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Creating Realistic Dynamic Food Webs using an Agent-Based Model

Introduction

Ecosystems are facing increasingly intense and frequent disturbances including climate change, land use change, and overexploitation. As a result, there is growing interest in quantifying the "stability" of a community – its capacity to withstand or recover from such disturbances (Van Meerbeek et al., 2021). Furthermore, species don't exist in isolated vacuums; within communities, they are connected by various modes of interaction such as competition, facilitation, and predation. A disturbance to even one species can propagate throughout the entire community through these links, producing community-level changes in species abundance and composition (Dunne et al., 2002). This has troubling implications for both ecosystem health and ecosystem function. Disturbances can cause biodiversity loss, but they can also precipitate the loss of ecosystem services if species providing these services are negatively impacted (Keyes et al., 2021). Ecosystem services are the benefits that people obtain from ecosystems, such as the provisioning of natural resources, regulating services including water filtration and carbon sequestration, and cultural benefits (Millennium Ecosystem Assessment, 2006). Understanding the interaction structure of these communities can help predict when large changes are more likely to occur in response to disturbance. Thus, it is imperative to evaluate community not just as a set of individual species, but as an ensemble that depends on the interactions of its species.

Many studies have investigated the robustness of a community to secondary extinctions, which are subsequent extinctions that occur due to loss of prey or other dependencies between species (see Dunne et al., 2002; Eklof et al., 2013; Keyes et al., 2021). In particular, there is substantial interest in relating how various aspects of food web structure can lead to differences in community robustness. Previous work in this area has largely used only static food webs. That is, they rely on the assumption that the food web of an ecosystem does not change over time except through the loss of extinct species and those species' interaction links. However, we know that this assumption does not always hold in reality. For example, predator species are frequently able to "rewire" their interactions to new prey species when their preferred prey is no longer available (Staniczenko et al., 2010). Perhaps more importantly, these studies typically consider food webs at the local meta-community level. This means that the species observed in a given community should be only a subset of the species that could feasibly persist there. A local extinction could lead to opportunities for invasion by species not currently present in the local community, introducing new species altogether to the food web. Under the static food web framework, we cannot incorporate this mechanism and capture the entire picture of community assembly, disassembly, and succession. Thus, we must move beyond this current model in order to more accurately represent and predict community dynamics following disturbance.

Agent-based models (ABMs) have been successfully used in a variety of research areas in biology and ecology, leading to new insights of how animals behave both individually and as a group, and interact with one another as well as their environment. However, most of these models have been developed to reproduce the behavior and decision-making process of each organism, and predict the aggregate patterns that subsequently emerge. While there is a rich theory of assembly and successional dynamics in ecological communities, ecologists have yet to take full advantage of the ABM framework here. Savage and Askenazi developed the ABM

Arborscape to explore community assembly following disturbance, though this model was specifically developed to model the successional dynamics of plant and tree species (Savage and Askenazi, 1998). As such, it does not model the immigration and establishment of mobile organisms in the community, and it also does not include any trophic interactions. Other studies make other simplifying assumptions, including spatial homogeneity (Hraber and Milne, 1997) and limited between-species interaction (Topping et al., 2003). Norling and Armstrong developed an ABM based on predation among species in a community and include mechanisms for both speciation and invasion (Norling, 2007; Armstrong and Norling, 2023). As a result, this model produces simulations of community dynamics over time as new species immigrate into the community, existing species evolve to better fit available ecological niches, and species go extinct due to predation and competition. However, the communities generated by this model show key differences in food web structure and complexity compared to empirical food webs.

I follow the general framework established by Norling and Armstrong and build an agent-based model of local community dynamics within a global community. By using a different model to generate the global species set and food web, I first aimed to create simulated local communities that more closely match empirical food webs. My second aim is to explore the factors that determine the dynamic behavior of food web evolution. I did not get very far with my second aim, as I ended up spending much more time debugging my simulator than originally anticipated! The end goal of this project was (and still is) to build a more flexible and ecologically realistic agent-based model of community dynamics to investigate how local communities will respond to disturbance and the drivers of ecosystem stability.

Methods

The first component of the model is the global community, defined as a food web $G = (V, E)$b. V is defined as the set of all species that could feasibly persist in a local community and E is defined as the set of all feasible pairwise trophic interactions between two species in V. Thus, each instance of a local community within this global community can be described by $g = (v, e)$, where $v \subseteq V$ and $e = \{(x, y) \in E \mid x, y \in v\}$. To generate an ecologically realistic global community, I implement the basic niche model as described in Williams and Martinez (2000). Originally proposed as a simple model of trophic interaction within an ecosystem, it builds on the cascade model (Cohen and Newman, 1985) by limiting the feeding range of each species. A key advantage is the simplicity of the niche model: it only requires the number of species S and the observed connectance of the food web, calculated by $C = \frac{L}{S^2}$, where L is the number of links in the food web. As a result, it is very easy to generate an arbitrary set of synthetic food webs that vary in their size and connectance. The niche model assigns a uniformly random niche value n_i to each species i in the ecosystem. The model then assigns species i a feeding range center c_i such that $c_i < n_i$, as well as a feeding range r_i drawn from a beta distribution with $\alpha = 1$ and β free. A species j is then eaten by species i if its niche value n_j falls within the feeding range $[c_i - \frac{r_i}{2}, c_i + \frac{r_i}{2}]$ of species i. Williams and Martinez (2000) derive a closed-form solution for the free beta distribution parameter β that yields a synthetic food web which achieves the specified connectance C in expectation.

For a specified number of species S and expected connectance C, I generate a global set of species along with their niche model values n_i, r_i, and c_i. The global community $G = (V, E)$ is then created based on the trophic interactions implied by the niche model values of each species. A species is designated as a plant species if its feeding range does not contain the niche value of any other species. I calculate the prey-averaged trophic level of each species in V,

following definitions in Williams and Martinez (2004). Each species i is then assigned a metabolism value m_i based on its trophic level relative to the maximum trophic level of any species in G. m_i is defined by an increasing, concave-down function such that plant species (with trophic level 1) have $m_i = 0$ and apex predators have $m_i = 1$. This reflects the assumption that carnivores must feed more frequently than herbivores, and that this energy requirement typically increases with trophic level.

For such a given global community, I simulate the dynamics of a local community with the agent-based model described here. An environment is initialized as an empty 100x100 array. A single organism occupies a single 1x1 cell, and its neighboring cells are considered the 8 cells directly adjacent to it (4 side cells and 4 corner cells). The environment is "looped" such that the left and right boundaries are connected and the top and bottom boundaries are connected. Each organism is described by its current location, its species, and its energy level. A single timestep follows the below sequence:

1. Choose a random species in V to add to the local community at a random unoccupied cell in the environment, with energy level = 1.
   a. The first species added to a newly initialized environment must be a plant species.
   b. For plant species, a neighboring unoccupied cell is one that is not occupied by any other species.
   c. For animal species, a neighboring unoccupied cell is one that is not occupied by any other animal species, but may be already occupied by a plant species.
2. The existing organisms in the environment are shuffled, and then for each organism:
   a. If the organism is dead (energy level = 0), skip over its actions in the timestep.
   b. If the organism is a plant:
      i. If the organism has no unoccupied neighboring cells, skip over its actions in the timestep.
      ii. Add 0.1 to its current energy level.
      iii. If the organism has energy level $e > 1$ and has unoccupied neighboring cells, reproduce.
      iv. The offspring is placed in a random unoccupied neighboring cell, set parent energy level = 1 and offspring energy level = $e - 1$.
   c. If the organism is an animal:
      i. If the organism has suitable prey in its neighboring cells as determined by the global food web G, randomly choose a suitable prey.
      ii. The probability of successful predation is given by Bernoulli trial based on how close the prey's niche value is to the center of the organism's feeding range.
      iii. If predation is successful, the organism moves to its prey's cell, increase organism energy level by 0.25•energy$_{prey}$, and set prey energy level = 0.
      iv. If predation is unsuccessful, the organism stays in its cell.
      v. If the organism does not have suitable prey in its neighboring cells, the organism moves to a random unoccupied neighboring cell.
      vi. If the organism has energy level $e > 1$ and has unoccupied neighboring cells, reproduce.
      vii. The offspring is placed in a random unoccupied neighboring cell, set parent energy level = 1 and offspring energy level = $e - 1$.
      viii. Decrease organism energy level by 0.1• m_i.
   d. Remove all dead organisms (energy level = 0) from the environment.

All models are implemented in R. I used a factorial experimental design for creating global communities, varying the number of species S as 25, 50, and 100 species, and expected connectance C as 0.1, 0.2, and 0.3. Due to time constraints, I could only generate one replicate global community for each (S, C) pair. After generating each global community, I initialized an instance of its local community and iterated it for 1,000 timesteps, with "snapshots" of the environment taken every 10 timesteps. At each snapshot, I record the species identities present in the local food web g and the abundance of each present species. I also compute the values of the following network structure metrics, as determined by the local food web:

- Number of species S present in the local food web.
- Connectance C of the local food web.
- The fraction T of species in the local food web that are top predators; that is, the proportion of present species that have no present predators.
- The fraction B of species in the local food web that are basal species; that is, the proportion of present species that have no present prey.
- The fraction I of species in the local food web that are intermediate species; that is, the proportion of present species that are neither top predators nor basal species.

Results

Figure 1 shows the number of total occupied cells in the 100x100 environment over time for a global community with $S = 50$ and $C = 0.1$. Though all local communities seemed to show cyclical dynamics to some extent, there was substantial variation in both amplitude and periodicity of cycles for different global communities. Additional replicates for each combination of (S, C) could help determine whether there are systematic differences in the cycles of productivity experienced for different global communities.
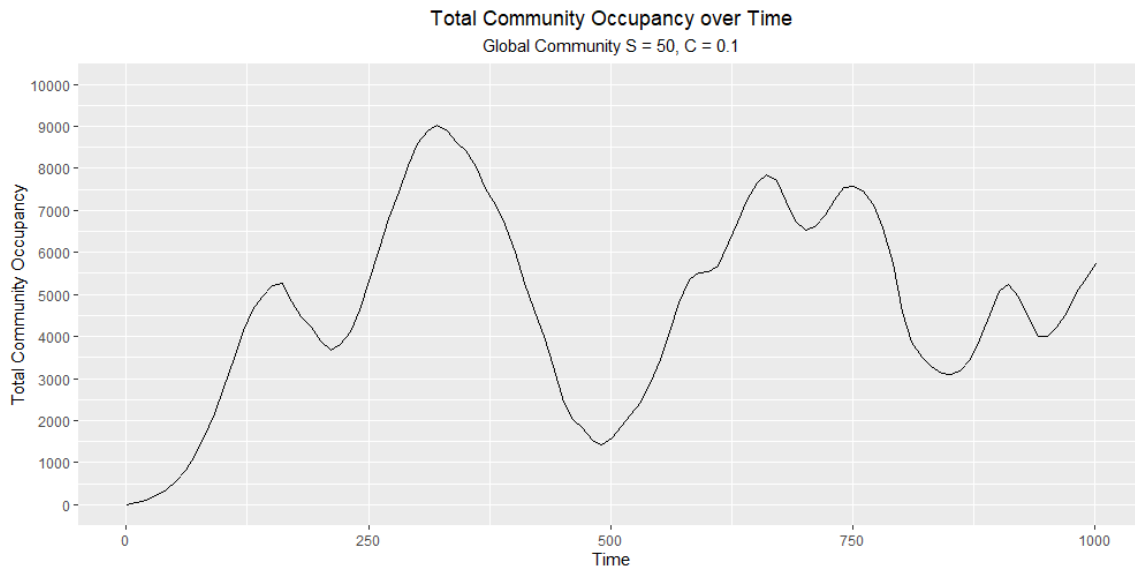

Figure 1. Total number of occupied cells in the 100x100 environment. All local communities exhibit cyclical dynamics to some degree, regardless of the parameter values for the global community.

Closer examination of community dynamics at the species level verifies that abundances for individual species are also cyclical in nature (Figure 2). This can be seen from snapshots of the environment for a global community with $S = 0.25$ and $C = 0.2$ at timesteps $t = 741$ and $t = 891$ (Figures 3a and 3b). Two plant species dominate the environment, with apparent competition occurring for space in the environment. The green species covers most of the environment at $t = 741$, and the environment transitions to one dominated by the yellow species at $t = 891$.
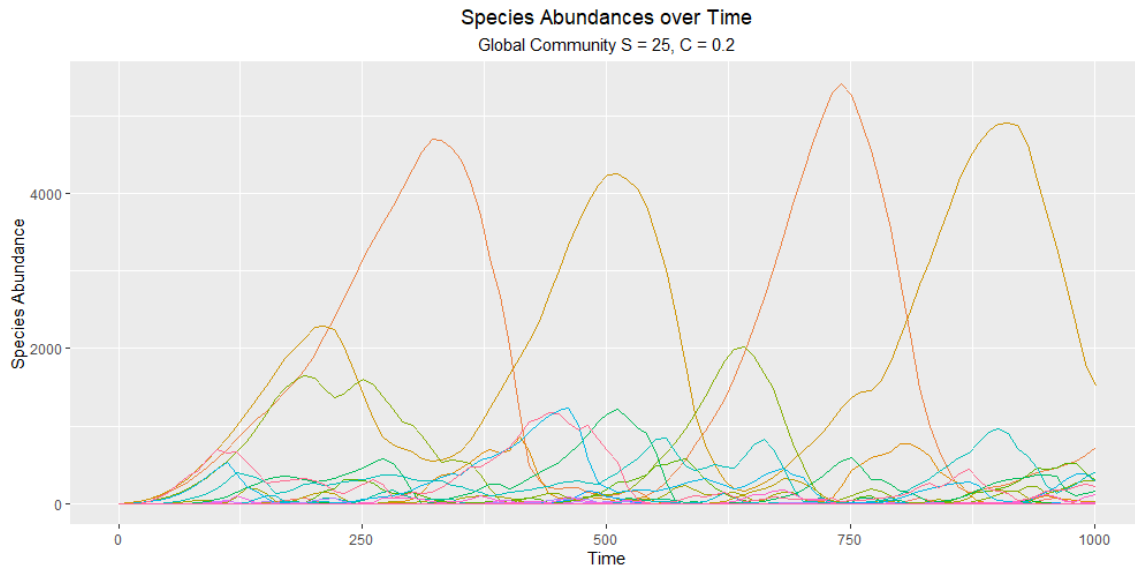
Figure 2. Species abundances over time for every species in the global community with $S = 25$ and $C = 0.2$.

Figure 3a. Visualization of a replicate's environment at $t = 741$.

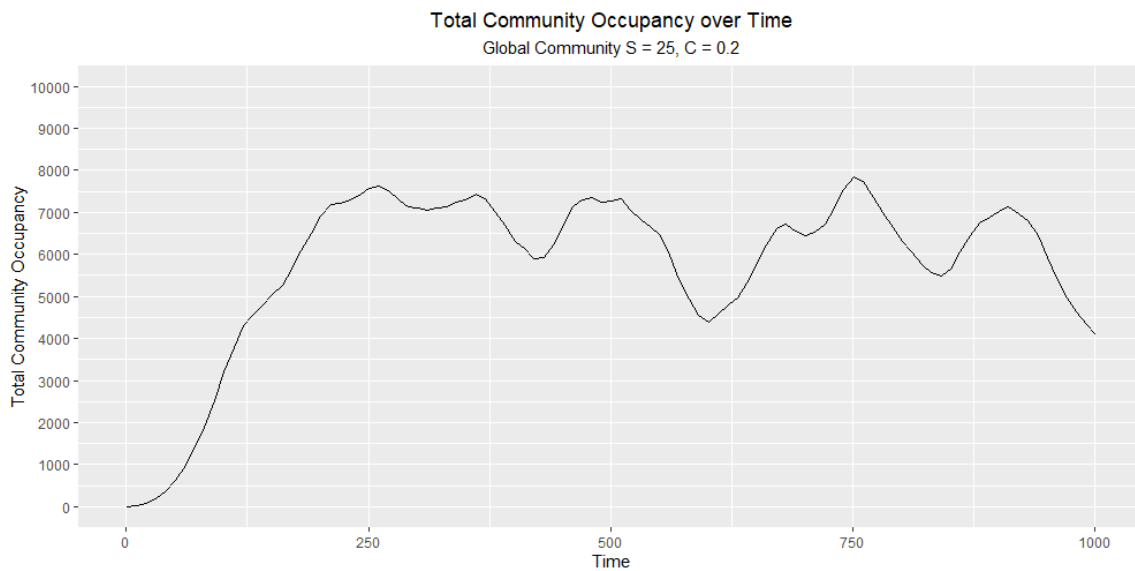Figure 3b. Visualization of the same replicate's environment 150 timesteps later, at $t = 891$.

Figure 3c. The total number of occupied cells over time for the same replicate.

This asynchrony in species abundances should lead to an overall stabilizing effect in community productivity, as there is always one species that is dominating the environment. Indeed, Figure 3c shows that the total number of occupied cells in the environment exhibits cycles with lower magnitude than the community described in Figure 1.

Figure 4 shows a snapshot of a local food web implied by the species present in the environment. In general, local food web size and connectance stays relatively stable over time though there is considerable turnover in the identities of present species. The size of the local food web did not seem especially sensitive to changes in the size of its global community. For global communities with 25 and 50 species, the size of the local food web typically fluctuated around 15 to 25 species. For global communities with 100 species, local food webs sometimes exceeded 30 present species (Figure 5a).
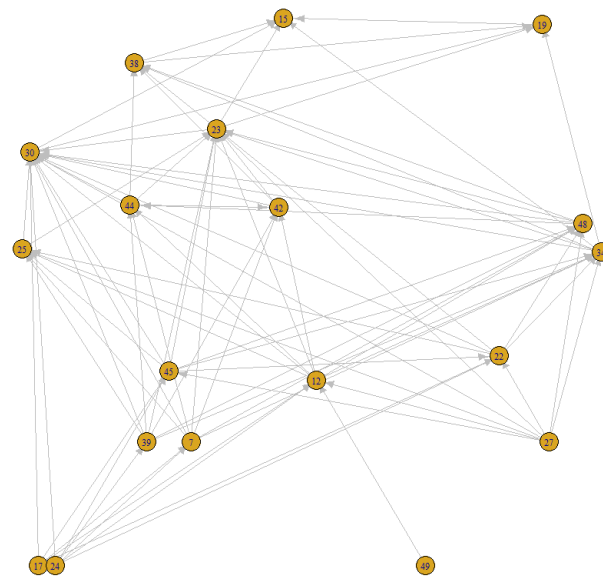

Figure 4. Local food web implied by the species present in the environment. Global community with $S = 50$ and $C = 0.3$.
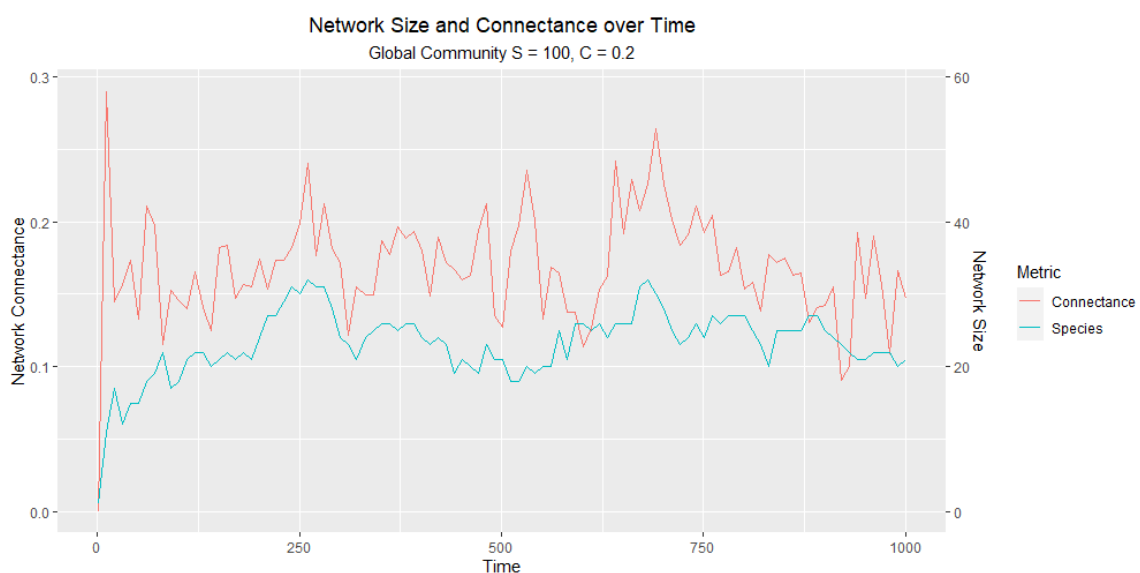

Figure 5a. Size and connectance of a local food web over time, for a global community with $S = 100$ and $C = 0.2$.

Local food web connectance seemed to covary more closely with the connectance of the global community. Global communities with $C = 0.1$ yielded local food webs with connectance values that fluctuated around 0.1 as well (Figure 5b). For global communities with $C = 0.2$, local food web connectance was typically 0.15. Lastly, global communities with $C = 0.3$ yielded local food webs with connectance values around $0.2 – 0.25$. Again, more replicates would clarify whether this correlation is systematic.
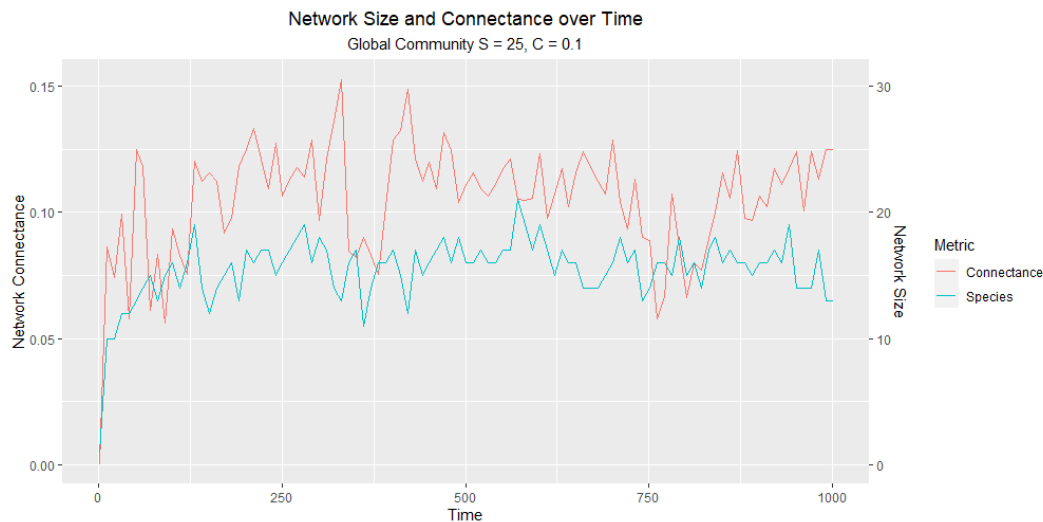

Figure 5b. Size and connectance of a local food web over time, for a global community with $S = 25$ and $C = 0.1$.

The mix of species types (basal, intermediate, and top) also tends to remain stable over time, and is typically well-balanced. It is rare for any one species type to exceed 60% of the present species in the local food web at any point in time, for all (S, C) combinations of the global community (Figure 6). Interestingly, for global communities with $S = 25$ and 50, we see much more distinct proportions of each species type as C increases (Figure 7a, 7b, and 7c). For both global community sizes, approximately 55% of all present species are Intermediate, 30% are Basal, and 15% are top. However, this pattern does not emerge for global communities with $S = 100$.
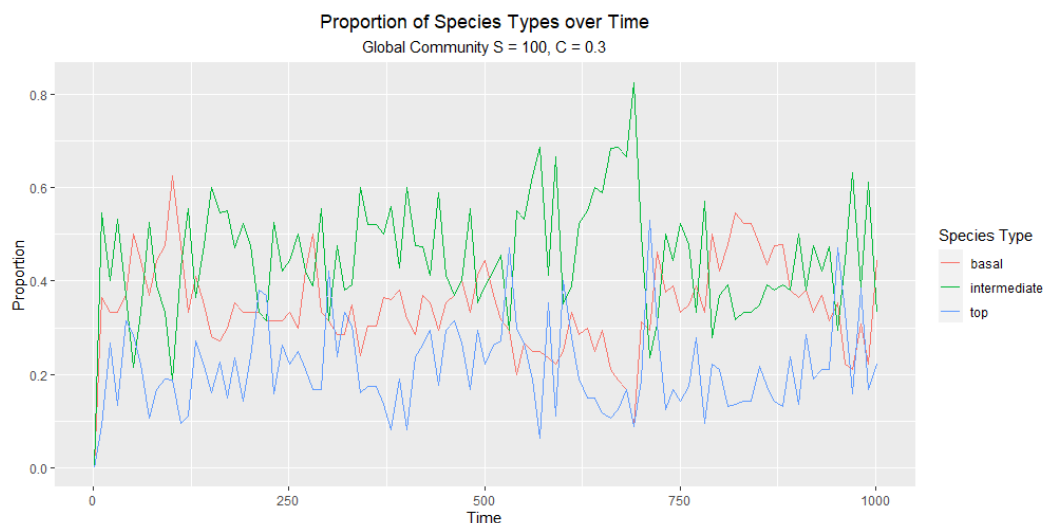

Figure 6. Proportion of total present species belonging to each species type, for a global community with $S = 100$ and $C = 0.3$.
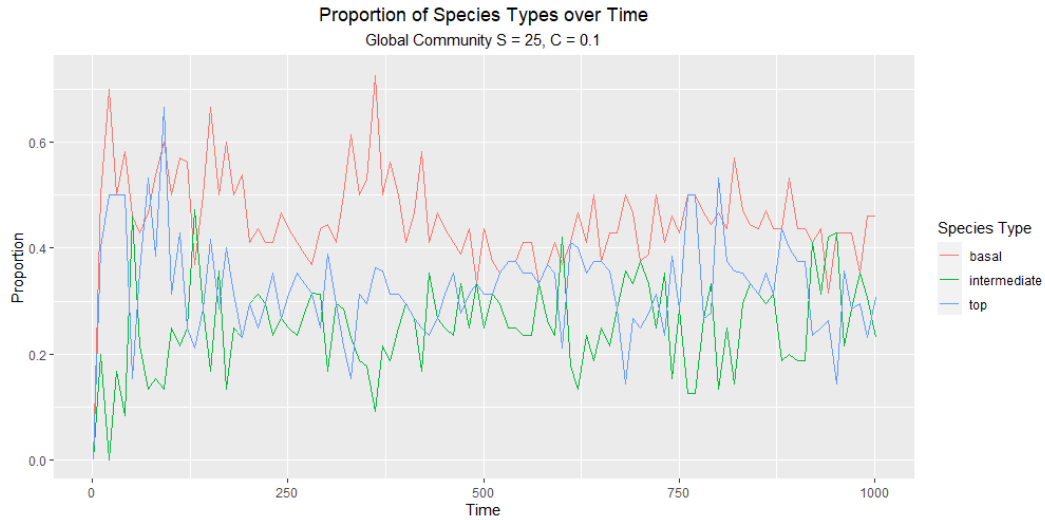
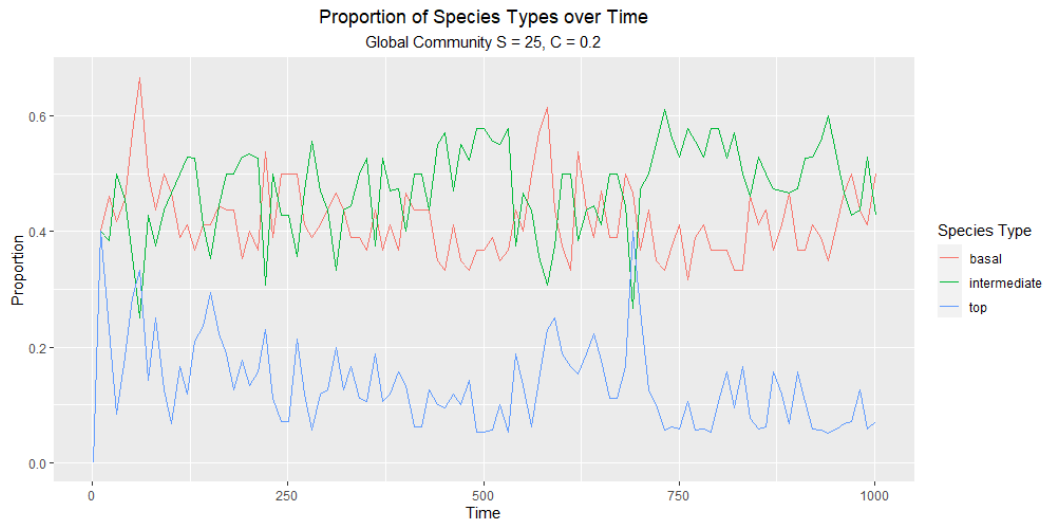Figure 7a. Proportion of total present species belonging to each species type, $C = 0.1$.

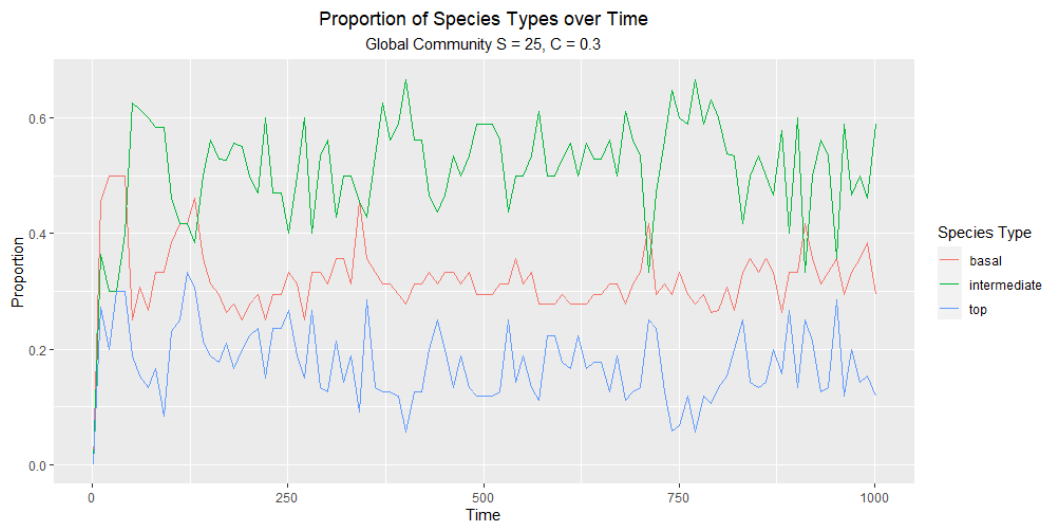Figure 7b. Proportion of total present species belonging to each species type, $C = 0.2$.

Figure 7c. Proportion of total present species belonging to each species type, $C = 0.3$.

Discussion

There are numerous directions for building on this preliminary analysis. First, there is obviously more that can be done with the current model by increasing the number of replicates and varying other model parameters. Next, there are other methods for generating the global community, including leveraging existing empirical community data. Lastly, there is opportunity for further investigation of how food web structure relates to community stability using this modeling framework.

 Due to the amount of time needed to iterate each replicate for 1,000 timesteps, I was only able to generate one replicate for each combination of (S, C) for the respective global communities. With more time, I would like to generate more replicates for each combination of parameter values. Doing so would yield a clearer picture of the roles that S and C play in influencing how the local environment and food web evolves over time. Importantly, it would verify that the general trends we observe here are not due to random chance. Additionally, there are many other parameters used in the model that can be varied to determine how they influence the results. This includes the parameters of the probability distribution that is used to determine whether a predator successfully consumes its chosen prey, the fraction of a prey's energy that is passed on to the predator, and scaling factor of metabolism that determines each specie's energy cost per timestep. Adjusting these parameters could lead to drastically different results. For example, the current simulations were conducted such that each organism lost $0.1 \cdot m_i$ per timestep. However, increasing this scaling factor would mean that predators at higher trophic levels will lose more energy per iteration of the simulation. As a result, predators (especially those at high trophic levels) will be less likely to persist in the local environment and possibly decrease the top-down pressure exerted on the community as a whole.

Another area of exploration is the mechanism used to generate the original global community. While the niche model has become a popular and widely used method of generating synthetic networks that resemble real-life food webs, it could be interesting to see whether we see qualitatively similar results when the global communities are generated using other models such as the cascade model or groups model (Allesina and Pascual, 2009). Perhaps the most interesting strategy is to use network data from empirical food webs. However, care must be taken to verify that the empirical food web was not constructed on a limited temporal and spatial scale. Well-studied long-term food webs built on observations from multiple sites are more likely to capture all species and interactions in an ecosystem, and thus represent a "global" community and not a merely local community. While utilizing empirical food webs would allow us to make more specific predictions about the effects of disturbances in a particular ecosystem, there may be less opportunity to attain more generalizable insights about the role of food web structure in promoting ecosystem stability.

Lastly, there is a rich literature in network science that should be leveraged in further exploring ecosystem stability. Here I only discuss the roles of food web size (S) and connectance (C), though there has been extensive work in relating other aspects of food web structure to stability. Cirtwill and Wootton (2022) identify certain motifs, specific subgraphs embedded within networks, whose presence are hypothesized to promote stability for the entire community. Modularity, the degree to which a network could be organized into distinct "groups," has also been shown to increase food web robustness (Stouffer and Bascompte, 2011). Future work should investigate how to manipulate other aspects of food web structure in generating the global community.

All source code, data, and additional figures are available on Github at https://github.com/heli8222/csci5423final.

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