. It is set at 0.005.
$S_{i,j}$ is the non-negative trait score of i against j, calculated by averaging the scores of i's traits against j's traits, and so $S_{i,j} = \frac{1}{10} \sum_{m=1}^{10} \sum_{n=1}^{10} \beta_{u_m, v_n}$, where u_m is the mth trait of species i and v_n is the nth trait of species j.
P_j is the set of species who are predators of j.
$\alpha_{i,k}$ is the symmetric competition strength of i against k. This is calculated using the equation $\alpha_{i,k} = c + (1 - c)q_{i,k}$, where c is our competition parameter describing how the strength of interspecific competition tails off between biologically-distinct species, and $q_{i,k}$ is the fraction of traits shared between species i and k.
2) Update the populations of the non-resource species, using the Euler method with step size 0.2, according to the balance equation:

$$\frac{dN_i}{dt} = -N_i + \lambda \sum_{j=0}^{n} N_i g_{i,j}(t) - \sum_{k=1}^{n} N_k g_{k,i}(t), \tag{2}$$

where the terms represent species i's natural death rate in the absence of predators, biomass gain due to predation and biomass loss due to being predated upon. Note that this model therefore assumes that natural mortality and metabolic efficiency are uniform across all species and trophic positions. The resource is considered to be species 0, so an autotrophic species i that gains energy from the resource will have $g_{i,0} > 0$.
3) Return the resource population to R/λ.

In the experiments described in this paper, the parameter b is not varied, whilst we will often examine the impact of the resource size, and the competition parameter c. As we shall see later, particularly in the section on perturbation effects, the main effect of c is to determine the system's willingness to tolerate low-population species in addition to better-established ones. If c is high, species with low populations will be excluded by the presence of high-population species.

3. Technical details and properties measured

3.1. Changes made to the original model

We make a number of changes and clarifications to the technical construction of the model. Rather than counting a feeding link if the functional response $g_{i,j}$ is greater than 1, we count it if the fraction of feeding effort $f_{i,j}$ is greater than $f_{min} = 10^{-6}$. Making this change ensures that species that make a low impact on others are permitted to remain as long as they can sustain themselves. This is more in line with the perspective of a field ecologist observing the contributions to diets, and assumes that a predator will focus on it's main prey, whilst discounting potential prey that would contribute a trivial amount to the predator's diet even if it would have a strong impact on the prey's population. If a species is ever unable to feed (no efforts greater than f_{min}), it is instantly removed from the system. This is necessary to ensure that the $B - I - T$ classification system for lifespans

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works correctly. If there are no links of sufficient strength in the entire network, or if no non-resource species remain, the simulation is immediately terminated. We also specify a maximum of 100,000 iterations in both the foraging and the ecological loops.

Finally, we implement a change to the parental selection algorithm in order to facilitate easy comparison with the spatial extension to the model that we shall undertake in future work. Instead of being chosen randomly, species are probabilistically selected to be the parent of the next mutation in proportion to their population or biomass as a fraction of the cumulative biomass of all non-resource species present. Implementing this change in the model results in reduced species diversity, as was noted in the original paper [1], because of the above-average difficulty of invading on the first trophic level where populations are greatest.

3.2. Data collection

For each simulation of the model, which we perform using the Fortran 90 programming language and analyse using MATLAB, we collect many food web properties in two ways. To produce time-series for a single simulation, most values are recorded every 20 timesteps (every "output step"). The exceptions are measures of stability (robustness and species deletion stability), as they are much more computationally expensive. Therefore they are calculated only every 500 evolutionary timesteps. Note that, as we shall see later when we perform some simulations where this data is recorded and output *every* timestep and we see that substantial variation in properties can occur within one or two timesteps, this introduces a problem inherent to field sampling of empirical data that some observations could be dependent on sampling frequency.

Many food web properties are often calculated using "trophic webs" in order to avoid false patterns created by inconsistencies in empirical data collection for different kinds of taxa (See the section of Dunne's review [40] on Species Aggregation for more information). In these, any pairs of taxonomic species with exactly the same set of predator and prey relationships are reduced to a single "trophic species". At each output step, we construct the trophic network in order to record its properties. To do this, a binary array of feeding links is created from the array of feeding efforts f, only counting those with $f > f_{min}$. However, it does not take into account the degree to which they are realised, and we note that some properties of the web can be sensitive to this threshold for counting feeding links [41]. Next, we delete any additional species with identical link structure to another. Population sizes and dynamics are not considered for trophic webs.

For both taxonomic and trophic webs we collect the following properties:

- Diversity, S, or the number of species in the food web including the resource.

- Fraction of Basal (only feed upon the resource), Top (no predators, but also *not* basal), and Intermediate (all other) non-resource species.

- The Link Density (L/S) and Connectance ($2L/S(S-1)$) of the network. Links L are only counted in the taxonomic web if the feeding effort is greater than f_{min}.

- The maximum and average shortest-chain trophic level (SCTL).

- The fraction of omnivorous species, who feed with $f > f_{min}$ on at least two species with different shortest-chain trophic levels.

- "Local Clustering Coefficient", which is the probability that two neighbours of a node (species) are directly connected (one of the species feeds upon the other), averaged over all species, and also averaged over all non-resource species.

- "Global Clustering Coefficient", which is the probability that a two-path in the food web is closed.

- Five variants of Robustness, which is a measure of community stability. To calculate this, we manually delete species one at a time, iterating the ecological loop in between, until the total number of extinctions (both primary and secondary) is at least half of the non-resource species. The fraction of non-resource species that had to be manually deleted is then the Robustness.
  - Random - delete species in a randomly-selected order. This process of randomly choosing deletion sequences is performed 100 times, and the mean robustness value is obtained.
  - High-C - delete species in order of most-to-least connected (at that moment, rather than how connected they were at the beginning). Where there are multiple options, choose randomly.
  - Low-C - as above, except that we delete species in order of least-to-most connected.
  - High-C Non-basal - delete species in order of most-to-least connected, excluding Basal species. If this is not possible due to only basal species remaining at a point before 50% total extinctions have occurred, do not return an answer. Where there are multiple options, choose randomly.

For taxonomic webs only we collect the following properties:

- Species deletion stability: the fraction of non-resource species that can be deleted without any further extinctions resulting when the population dynamics are subsequently iterated.

- The average number of secondary extinctions that occur when a single species is deleted. (Averaged over all species deletion tests, including those that result in zero secondary extinctions.)

- The average population (equivalently, biomass) of each non-resource species in the web.

- Snapshots of the web at various points during the simulation.

- The average and cumulative population throughout the simulation subdivided by Basal-Intermediate-Top classificiation, and by shortest-chain trophic level.

- The number of extinctions between subsequent evolutionary timesteps, used to construct the frequency distribution of extinction events of different sizes.

- The average fraction of traits which overlap between pairs of distinct species in the first, second and third (shortest-chain) trophic levels, assuming species exist at these levels.

- The maximum and average prey-averaged trophic level (PATL), also called Trophic Height or flow-based trophic level in the literature, this is calculated recursively by averaging over the prey-averaged trophic levels of a species' prey, weighted according to the fraction of effort that the species devotes to feeding on them. We use a method detailed by Levine for this [39], until at least 99% of the flow of biomass (energy) to each species is accounted for. This is necessary in Webworld, where looping (closed cycles in the feeding network) is a possibility.

- All of the prey-averaged trophic levels occupied at every output step.

Next we consider the frequencies of species invasions and extinctions, and their evolutionary lifespans. In particular, we calculate properties for species which could be classified at the appropriate time in the following species groups: Basal, Intermediate, Top, Unclassifiable BIT, Shortest-chain Trophic Level 1, 2, 3, 4, 5 or greater, or unclassifiable shortest-chain trophic level. In some cases species cannot be classified at the time when this data is collected, as trophic level and BIT classifications are not fixed for a given species. The following five properties are calculated for each of these ten groups for every 10,000 time step period, and also over the entire simulation. In all cases, species are only counted if they successfully invaded the system (therefore having lifespan greater than one evolutionary timestep):

- The average lifespan of species born in the time period, and who were most commonly assigned to that species group during their lifetime.

- Turnover, which is the number of deaths of species that occur during the time period, who were counted as part of that species group at or just before their death.

- The frequency of speciation events during the time period, where the parental species was part of the species group at the time of speciation, and which resulted in the child successfully invading the system.

- The previous property expressed as a fraction of total (successful and unsuccessful) speciation events to parents of the group during the time period. In other words, the rate of successful invasions of children of the species group during that time period.

Additional information is collected at the end of the simulation:

- A visual representation of the final Food Web.

- Degree distribution of both final Taxonomic and Trophic webs.

- Histogram of the frequency distribution of the logarithms of the populations of non-resource species at the end of the simulation.

- A representation of the phylogeny (genetic ancestry) of those species which exist at the end of the simulation, indicating the creation time, extinction time, and parent species of each species in the direct ancestral lineage of the final species.

4. A Single Simulation
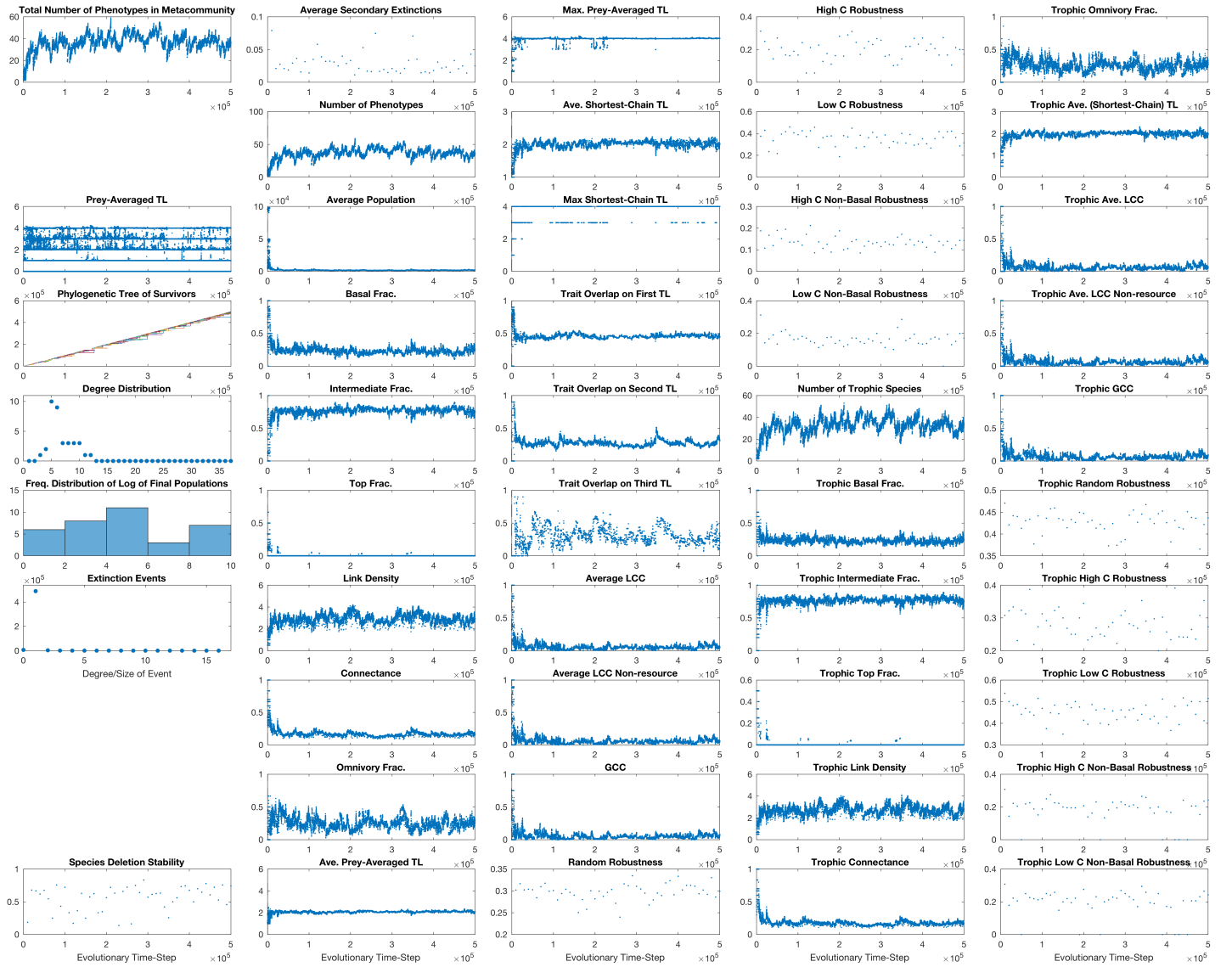
An example data set for one simulation follows:

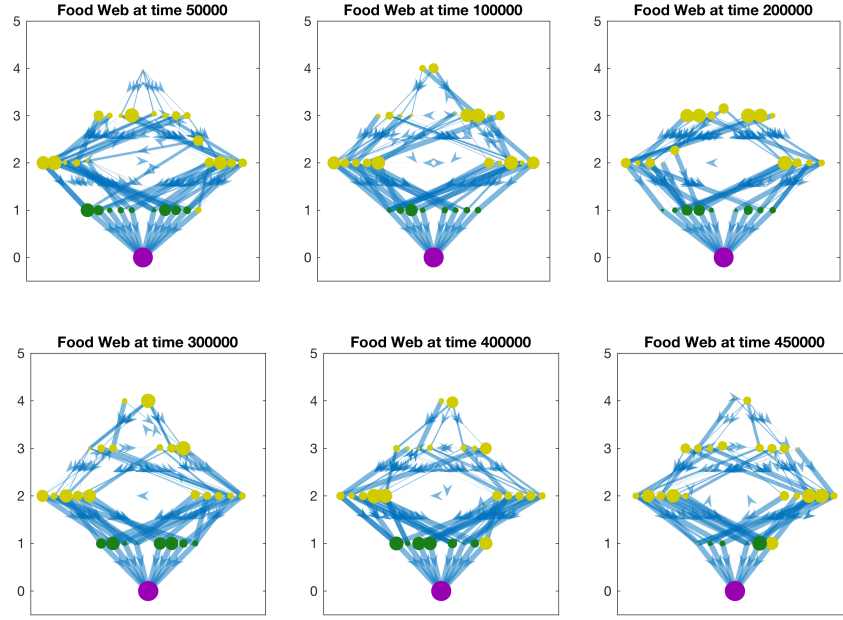Figure 1: All Properties for One Simulation

Figure 2: Food Web during One Simulation:
- Height is representative of prey-averaged trophic level.
- Colour: purple for the resource, green for Basal, yellow for Intermediate, red for Top.
- Size of nodes is directly proportional to the logarithm of biomass/population.
- Thickness of feeding links corresponds to predatory effort.

(a) Diversity   (b) Trophic Diversity   (c) Link Density   (d) Connectance

(e) Random Robustness   (f) Prey-Averaged Trophic Levels   (g) Cumulative Population of B-I-T   (h) Cumulative Population of SC Trophic Levels
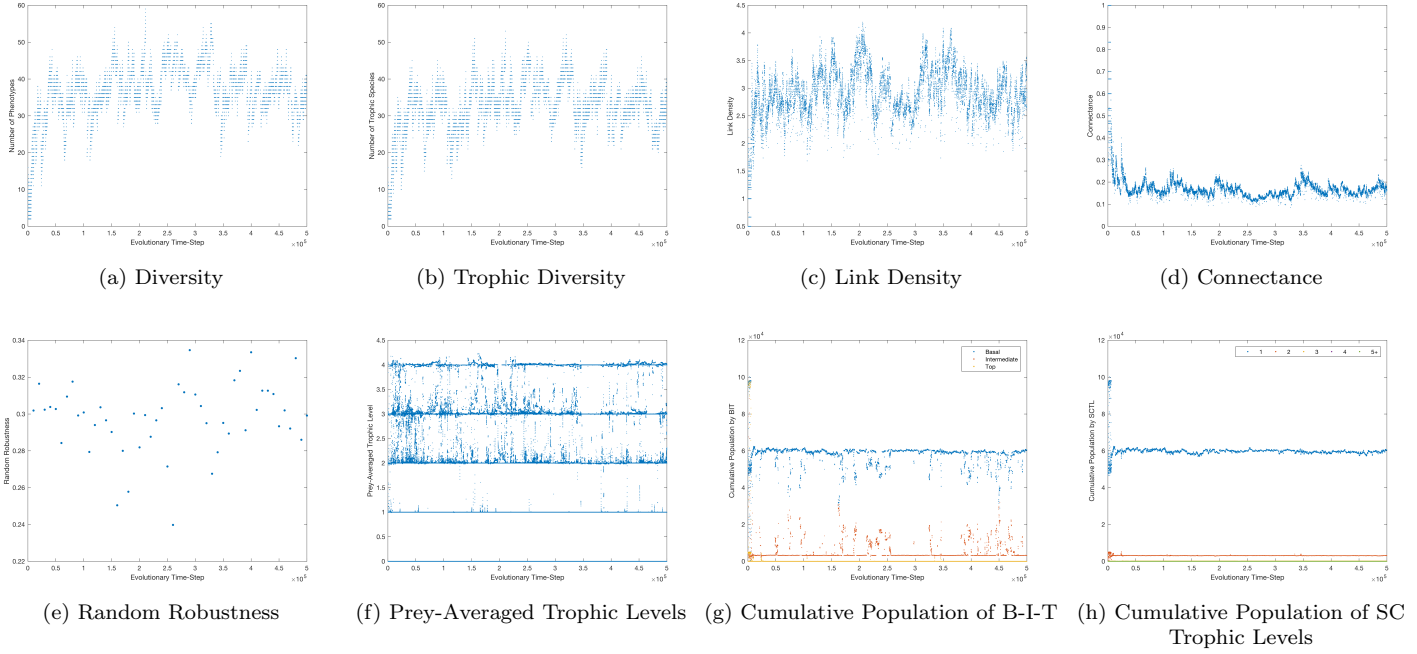
Figure 3: Selected Properties for a Single Simulation

The vast majority of biomass is made up of species that are Basal (Figure 3(g)) and/or on the first shortest-chain trophic level (Figure 3(h)). That is, species which feed on the resource only or at least in part, respectively. This is not surprising, as the ecological efficiency only allows 10% of biomass to be passed up the food chain at each trophic level.

Beyond the initial period of the first 500 timesteps, robustness to random species extinctions has no clear pattern in evolutionary time. However, it decreases substantially at several points after 150,000 timesteps (Figure 3(e)), indicating that ecological communities which we may consider "highly-evolved" nonetheless remain relatively vulnerable to external perturbation in terms of sequences of species extinctions.
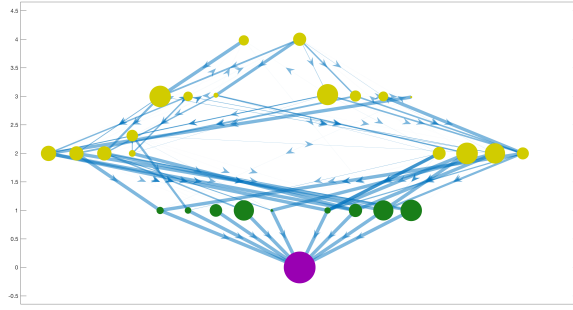
Figure 4: Final Food Web: - Height is representative of prey-averaged trophic level.
- Colour: purple for the resource, green for Basal, yellow for Intermediate, red for Top.
- Size of nodes is directly proportional to the logarithm of biomass/population.
- Thickness of feeding links corresponds to predatory effort.

Let us consider the food web that is present at the end of the simulation (Figure 4). There are nine species on the first trophic level, all of whom are basal (they do not feed, even in part, on any non-resource species) and so they are highly adapted to focus on exploiting the resource. The remaining 17 species have prey-averaged trophic heights of between 2 and 4. As is fairly typical for our Webworld simulations, there are no "Top" species , so there are necessarily examples of feeding loops in this network. In fact we can see that a species with the highest trophic height is being weakly predated upon by at least one species with approximate trophic height of 2. Other researchers have found looping and a non-strictly-hierarchical food web structure to be beneficial to the ability of a network to evolve further using networks generated by a model similar to the Cascade and Niche models [42]. Furthermore, in a study of soil food webs, loops comprised of weak links were found and the authors proposed a mechanism by which "weak links prevent complex food webs with long loops from being unstable" [43]. In general, although early food web ecology assumed looping and cannibalism to be very rare phenomena, more recent and reliable studies from the 1980's onward showed that this is not the case [40] and that feeding loops are quite possible, with the result that top species may be rare or non-existent in a sufficiently large and well-resolved food web.
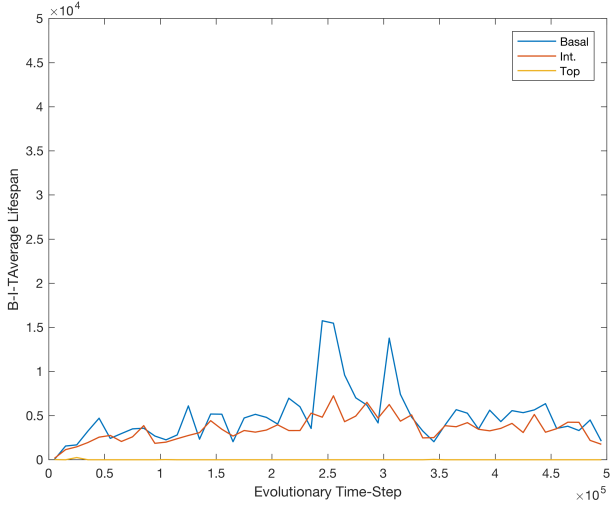
(a) B-I-T
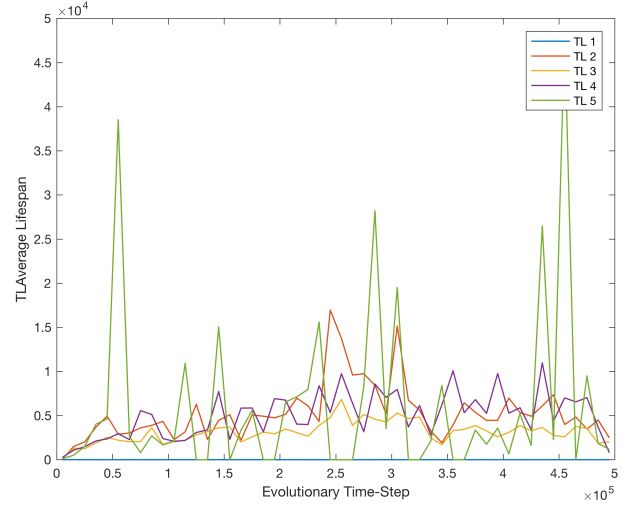
(b) SCTL

Figure 5: Evolutionary Lifespan

In Figure 5, we show the average evolutionary lifespans (that is, how many evolutionary timesteps a species persists for) of species in the simulation, classified in two ways: First, by Basal-Intermediate-Top and second by trophic level. Since these properties can vary over time for a single species, we calculate the average lifespan for species that were born in each period of 10,000 evolutionary timesteps and who were *most often* assigned this particular $B - I - T$ or trophic level classification. Basal species, with the largest populations and the only food source that is not potentially subject to change, naturally have the longest lifespans in each time period (Figure 5(a)). It seems that there are a small number of species who have trophic level of 5 or greater for much of their lifespan who are very long-lived, perhaps because their small population reduces the likelihood of them being chosen for speciation, and the lack of competition compared to lower trophic levels. Since the Top species clearly do not benefit from these long evolutionary lifespans, it seems that either there are many Top species on lower trophic levels with

shorter lifespans, or else that the long-lived high trophic level species are able to endure a small amount of predatory effort from some other species. Either way, we need to keep the limitations of how this data is collected in mind - for example, a species is classified as "Basal" during a time period, and contributes its lifespan to that particular average, if it was basal at output steps (every 20 evolutionary timesteps) only at least once more often than it was intermediate or top during the observation points in this period.
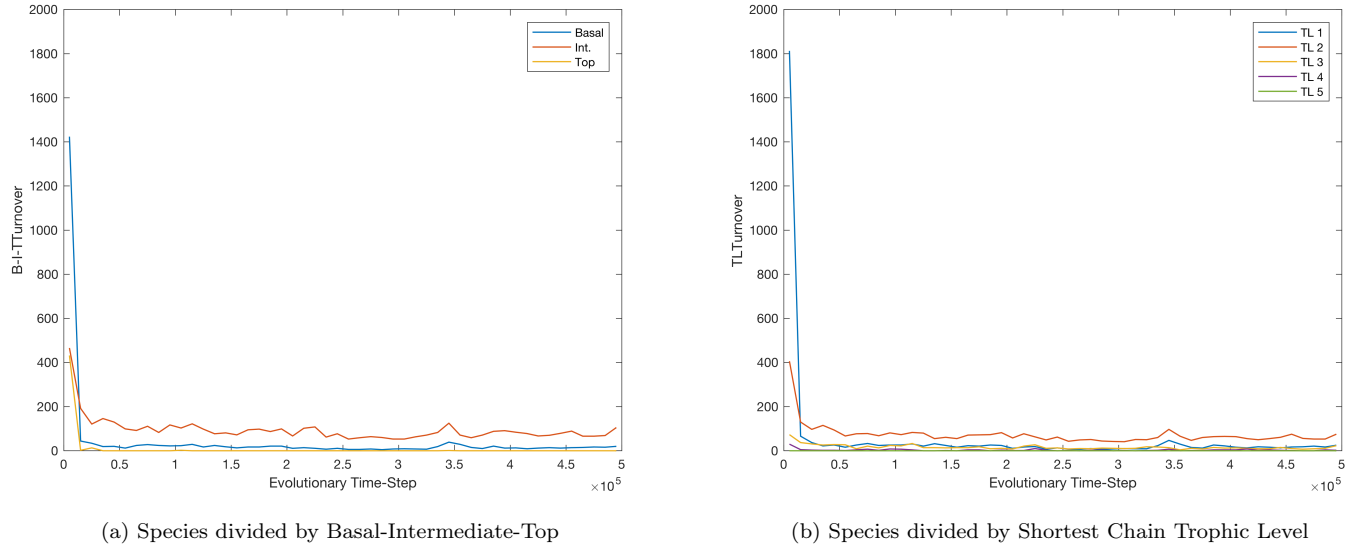

(a) Species divided by Basal-Intermediate-Top

(b) Species divided by Shortest Chain Trophic Level

Figure 6: Turnover

(a) Species divided by Basal-Intermediate-Top

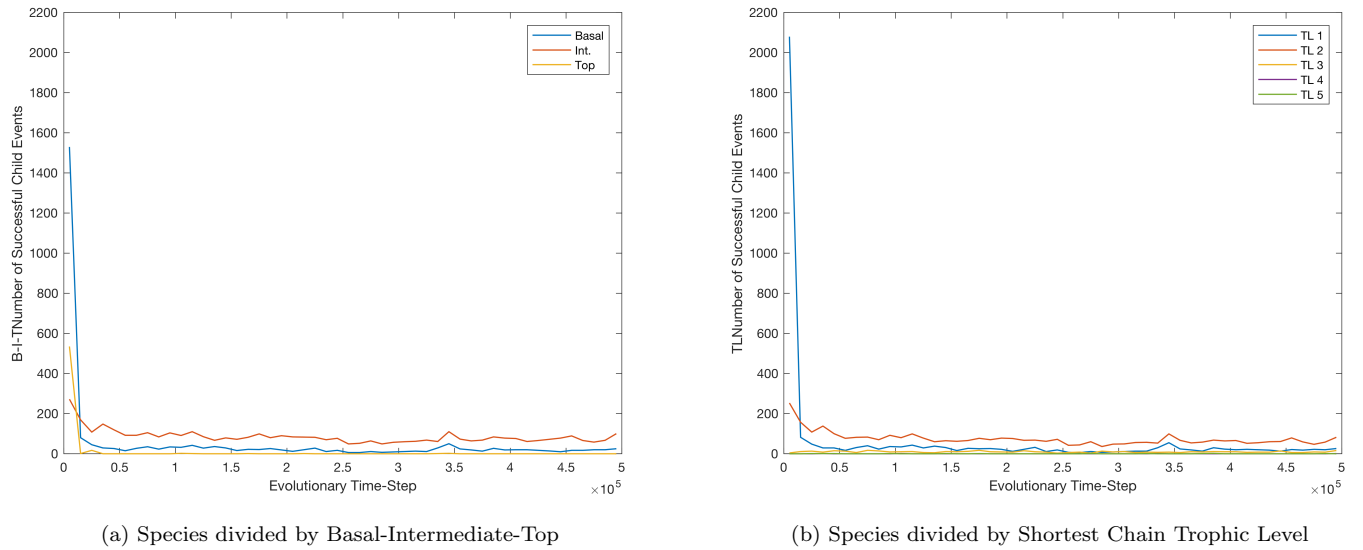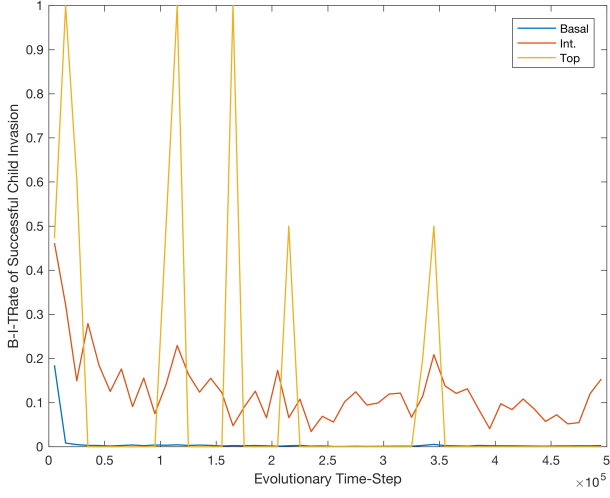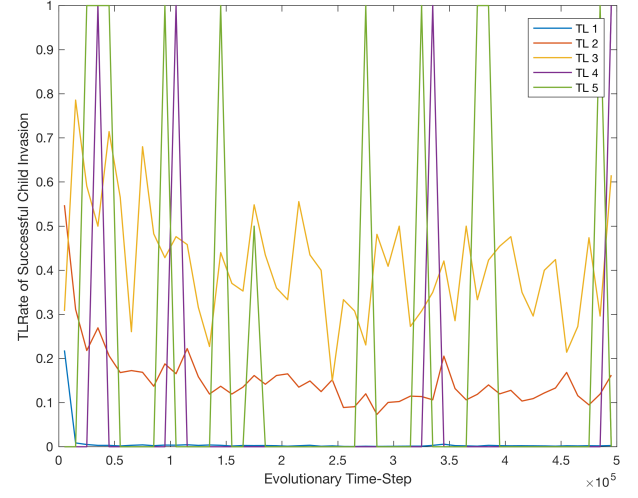(b) Species divided by Shortest Chain Trophic Level

Figure 7: Number of Successful Child Invasions

Figure 6 illustrates the frequency of species extinctions (turnover) over periods of 10,000 evolutionary timesteps, restricted to those species which had successfully established in the food web for at least one timestep. In this case, species are counted according to their $B - I - T$ or trophic level classifications immediately prior to their demise. The number of successful invasions (Figure 7), and extinctions (Figure 6), of already-established species, is much greater within the first 20,000 evolutionary timesteps than any other point in the simulation. This matches with the diversity time-series where we see that in this time the system undergoes severe fluctuation in a transient "pre-complexity" stage before it finds a suitable arrangement of species which allow the development of a more complex web to take off. After this period, the number of invasions and extinctions does not seem to change much over the remainder of the simulation.

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(a) Species divided by Basal-Intermediate-Top

(b) Species divided by Shortest Chain Trophic Level

Figure 8: Rate of Successful Child Invasions

Figure 8 illustrates the fraction of the children of species in the different subgroups which successfully join the ecosystem. As was found by previous authors [30], we see that once the system's early fluctuations have come to an end, for the remainder of the simulation the children of species on the second and third trophic levels (and similarly, intermediate species) have the best consistent chance of invasion. Since they also have consistently higher frequencies of extinction, it seems likely that intermediate species are being constantly replaced by other similar species who occupy the same position in the web. Those on higher levels are occasionally successful, but it should be noted that the absolute number of invasion events for children of parents on those levels is extremely low by comparison.

5. Averaged data collected for the general model

Next, we consider twenty parameter sets: five values of c (0.4, 0.5, 0.6, 0.7, 0.8) and four values of R (10^{-4}, 5×10^{-4}, 10^{-5}, 2×10^{-5}). For each pair of these values, we perform 30 simulations of 120,000 evolutionary timesteps, and calculate the mean properties over the final 10,000 iterations of all 30 experiments. For stability measures, we reduce this to the final 100 evolutionary timesteps. Two additional properties are also presented here, which are calculated over the *entire* simulation:
- *Average Lifespan*: the average number of evolutionary timesteps that a species survives for.
- *Average Diversity over all time*: this is the average diversity (number of species) throughout all 120,000 timesteps of each of the 30 simulations, so we can see if the web at the "end" is on average any different to the web that is present for "most" of the simulation.
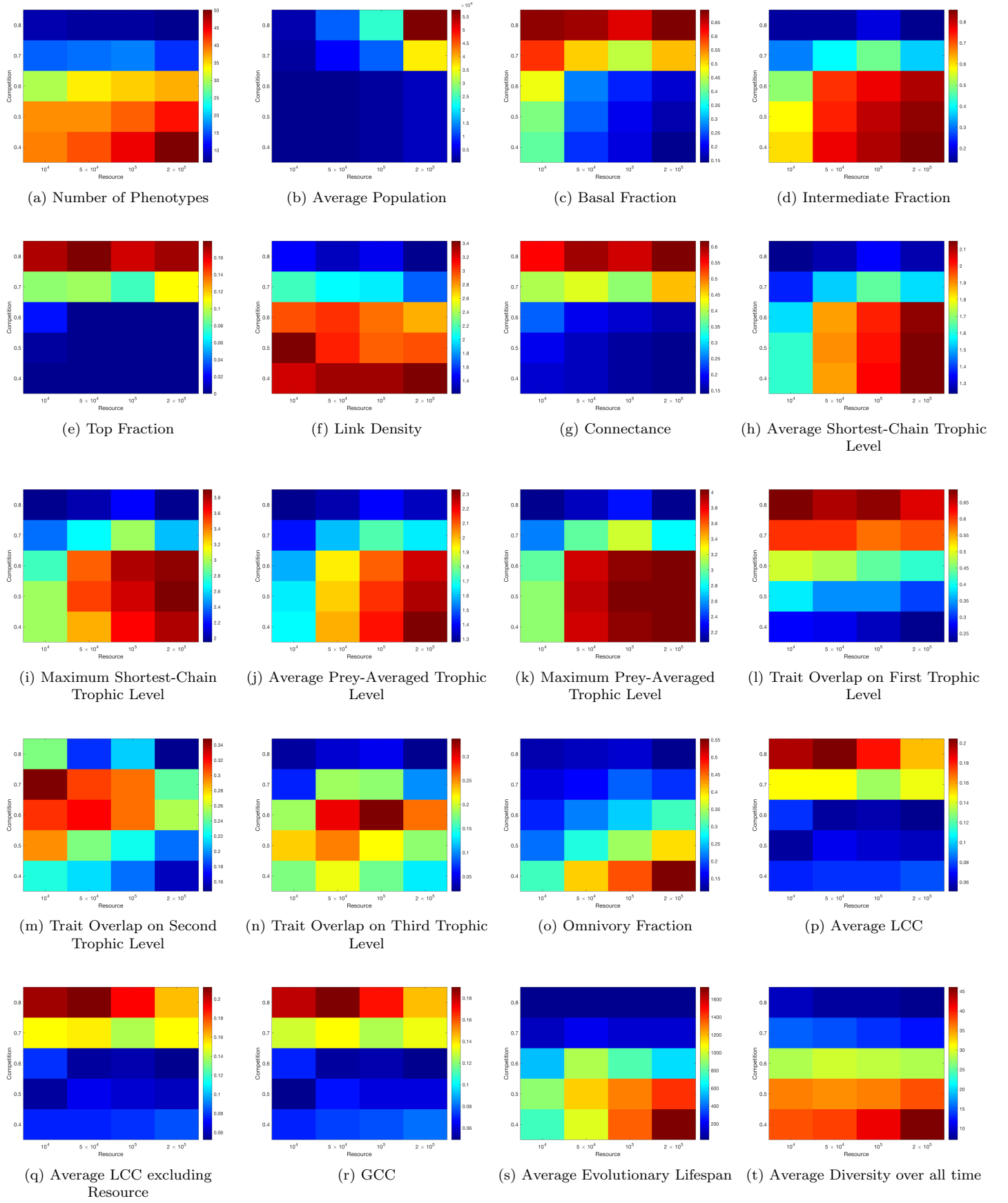
(a) Number of Phenotypes

(b) Average Population

(c) Basal Fraction

(d) Intermediate Fraction

(e) Top Fraction

(f) Link Density

(g) Connectance

(h) Average Shortest-Chain Trophic Level

(i) Maximum Shortest-Chain Trophic Level

(j) Average Prey-Averaged Trophic Level

(k) Maximum Prey-Averaged Trophic Level

(l) Trait Overlap on First Trophic Level

(m) Trait Overlap on Second Trophic Level

(n) Trait Overlap on Third Trophic Level

(o) Omnivory Fraction

(p) Average LCC

(q) Average LCC excluding Resource

(r) GCC

(s) Average Evolutionary Lifespan

(t) Average Diversity over all time

Figure 9: Averaged Data of Taxonomic Webs

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(a) Number of Trophic Species

(b) Basal Fraction of Trophic Web

(c) Intermediate Fraction of Trophic Web

(d) Top Fraction of Trophic Web

(e) Link Density of Trophic Web

(f) Connectance of Trophic Web

(g) Average Shortest-Chain Trophic Level of Trophic Web

(h) Maximum Shortest-Chain Trophic Level of Trophic Web

(i) Omnivory Fraction of Trophic Web

(j) Average LCC of Trophic Web

(k) Average LCC excluding Resource of Trophic Web

(l) GCC of Trophic Web

Figure 10: Averaged Data of Trophic Webs

(a) Species Deletion Stability

(b) Average Fraction of Secondary Extinctions

(c) Average Random Robustness

(d) Most Connected Robustness

(e) Least Connected Robustness

(f) Most Connected Non-Basal Robustness

(g) Least Connected Non-Basal Robustness

(h) Trophic Average Random Robustness

(i) Trophic Most Connected Robustness

(j) Trophic Least Connected Robustness

(k) Trophic Most Connected Non-Basal Robustness

(l) Trophic Least Connected Non-Basal Robustness

Figure 11: Averaged Stability Properties

The mean properties resulting from these experiments are presented in Figures 9-11. Firstly, it is evident that diversity increases with resource and decreased competition, as could be expected. Connectance looks like it might be approaching a rough constant (~ 0.12) for large networks, and we shall investigate this in more detail later as it is of some historical significance. Compared to other properties, which are strongly controlled by Competition, Resource amount has more influence on the trophic levels reached (due to ecological efficiency, more resource allows higher levels to be reached). Most properties for trophic webs (Figure 10) follow simialr patterns to their taxonomic counterparts, with diversity shifted downward by approximately 10% and corresponding increases to connectance. We verify that in all cases, as reported by previous authors [30], both the foraging and ecological loops rapidly converge to within the required tolerances as the limit of 100,000 iterations is never reached in either loop in any of the 600 simulations performed. This also means that chaotic regimes are not evident in the population dynamics.

As explained in the original papers, c controls the degree to which interspecific competition drops off as the species pairs share fewer traits - so high c means stronger interspecific competition, which results in fewer species and therefore higher average populations given the same resource input. Very strong interspecific competition encourages specialised predation - reducing both Link Density (Figure 9(f)) and Omnivory (Figure 9(o)). As c increases, for any given pair of non-identical species, the strength of competition between them increases. However, the more different they are, the greater this increase will be. Furthermore, note that the increasing competition will only affect realised feeding links. At low c there could be species who are mostly on the second or third trophic levels but who expend a small fraction of effort on the resource as its biomass is so large and dependable. These species may therefore be dissuaded from attempting to generalise by the increasing competition, and focus soley on their other prey. Thus, only a few similar, very well-adapted species remain on the first trophic level, and so the trait overlap increases (Figure 9(l)). This is in accordance with the rationale of the original paper: "When c is small there is much weaker competition between [phenotypically] distant species; hence, we would expect greater diversification of the ecosystem when c is small" [1].

In large food webs, there are likely to be very few top and basal species relative to the number of intermediate species. In

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addition, as the average trophic levels are reduced by this increase in competition, top species in these cases are likely to be at lower trophic levels and thus have larger populations than when c is low. This explains the increase in these fractions at high c, despite the fact that top species generally have low populations and would be vulnerable to extinction at high c: this would only be the case in larger webs with higher trophic levels.

Regarding stability and long-term evolution, for sufficiently large food webs, approximately 60% of species can be deleted from the network without incurring any additional extinctions (species deletion stability (Figure 11(a))), and on average (including the deletions with no effect) a species deletion results in the extinction of 0.02-0.03 of the remainder of the web (Figure 11(b)). This matches the result of a previous study that found average secondary deletions of 2.1% [29] using the Webworld model. For very small food webs with $c = 0.8$, both species deletion stability and the fraction of secondary extinctions increase - so whether larger webs are more or less stable depends on how stability is measured. Our other test of stability, Robustness, in all of its variants follows the pattern of species deletion stability with the food web parameters: it increases as the competition parameter increases. The pattern with the resource amount is less clear, but for low c robustness increases as R decreases.

We find that average evolutionary lifespan corresponds with the pattern of diversity, increasing with lower Competition (this reduces competitive pressure and turnover) and, to a much lesser extent, higher Resource. Interestingly, average diversity over all time (over all 120,000 times steps for each of the simulations (Figure 9(t))) is very similar to final average diversity (Figure 9(a)), which suggests that the food webs do quickly reach a dynamic equilibrium in that there is not much average difference between the diversity over the final 10,000 iterations and the diversity over the full 120,000 iterations including the very beginnings of the web.

We also considered some properties of interest in the inderdisciplinary field of Complex Network Theory. We find that both the Local and Global Clustering Coefficients vary between 0.06 and 0.20, and appear to approximate 0.07 for large networks. This is in general agreement with the study of local clustering coefficients for 16 large empirical food webs that vary between 0.02 and 0.43, with all but 3 of these between 0.02 and 0.16 [44].

6. Link-Species relationship

The relationship between the number of feeding links and the diversity of an ecosystem has been of interest to theoretical ecologists for some time, and a scaling law of the form $L = aS^b$ had been sought as a candidate for one universal law underlying and constraining the structure of all real food webs. Previously, researchers studying empirical food web data had proposed exponents of 1 (with a constant link density of approximately 2.0), known as the link-species scaling law [3], and then following this others suggested an exponent of 2 (resulting in a constant value for connectance equal to 0.1) [40]. We analyse the data set from Section 5 to determine which, if either, relationship is demonstrated by the food webs assembled by the Webworld model.
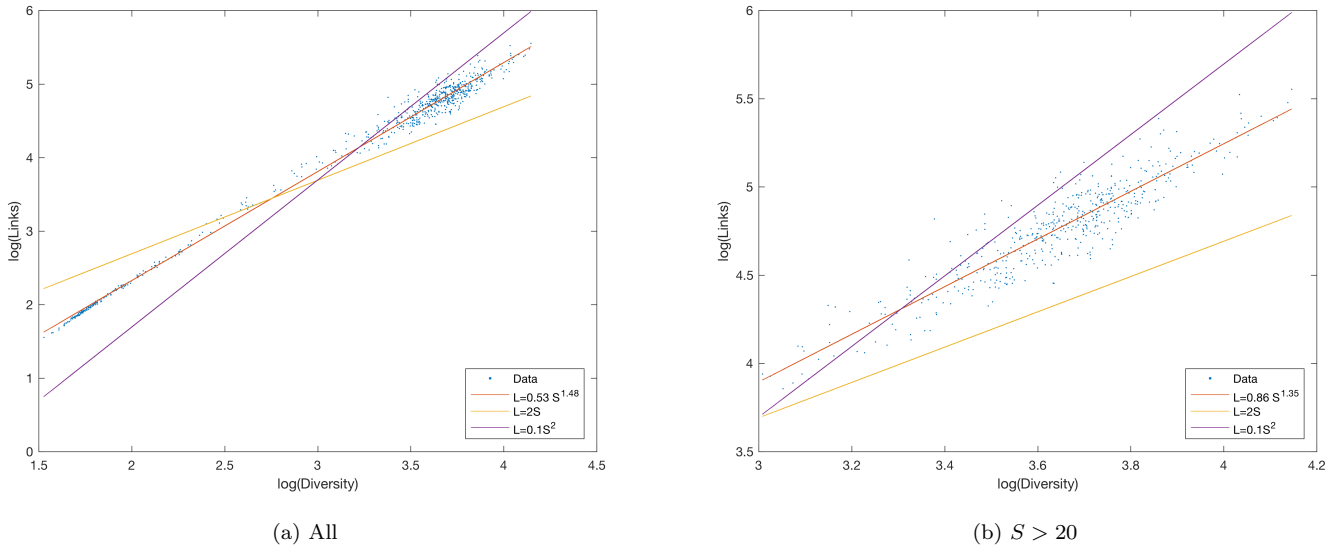

(a) All

(b) $S > 20$

Figure 12: Link-Species Relationship for Taxonomic Webs'

Data over all 600 simulations (Figure 12) supports neither the constant connectance hypothesis, nor the link-species scaling law, both for all simulations and only for those with $S > 20$. In both cases an intermediate exponent ($b = 1.48$ and $b = 1.35$ respectively) is supported. This is still coherent with some empirical data that supports an exponent of around $b = 1.5$, as summarised in Dunne's 2006 review [40] which catalogues recent historical thought on the link-species relationship in detail.

(a) L/S - Diversity Correlation

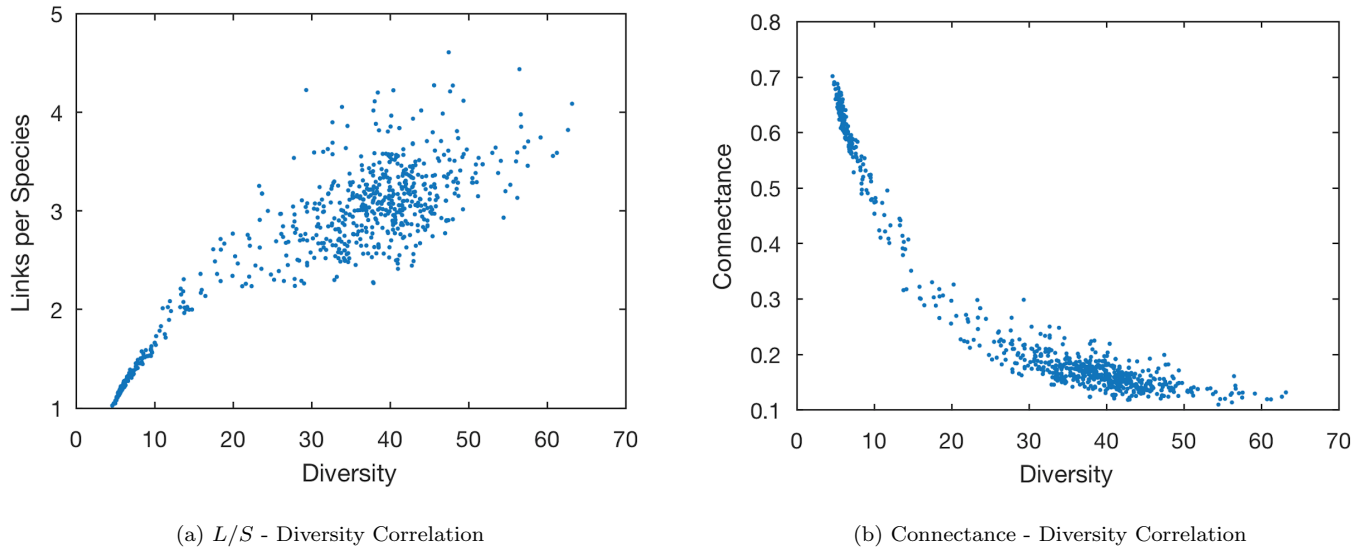(b) Connectance - Diversity Correlation

Figure 13: Correlations of Taxonomic Webs

Figure 13 shows the results of the average final species diversity plotted against link density and connectance respectively. Clearly, the 600 simulations we have performed do not have a uniform distribution of final species diversity. In particular, the intervals 5-10 and 30-50 are greatly over-represented, whilst there are relatively few data points in the 10-30 and 50-65 intervals. In order to address the effect that this may have, we sample 10 points from every interval of 10 species, so that the large numbers of data points no longer dominates the correlations.

(a) All

(b) $S > 20$
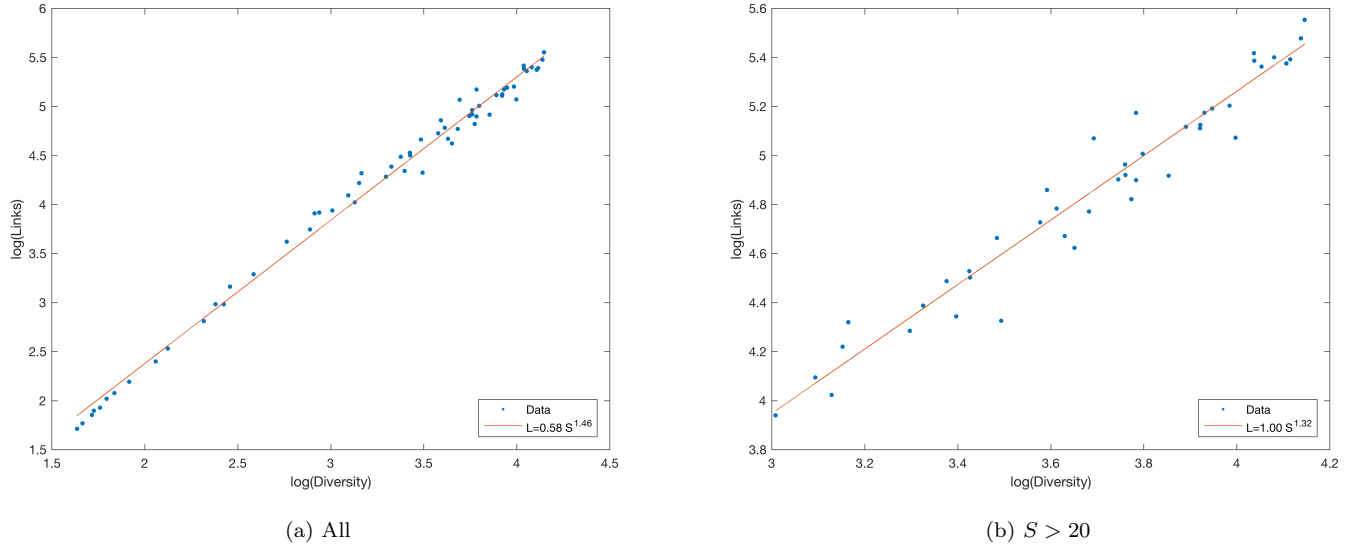
Figure 14: Taxonomic log(Links) - log(Diversity) Best Fit, uniformly sampled

Repeating the previous analysis with data uniformly sampled from these intervals of S returns an exponent of $b = 1.32$ when we restrict the diversity to $S > 20$, and $b = 1.46$ when the full range is admitted (Figure 14).

We also undertake similar same analysis of the relationship between trophic diversity and the number of binary feeding links present in the trophic webs. In this case, we obtain exponent estimates of 1.52 for the full trophic web set, 1.42 for the full set of trophic webs with more than 20 trophic species, 1.50 for a uniformly-sampled set, and 1.48 for a uniformly-sampled set restricted to at least 20 trophic species.

Finally, we investigated the link-species relationship of food webs constructed using a version of Webworld where the parents of mutants are selected randomly, rather than probabilisitically by biomass as is the case for experiments presented in this paper. In this case, we found exponents of $b = 1.39$ for all data, and $b = 1.37$ when restricting our study to webs with diversity

$S > 20$. In summary, across both taxonomic and trophic cases, with and without restricting to uniformly-sampled subsets, and with or without excluding small food webs, we report an estimated exponent b of between 1.32 and 1.52 for the $L = aS^b$ relationship, indicating that the networks constructed by the Webworld model support neither constant link density ($b = 1$) nor constant connectance ($b = 2$) hypotheses.

6.1. Sensitivity of the Exponent to Link-Counting

We consider the sensitivity of the exponent to the parameters involved when counting feeding links. In particular, we calculated the exponent over 600 simulations (30 for each of the same 20 parameter choices), for six data sets where f_{min} (that is, the minimum effort designated for potentially valid feeding links) took different values spanning several orders of magnitude. This experiment revealed that the diversity of webs constructed by Webworld can be strongly affected by this parameter, as increasing it to 10^{-4} and larger resulted in much greater species diversity (200-300 species).
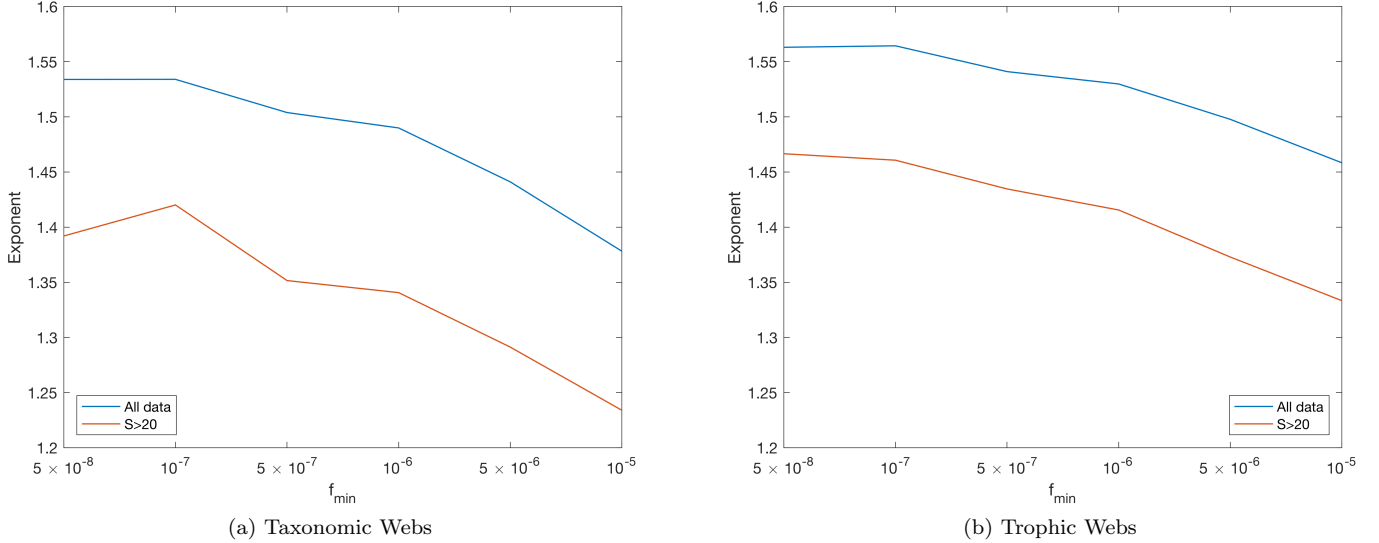

(a) Taxonomic Webs (b) Trophic Webs

Figure 15: Effect of Varying f_{min} on Link-Species Exponent

Unsurprisingly (Figure 15), lower values of f_{min} increase the number of links counted relative to the number of species, and result in larger exponents. However, all results continue to support an intermediate value. Finally, we return to the original dataset of 600 simulations (with $f_{min} = 10^{-6}$) and introduce a new link-strength threshold which is varied between f_{min} and 1.0, where only the strongest feeding relationships are "observed". Species who are not observed either feeding, or being fed upon, are discounted. This process mimics the result of a field researcher recording the same food web with different levels of sampling effort, which is known to potentially have significant effect on the results of empirical studies [41].
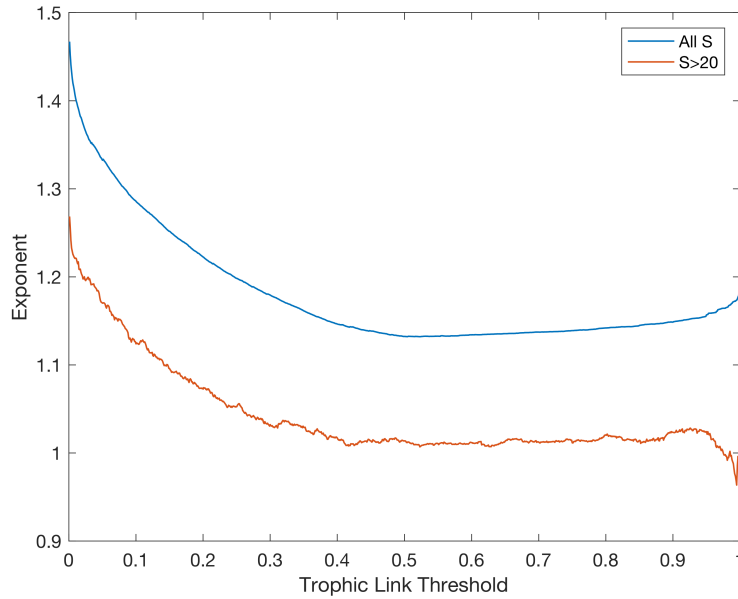
Figure 16: Effect of Sampling Effort on observed Link-Species Exponent

Increasing the minimum effort required for observation reduces the number of links faster than the number of species, and so the exponent decreases (Figure 16). This effect was found by other researchers analysing empirical data in the 1980's [45, 46], and as a result they were able to attribute apparent empirical support for the link-species scaling law to previous data being poorly-resolved. We note that the webs constructed by Webworld support an intermediate exponent provided that the threshold is sufficiently small, however if small webs are discounted then a finer resolution of the web is needed, as such small webs tend to have higher connectance and therefore contribute to raising the exponent.

7. Robustness

Next we consider what contribution the Webworld model could make to the stability-complexity debate in theoretical ecology. A previous study considered the stability of the model's networks in terms of species deletion stability and resulting secondary extinctions [29]. However, the robustness form of stability has not yet been employed using this model. This measure, as described in Section 3.2, is calculated in the following manner. For a taxonomic food web with population dynamics, we artificially delete a species from the food web and iterate the ecological loop to determine if species' removal results in the extinction of any further species (secondary extinctions). This process is repeated until the combination of artificial deletions and secondary extinctions has resulted in the removal of at least half of the original food web (discounting the resource). The robustness of the web is then the fraction of the web that had to be artificially deleted in order to achieve this. Thus, the least possible value is $1/S$, where S is the number of non-resource species. To calculate the robustness of a trophic web, which lacks explicit population dynamics and has only binary feeding links, we artificially delete species as normal and then secondarily remove any additional species which no longer have a path to the resource.

Findings from empirical data (Dunne et al 2002 [47], Dunne et al 2004 [48]), and the Cascade, Generalised Cascade, Niche and Nested-Hierarchy Models (Dunne and Williams, 2009 [49]) had suggested a positive relationship between robustness and connectance. Here, we test the relationship between several kinds of robustness and connectance, in addition to diversity and link density. In particular, we vary the methods of selecting the order in which species are to be artificially deleted: randomly, in the order of most-to-least connected ("High-C"), in the order of least-to-most connected ("Low-C"), and the latter two forms but excluding the possibility of selecting a basal species for deletion. In this, we are following the previous authors, who highlighted the potentially highly destabilising effect of removing a well-established basal species.
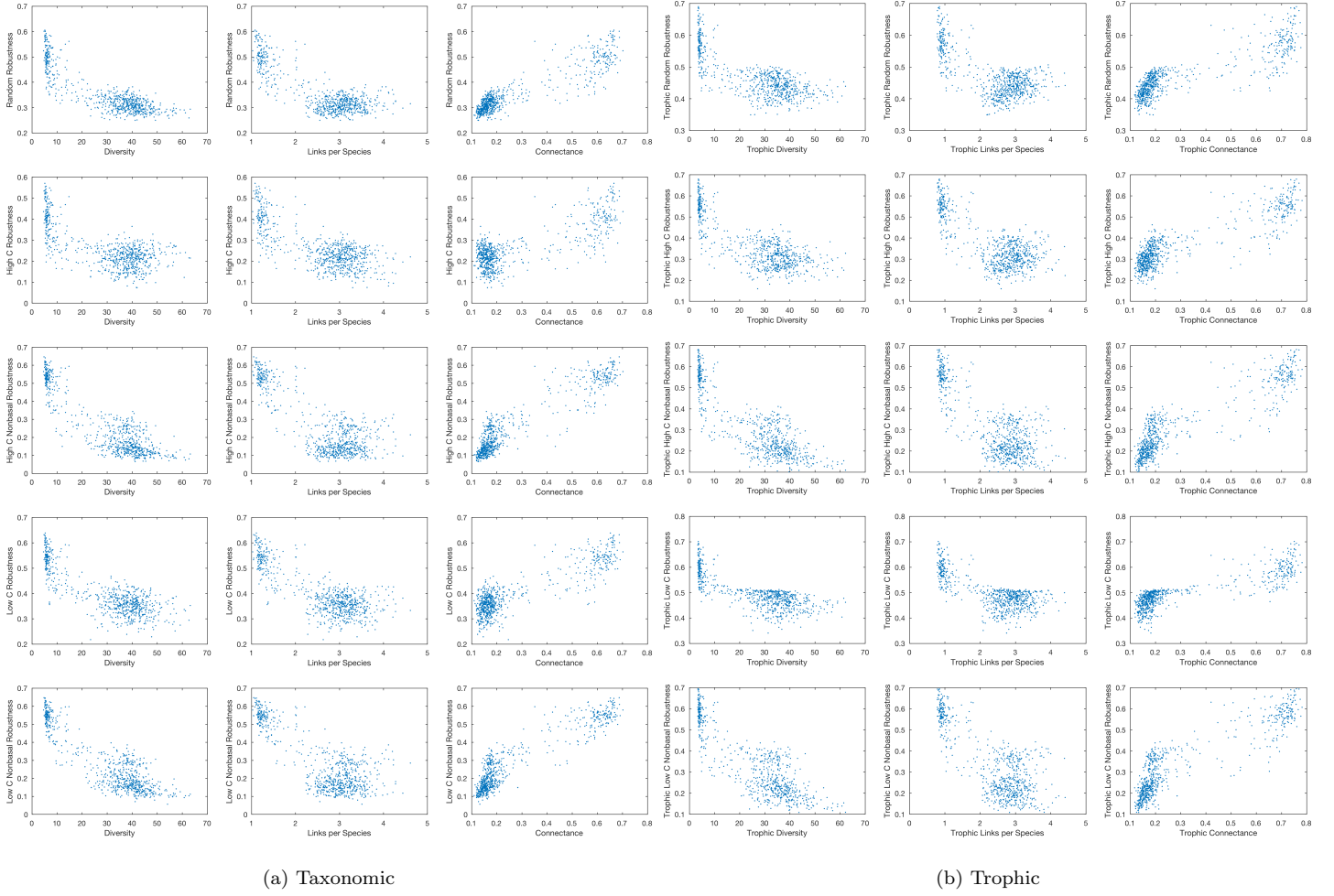
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(a) Taxonomic   (b) Trophic

Figure 17: Robustness Correlations

Robustness	Variable	Correlation Coefficient
Random	Diversity	-0.851
	Link Density	-0.800
	Connectance	0.910
High-C	Diversity	-0.704
	Link Density	-0.749
	Connectance	0.782
High-C Nonbasal	Diversity	-0.882
	Link Density	-0.808
	Connectance	0.931
Low-C	Diversity	-0.820
	Link Density	-0.792
	Connectance	0.869
Low-C Nonbasal	Diversity	-0.891
	Link Density	-0.805
	Connectance	0.926

Table 1: Taxonomic

Robustness	Variable	Correlation Coefficient
Random	Diversity	-0.765
	Link Density	-0.698
	Connectance	0.852
High-C	Diversity	-0.799
	Link Density	-0.759
	Connectance	0.878
High-C Nonbasal	Diversity	-0.856
	Link Density	-0.802
	Connectance	0.905
Low-C	Diversity	-0.776
	Link Density	-0.727
	Connectance	0.837
Low-C Nonbasal	Diversity	-0.863
	Link Density	-0.790
	Connectance	0.895

Table 2: Trophic

We find (Figure 17) that in the 600 evolved webs from the Webworld model, it appears that robustness of all kinds decreases with diversity and link density, for both taxonomic (Table 1) and trophic (Table 2) webs. For example, there are correlation coefficients of -0.851 and -0.765 for the robustness of taxonomic and trophic webs respectively to the randomly-ordered deletion of species from the web. However, robustness has a strong positive correlation with connectance, and in all cases this relationship is stronger than the negative relationship with diversity and link-density. In all but one case (the robustness of taxonomic webs to deleting species in decreasing order of connectance, labelled as "High-C") we find that the link density has the weakest

correlation of the three properties. Furthermore, for taxonomic webs robustness to deletions in order of most- or least-connected has a weaker correlation with connectance than the robustness to species deletion in random order, but both correlations with robustness to ordered species deletion increase in strength if basal species are excluded. For trophic webs, ony Low-C robustness has a weaker correlation with connectance than random robustness, but again both it and High-C robustness increase when excluding basal species from deletion.

8. Effects of Perturbation

To study the effect of a decrease in resource input on a developed web, akin to habitat destruction or the loss of resources in a real ecosystem, we allow the web to develop for 100,000 evolutionary timesteps, before dropping the size (biomass) of the resource by 10%, 20%, ..., 90%, where a decrease of 100% would remove the resource altogether and necessarily result in the total annihilation of the ecosystem. In all other experiments, as described in Section 2.1, the scores of the traits against each other are given by an antisymmetric matrix, with non-diagonal elements drawn from a normal distribution. However, for this experiment, we compare the effect of resource loss between webs constructed using this trait matrix, and a version tested originally by Lugo and McKane [33]. In the latter case, the score of trait A against trait B is +1 with probability 0.25, -1 with probability 0.25, and 0 with probability 0.5, and the matrix is again antisymmetric. This results in a matrix with each trait having a non-neutral relationship with approximately half of all the other traits, rather than having a relationship with *all* other traits (and thus, there existing a potential feeding relationship between any conceivable pair of species) which is the case in the usual description of the model. The effect of this change will therefore be to reduce the flexibility of species' feeding habits, so stronger consequences can be observed from an unexpected perturbation of the system.

(a) Regular Trait Matrix   (b) Alternative Trait Matrix (0.5 Connectance)
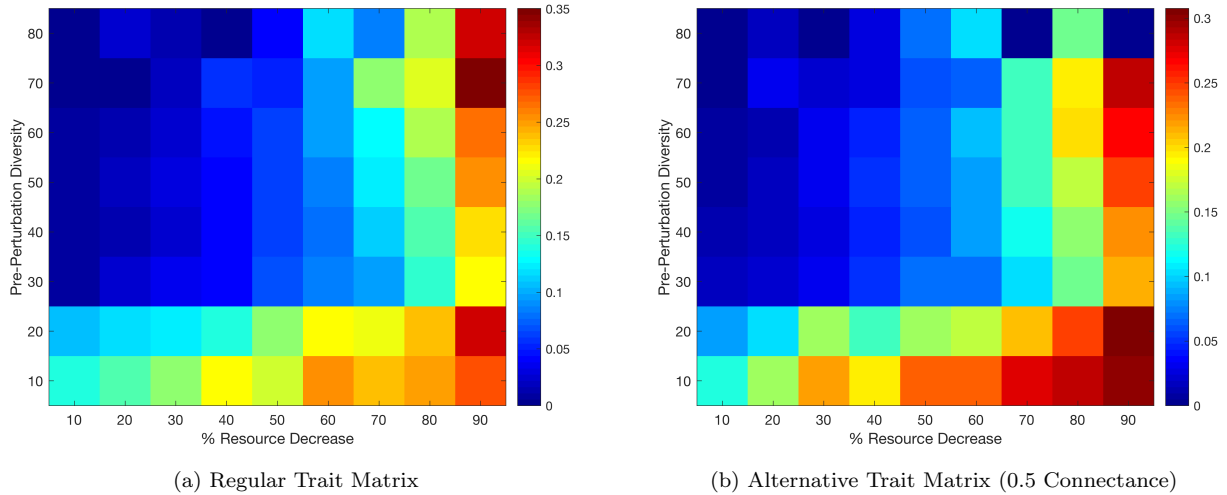
Figure 18: Fraction of extinctions by prior diversity and magnitude of perturbation.

In both cases, there are no very strong correlations between any prior properties of the food webs and the fraction of species lost as a result of the perturbation, although it tentatively appears that food webs with low diversity (Figure 18) and high c (not shown) generally suffer more extinctions. When these smallest webs ($S < 10$) are excluded from consideration, those remaining which possess above-average robustness prior to the perturbation tend to lose fewer species. As would be expected, food webs that were subjected to stronger perturbation suffered greater loss of diversity, and extinctions were amplified in the set of webs that were constructed using the less flexible alternative trait matrix. We find that average populations of present species decrease monotonically with the magnitude of percentage decrease in resource biomass. In most cases, robustness to random species deletions increases substantially as a result of resource perturbation, perhaps as "loose" species are dislodged and a more robust web remains. The fewer species (higher c) and greater the perturbation, the larger the robustness increase.

9. Long-term Behaviour and Criticality

We examine the long-term behaviour of the model with a single simulation that lasts for 100,000,000 evolutionary timesteps and records the number of species at every timestep, with parameters $R = 1 \times 10^5$ and $c = 0.5$. Figure 19 shows the number of species at every individual timestep, and superimposed at time step n the rolling average of the number of species over the interval $[n - 99999, n]$. As we can see, the range of the number of species in the system remains substantial over the entire course of the simulation, and it is not clear that the system reaches a "dynamical stationary state" as was concluded in earlier studies [1], without the term become rather loose. It was thought that "no more than a few species go extinct at the same time" in response to speciation [37]. However, in this experiment a maximal extinction event of 31 species in a single iteration was found to occur

at one point, after 15,403,392 evolutionary timesteps, and from 48 to 18 resident species (not including the invader). This large event, in which more than half of the existing ecosystem was destroyed, was preceded by almost 500 invasion events that caused either zero (the invading mutant joins the ecosystem with no resulting extinctions) or just one extinction (the invader either dies or replaces exactly one resident species). This is entirely due to a combination of the internal population dynamics, which are fully deterministic, and external perturbation limited to invasion of the system by a single, minimum-population species. Statistical analysis of the fossil record by paleobiologists has shown evidence of self-similarity consistent with a model that does not require extreme, qualitatively distinct perturbations (usually hypothesized to be meteorite strikes) to prompt the largest extinction events [50], and some dynamical models have been constructed which support this theory [51]. While the original publication of Webworld used a single simulation's data as evidence of an exponential distribution of extinction events, which would not be consistent with Self-Organised Criticality, our results show that the food webs generated by the model can undergo great changes after sufficiently long periods of time. Furthermore, in an additional long simulation of 20,000,000 evolutionary events (with $R = 5 \times 10^4$ and $c = 0.6$), the number of species dropped to as low as one non-resource species, the same as the initial state of the system, after more than 17,000,000 evolutionary timesteps had elapsed.
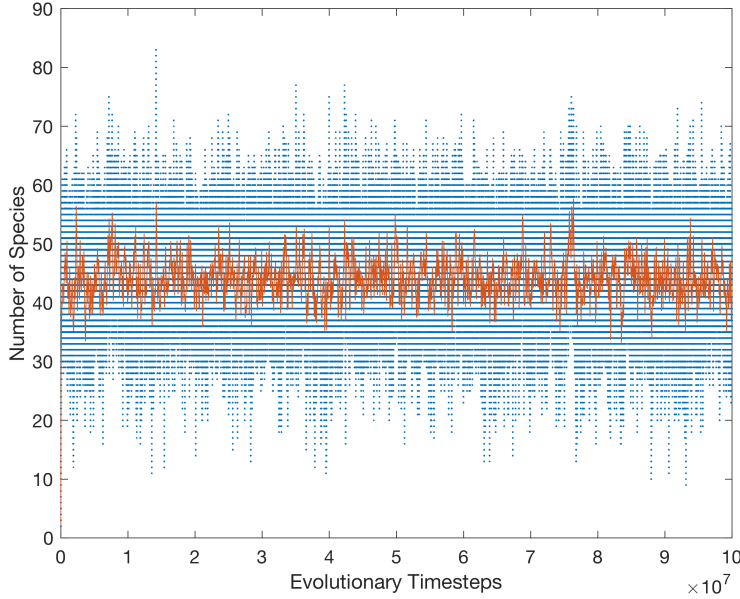

Figure 19: Number of Species over a very long simulation

We fit two candidate models for the distribution of non-zero extinction events between invasions, shown in Figure 20. Let s be the size of the extinction, and $N(s)$ the frequency of this event in the long simulation. Whilst 31 is the largest extinction event, 23 is the largest that is reached without having to skip some events of frequency zero. However, we will further restrict the range of points that we consider when fitting the curve to the most reliable data set beyond the initial peak at $s = 1$. For $s > 15$ it is not clear that the statistical frequency of events has been achieved, therefore, we will fit our models to the data between events of size 5 and 15.

First, a power law relationship, of the form $N(s) \propto S^b$ is found with exponent $b = -5.07$, an R^2 value of 0.976 and a Mean Squared Error of approximately 3.37×10^7. Then, an exponential relationship is tested, of the form $N(s) \propto b^{-S}$. This returns $b = 1.82$, with an R^2 value of 0.990 and a Mean Square Error one order of magnitude smaller, at 6.17×10^6. These are both apparently very strong fits, and it does seem that an exponential law is slightly favoured. However, consider the log-log and log-linear plots for the power and exponential laws respectively (Figure 20(a) and 20(b)). For the power law, the data curves over and then under the fit, whilst for the exponential law the data curves around the graph in the opposite manner. Because of these clear patterns, and the strength of both fits, it is likely that the true distribution of the data is governed neither by a single power law or exponential law. It perhaps could be a linear combination of power and exponential terms, but we lack sufficient data to reliably fit such a law at this time. However, we can say that this data, more reliable than any previously employed does not fit exponential decay as previously supposed [1]. One possible reason for this discrepancy could be due to a choice concerning numerical stability. As described in Section 2.2, in our experiments a speciation event occurs after every population has reached a steady state within a tolerance of 1.0 as this is the minimum unit for a population. The 2001 paper that described Webworld in its current form did not specify this parameter, so we cannot discount the possibility that if a much smaller value was used then different results could be yielded.

(a) Extinctions of 5-15 species: Power Law   (b) Extinctions of 5-15 species: Exponential Law   (c) Extinctions of 5-15 species: Distribution of Extinction Events
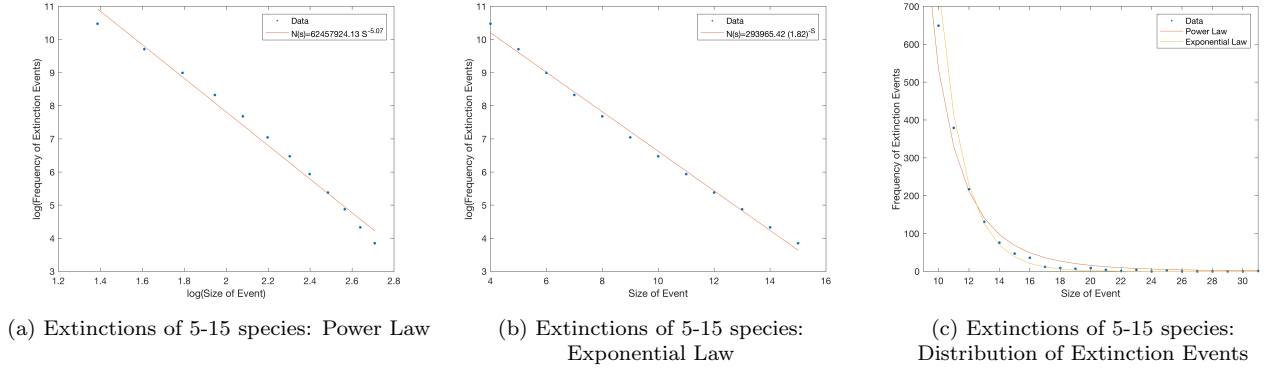
Figure 20: Fitting relationships to the distribution of extinction events

10. Hurst exponent and Box-counting dimension of Diversity time-series

For a range of parameter choices, we consider some long simulations and calculate the Hurst exponent of the number of species and of the average non-resource species population. This a nonlinear dynamics quantifier usually applied in studies of financial time-series but also suitable for ecological studies (e.g. [52, 53]). To determine its value, we calculate the Box-Counting dimension, B, and then the Hurst exponent is equal to $2 - B$. This investigation also provides an opportunity to examine the variation in species diversity over 80 long simulations with 5,000,000 timesteps and the number of species being output at every single timestep. A rolling average over 50,000 evolutionary timesteps is superimposed in each case. For each of 16 parameter sets (4 choices of c and 4 choices of R), we average data over 5 simulations.

(a) Over the final 50,000 timesteps   (b) Over all timesteps
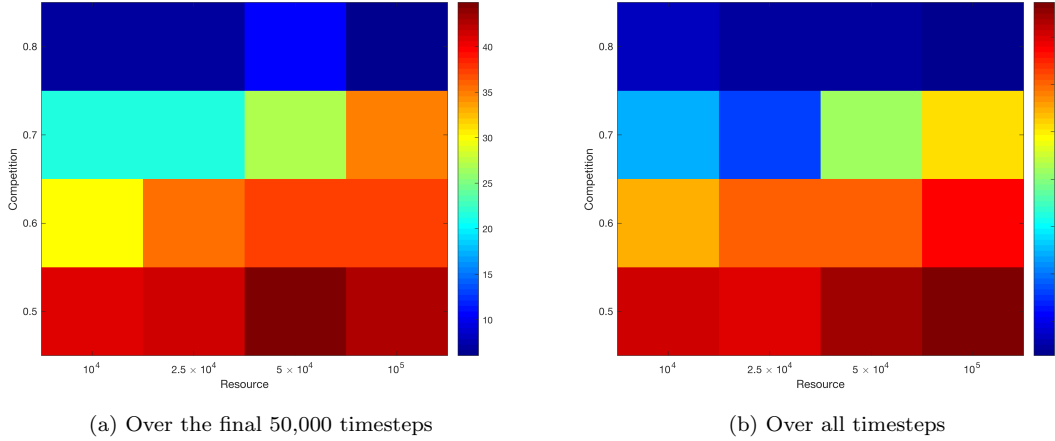
Figure 21: Average Species Diversity

From these experiments, we observe that again the competition parameter has a large influence on the results (Figure 21), although note that the range of resource populations in these experiments is more restricted than was previously the case. Simulations with $c = 0.5$ generally occupy a high-diversity state, those with $c = 0.8$ are restricted to low diversity (but given the consistently higher box-counting dimension, they experience frequent small-amplitude variation there), and whilst simulations with intermediate c (0.6, 0.7) usually occupy high diversity (~ 40 species) configurations, they may intermittently collapse down to low diversity configurations - thus experiencing larger potential fluctuations over very long timescales.
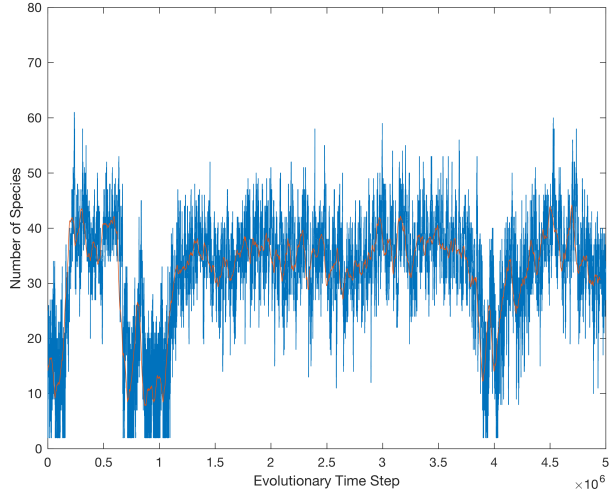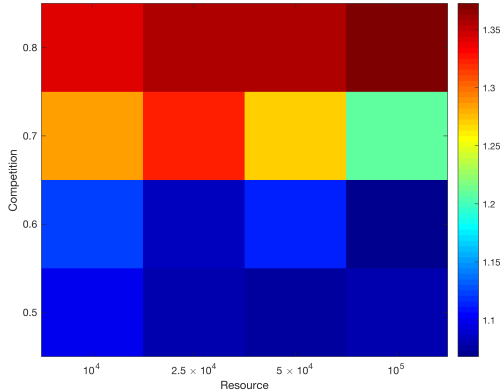
(a) $c = 0.6$, $R = 5 \times 10^{-4}$
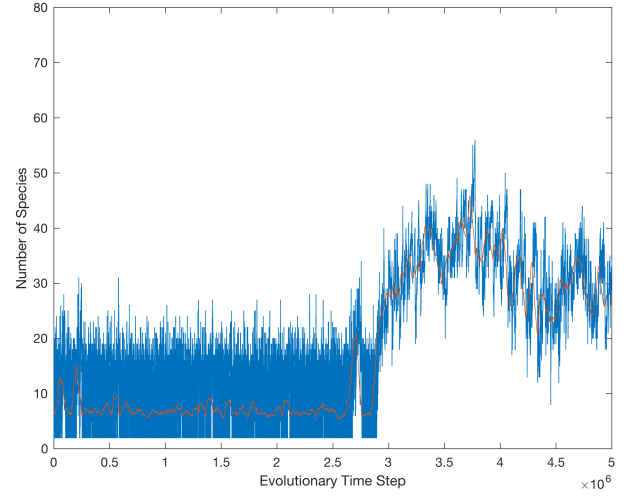
(b) $c = 0.7$, $R = 10^{-4}$

Figure 22: Examples of Long-term Change

It may take much longer simulations than were originally tested in order to understand the behaviour of a parameter set. For example, consider Figure 22(b), where a qualitative change in the behaviour of the system does not occur until almost 3,000,000 evolutionary timesteps have elapsed.

(a) Box-counting Dimension
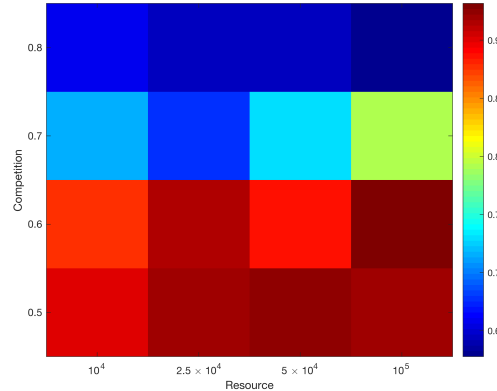
(b) Hurst Exponent

Figure 23: Properties of the Diversity Time-Series

For all parameter choices, the box-counting dimension of the diversity time-series takes a non-integer value between 1.1 and 1.4 (Figure 23(a)), in agreement with analysis of the fossil record that indicates a fractal time-series of species diversity in the Earth's history [50]. In all cases, the average Hurst exponent over all the simulations is greater than 0.5 (Figure 23(b)). This indicates that in general trends are likely to persist, in that an increase in diversity is more likely to be followed by another increase, and a decrease more likely to be followed by another decrease. When the competition parameter is low ($c = 0.5$), the Hurst exponent is particularly large, suggesting that for these parameters we are more likely to see monotonic or stable patterns in diversity, rather than wild fluctuations.
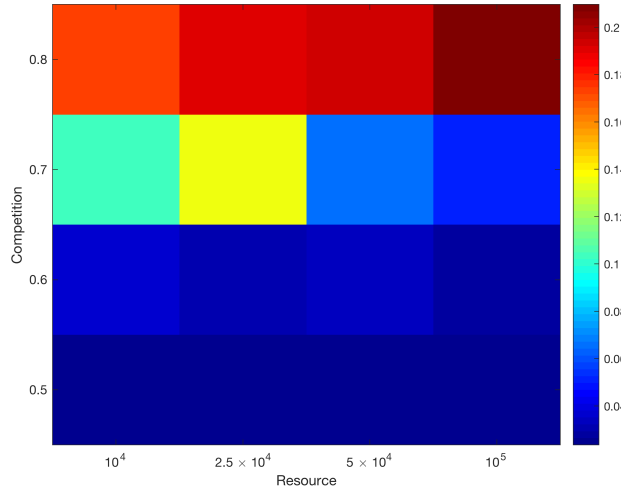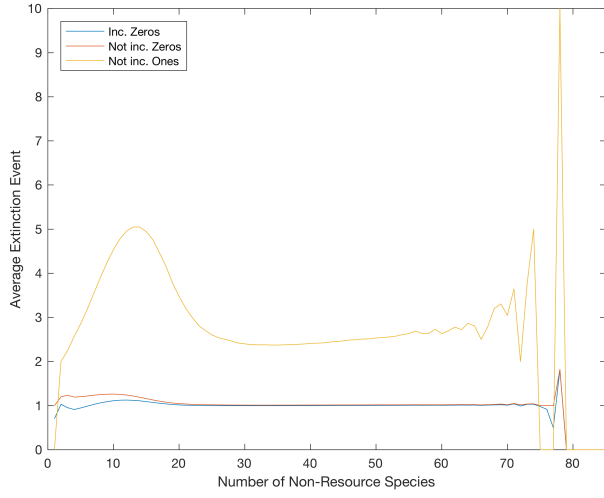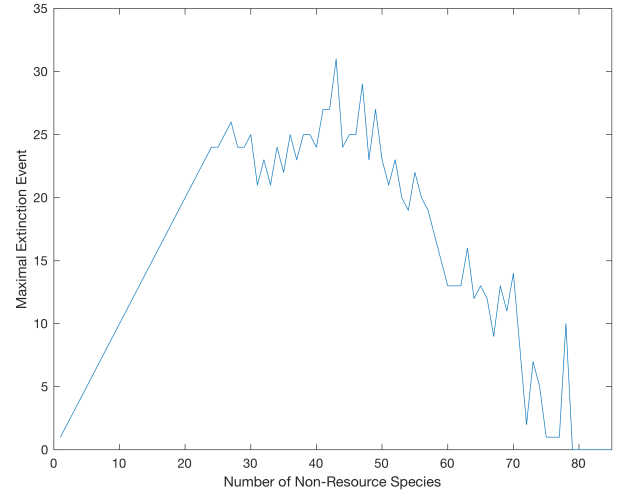
Figure 24: Average Fractional Extinction event sizes per Model Parameters

(a) Average

(b) Maximal

Figure 25: Absolute Extinctions per Prior Number of Non-resource Species
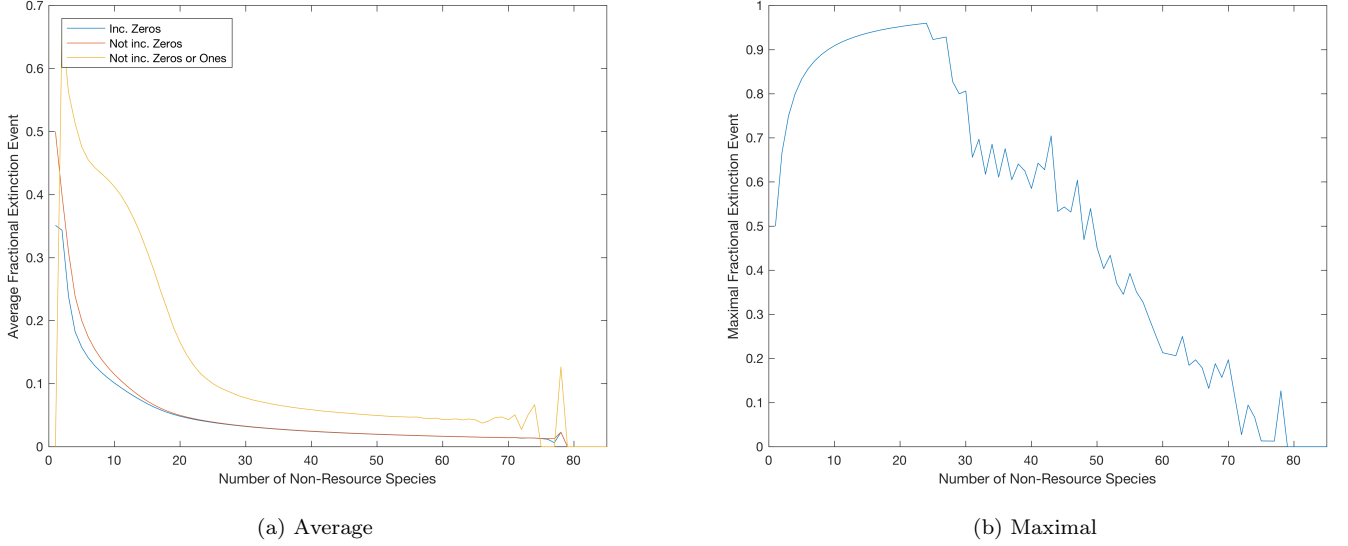
(a) Average

(b) Maximal

Figure 26: Fraction of Web extinction per Prior Number of Non-resource Species

We see (Figure 24) that high c systems suffer much greater fractional extinctions as a result of the perturbation to the system induced by the speciation mechanism. This is in agreement with the experiments in Section 8, where such webs were more susceptible to extinctions caused by perturbing the resource. In this case, low c systems allow greater species diversity, as we see from Figure 22. When zero-extinction events are excluded from consideration, all values are scaled up slightly but the pattern remains the same. Higher diversity networks appear to be more stable to the addition of new species (Figures 25-26), although they are negatively correlated with Robustness (Figure 17). How to resolve this tension is not obvious, although a case could be made that the correlations for diversity (as opposed to those for connectance) are strongly determined by outliers at very high and very low diversities. Provided that all other factors (in particular, R) are constant, higher diversity networks will necessarily have lower average populations as the total biomass is constrained by R and λ. Uniformly decreasing the populations of all species as the perturbation of resource decrease propagates through the system will therefore cause more extinctions in a high diversity network, but this is quite a different proposition to testing the ability of species to adapt to a change in the composition of the food web such as the removal of one of its competitors or prey species.

The stability-diversity relationship of food webs has been of interest since May's result [54] that, using linear stability analysis, larger networks are less stable. We test the number of extinctions that result from the perturbations caused by invasion events. From almost 4×10^8 total invasion events over 80 simulations, the average fractional extinctions decline as a function of prior species diversity (Figure 26(a)), as do maximal fractional extinctions for S greater than 25 (Figure 26(b)), suggesting that sufficiently large networks have greater stability. The maximal absolute extinction events peaked at approximately $S = 45$ and declines for larger prior species diversity (Figure 25(b)). However, we should note (Figure 21) that the largest average diversity for any parameter set in this experiment was also around $S = 45$. Therefore, there are likely to be relatively few events with prior diversity much greater than this, so if a "large" or maximal extinction event per prior diversity has a set small probability of occurrence then it may simply be that we do not observe these in our simulations for high levels of prior diversity.

11. Trait Frequencies

We return to the simulation from Section 4, and examine the frequencies with which each of the 500 traits occur according to the number of present species which possess them at each evolutionary timestep (*not* accounting for biomass). We also present the corresponding phylogenetic graph of the final species in the simulation (Figure 27(a)), showing the period over evolutionary time for which they and their direct ancestor species exist continuously in the system (horizontal line) as well as the relationship to their parent species (vertical line. We also plot the lifespans over evolutionary time of the 500 species who persisted for the longest periods of evolutionary time (Figure 27(b)) out of any in the simulation. As is typical for this model, species are constantly being replaced by invaders, and no species is able to persevere for a significant portion of the simulation.
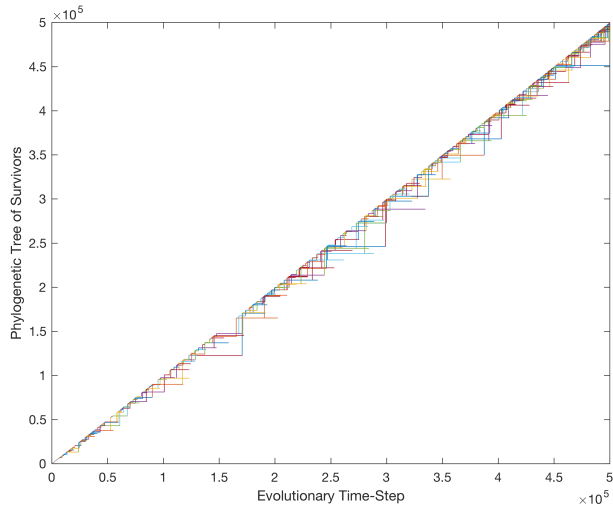
(a) Ancestry of Final Food Web
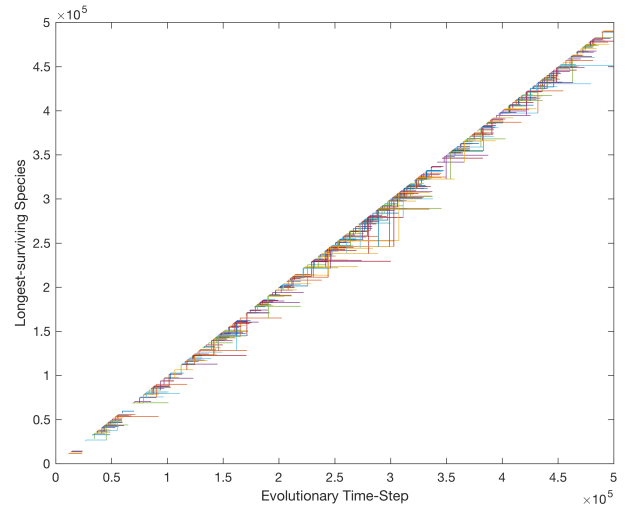
(b) 500 Longest-surviving Species

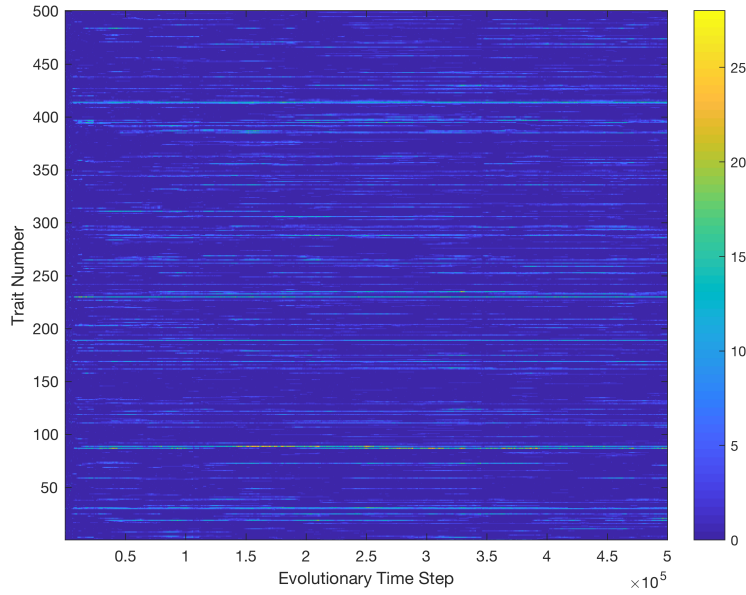Figure 27: Phylogenetic Trees for simulation

Figure 28: Trait Frequencies during the Single Cell Simulation

We observe (Figure 28) that despite the constant turnover of species shown in the phylogeny plots, some traits are the most popular and remain so throughout the entire simulation, probably because they score well against the resource. Analysing the equivalent plots for the many long runs in Section 10, it seems that the patterns of preferred traits are very clear for low c, but become obscured as c increases. The question then is, what is the mechanism by which species are constantly replaced as evolutionary time elapses, whilst maintaining the pattern of popular traits?

To investigate this, we first consider the average and maximum scores for realised predatory relationships, both in general and against the resource specifically. We collect this data for a 300,000 timestep simulation.
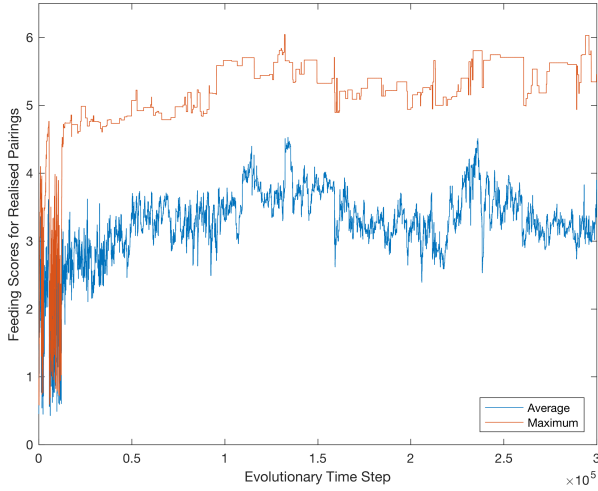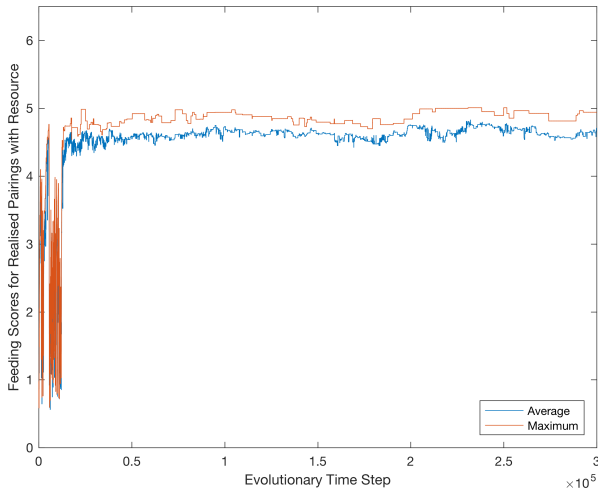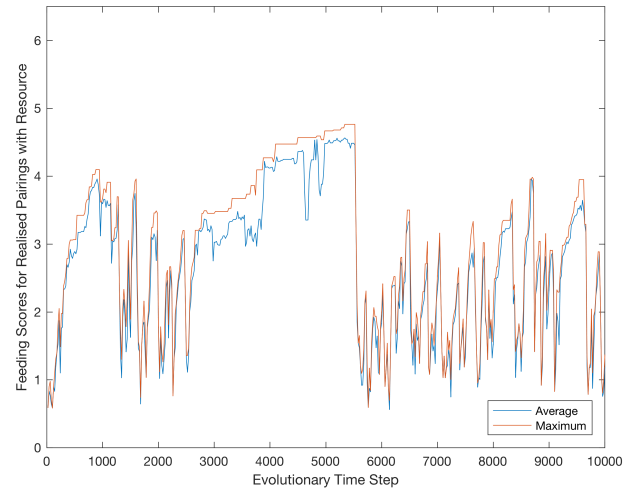
(a) Whole Simulation
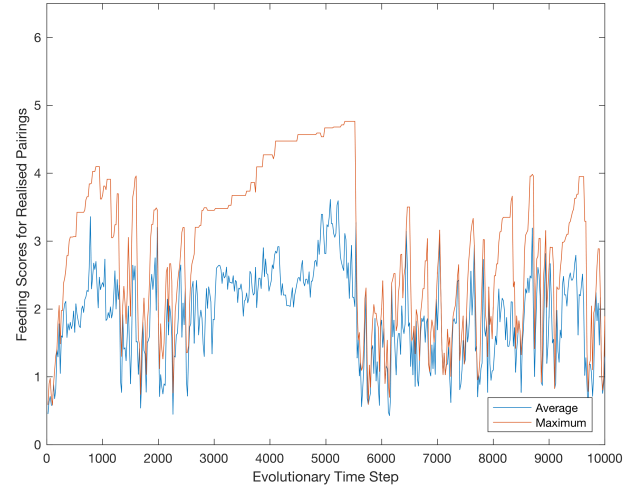
(b) Early Simulation

Figure 29: Feeding Scores of Realised Predator-Prey Relationships

(a) Whole Simulation

(b) Early Simulation

Figure 30: Feeding Scores of Realised Feeding Relationships against the Resource

As we saw in Section 4, early in the simulation the network is in a "pre-complexity" or transient state where it attempts various arrangements before finding one that allows a more complex web to be built. During this period the diversity goes through cycles of building up and then collapsing down (Figure 3(a)). This may be repeated several times until a stable set of species is found. The average realised feeding scores undergo a very similar pattern in the early stages of the simulation (Figure 29(b), 30(b)). However, we see that after a long time the species in the system have become well-adapted to feeding on the resource, and the scores no longer vary much with time compared to the full set of feeding relationships (Figure 29(a)). These general relationships do show some cycling, with the maximum and average feeding scores around the 130,000th time step not being matched again until after 240,000 timesteps. What is driving this system to keep changing its species composition if it is not improving overall? It seems that some species invasions, although the species itself is well-adapted, are not beneficial to the rest of the community, and it may take hundreds of thousands of speciation events to recover the system from such an invasion. Is a cycle of the same small number of species occuring? Analysing one example of the long runs from the previous section, we find 150,000 unique species occur in the first 155,260 steps of evolutionary time. These consist of 13 examples of a species occuring 4 times, 227 species which occur 3 times, and 4767 species that are repeated once. The remaining 144993 species only appear once within that evolutionary timeframe. So it seems that whilst some species are being repeated, it is not occuring often enough to account for the entire cyclical behaviour of the network.

The populations of species on higher trophic levels are often small enough that being selected as the parent for speciation could result in extinction due to the parent losing 1.0 of its population. To ensure that this is not the cause of the evolutionary turnover, we performed an additional set of simulations where the parent loses only 10^{-6} of its population at speciation. The phylogenetic graphs of these simulations are slightly sparser, indicating that the parental-extinctions do contribute to evolutionary turnover, but the effect of continual species turnover continues. Invasion, not forced extinction due to low-population species being selected for mutation, is the main driver of turnover. We also note that using the current speciation mechanism, these low-population species are also much less likely to be selected for mutation anyway. One paper [30] studied the statistical impact of speciation in the Webworld model in some detail. In particular, they found that the parents, prey and other (non-parental) competitors of the newly-added species are more likely than average to go extinct as a result of the invasion. This indicates that both predation and competition from the invader is unseating established species and driving the turnover. They offer the following justification for the process: "New species on level one, for example, can out-compete older level 1 species, leading to their extinction, and possibly to the extinction of any level two species that fed on the old species (an upwards effect). However, a new level 2 species could arise that is a better adapted predator that causes its level 1 prey to go extinct (a downward effect) . . . With coevolutionary effects in both directions, species that are successful at one time do not remain successful for ever."

We note some observations from the original paper [1]: (a) the inclusion of adaptive foraging prevents the model from reaching a state where better-adapted species cannot invade, (b) Basal-only systems reach an uninvadable state. This means that even though competition was noted in Quince et al's work [30] to be an important factor of species displacement at invasion, it cannot be sufficent since it is present in the basal-only simulation. This reinforces the conclusion of that study that both predation and competition by new species on established ones are components of the driving mechanism of species replacement. Drossel et al also observed (c) that there are multiple uninvadable basal-only states, and they usually do not include the best-scoring species unless c is very high and so the relative pressure to choose having the best feeding scores over avoiding competition is increased.

We hypothesise that the resource's traits favour some area of the 500-dimensional fitness landscape. Competition constrains the size of this landscape that can be occupied at any given time, and then either the pressure of predation drives an evolutionary cycling effect within this restricted favourable region of the fitness landscape, unless a well-adapted invader destabilises the community such that the driving mechanism is an attempt to recover to the optimal state that existed prior to this invasion.

To test the influence of the resource on the resulting traits of species in the system, we develop an index to quantitatively measure the similarity of trait distribution between a pair of ensembles: Across the final 100 evolutionary timesteps of a simulation, we count the number of times that a given trait is among the 10 most common traits by species. The 10 traits which satisfy this criteria most often are the top 10 traits for that simulation. Then for a given pair of simulations, we count the occurrences of pairs of the same traits, and normalise by dividing by 10. So for example an index of 0.3 means that there are three traits that occur in the top 10 for both simulations. We perform 90 simulations with the same resource and same trait matrix, 90 simulations with the same resource, trait matrix, and first species, and finally a control set of 90 simulations with the same trait matrix only. In all cases, $R = 1 \times 10^5$ and $c = 0.6$. We compare the average trait comparison index across all $(90 \times 89)/2$ pairs of ensembles between these three sets in order to determine if the resource, first species or neither give rise to the same final subset of traits.

Fixed Features:	Score Matrix	Scores and Resource	Scores, Resource, Initial Species
Average Index	0.0297	0.4365	0.4533
Average Final Diversity	39.7	38.5	38.4

Table 3: Trait Index of 90 simulations for three scenarios

Given that the number of species present in the final food web is usually between 30 and 50, these results (Table 3) provide compelling evidence that the choice of resource, representing the external environment in this model, has a strong determinative effect on the final composition of the food web in terms of the traits that are commonly present, even though the species themselves are subject to constant change. Keeping the first species, which could be thought of as the initial condition of the simulation, constant has a relatively minor cumulative effect by comparison.

12. Frequency of Success and Collapse

For all data presented in this paper apart from this section, if the simulation fails to complete due to the extinction of all non-resource species, the experiment is considered a failure and restarted, in order to only compare complete simulations. For this next experiment however, we allow simulations to collapse altogether as we test the ability of a drawn resource and initial species to result in a viable ecosystem. 10,000,000 experiments are performed where we draw initial species and run the simulation with $R = 5 \times 10^4$ and $c = 0.6$ for 10,000 evolutionary timesteps.

Total failure rate:	0.619
Fraction which fail in the first evolutionary timestep:	0.571
Fraction of successes with 10 or more non-resource species after 10,000 steps:	0.518
Fraction of successes with 20 or more non-resource species after 10,000 steps:	0.035

Table 4: Success and Failure rate of Webworld simulations

In all of these simulations (Table 4), if any one of them failed within the 10,000 timesteps tested, the failure *always* occurred within the first 10 evolutionary timesteps.

Next we performed more than 1500 simulations of 1,000,000 evolutionary timesteps with $R = 10^4$ and c in the range $[0.59, 0.90]$, finding no instances of total extinction occurring after the first 10 timesteps. Finally, when we sought 500 successful simulations with 120,000 timesteps, only 54 failed. Of those, 23 failed within the first timestep, and the remaining 31 all failed within the first 10. Together with the statistical results from the 10,000,000 short-simulation experiments performed above, we can be confident that total annihilation beyond the 10th timestep is extremely rare, if even possible.

13. Conclusions

We have collected many new ecological properties of food webs constructed by the Webworld eco-evolutionary food web model, including time-series of the species composition and average and maximum trophic levels, and studying the trophic webs as well as taxonomic webs. Network properties including clustering coefficients are given for the networks it generates, and an intermediate exponent between link-density scaling and constant connectance is found to be supported for a variety of implementations. We have studied the long-term evolution of model networks in new detail, analysing the popularity of certain traits for a given simulation, and the frequency of distribution of extinction events in much longer simulations than previously considered. In particular, it appears that neither a power law nor an exponetial law is supported by the data.

With the progress of complex networks as a discipline in recent years, theoretical ecologists have stressed the need for studies of the response of model networks to perturbation to be based on webs featuring realistic structure and the response of population dynamics that are not too simplistic. In this paper, new results are obtained pertaining to the stability of food webs generated by the Webworld model, and to the stability-complexity debate in general. We collect community robustness results for the first time using this model, finding support for the hypothesis that (in all its forms) it increases with connectance. However, it decreases with diversity and link density. Consistent with this, robustness is greatest for low Resource, high Competition parameters - which produce low diversity, high connectance food webs. Therefore in this sense, large food webs are less stable. Similarly, species deletion stability decreases with diversity, approximating 0.6 for large webs. However, we find that whilst the likelihood of no additional extinctions decreases, it is also true that the average size of the secondary extinction events as a fraction of the web decreases. Therefore, using this measure of stability, as diversity increases the webs could be said to increase or decrease in stability depending on the precise definition employed. This is symptomatic of many questions regarding food web patterns and ecological modelling, where a variety of definitions and measures often yield seemingly contradictory results. Next, we considered the effects of a serious perturbation to the environment by reducing the resource species' biomass. The effects of this are not particularly surprising: the greater the reduction, the more severe the consequences for the ecosystem. We do find that systems with higher c and therefore lower diversity generally suffer greater diversity loss. Finally, we studied the size of extinction events resulting from invasion events. Previous papers have considered the size distribution of such events for single simulations, however we looked at fractional extinctions as a function of prior diversity and other food web properties. For both the average and maximal cases, a clear decrease is observed beyond $S \approx 25$, so in this sense larger food webs are more stable to the perturbations caused by invasion of species similar to those already present in the network.

For our future work, we have constructed a spatially-explicit metacommunity variant of the Webworld model, and are studying the impact of different mechanisms for species dispersal between sites on the local networks. However, other possibilities for study in the non-spatial model could include systematically testing the effect of varying the thresholds for numerical convergence, or introducing mutations of variable size within a simulation. A further possibility would be incorporating age and stage-structuring of species, or the model could be combined with explicit modelling of body-size as used in other eco-evolutionary models [10, 11] in order to allometrically scale the ecological efficiency and mortality rates of different species.

14. Funding

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