Contents

1   Introduction

The ability to model and predict the effects that the changes in climate will have on ecosystems is a field growing in importance as the impacts of climate change continue to escalate. The relationship between the biodiversity of an ecosystem and its susceptibility to environmental changes is of particular interest due to the rapid decline of biodiversity across the globe. We present two complementary mathematical models of these effects on a simple plant ecosystem, where we consider the effects of changing precipitation. The modeling is centered on three key effects biodiversity can have a system: niche efficiency, the insurance hypothesis, and increased adaptability.

Niche efficiency is the concept that interspecies competition is generally less strong than intraspecies competition because different species tend to occupy different niches in the ecosystem, and so require different sets of resources [4]. This effect has been measured and modeled in multiple plant systems, often leading to diverse ecosystems having increased productivity compared to less diverse ones [6,7]. The magnitude of this effect will be a key variable in our modeling, represented as reduced interspecies competition relative to intraspecies competition.

The insurance hypothesis is the idea that a diverse ecosystem is more robust against a variety of environmental changes, since is is more likely that there exists a species with traits adapted to a set of changes [1]. Overall, this suggests that increased diversity tends to reduce variation in ecosystem level metrics (total biomass, population, etc.), although it may decrease stability for individual populations. This effect will be modeled using stochastic simulations and replicate ecosystems, as was done in [8].

Finally, the observations provided by the COMAP competition suggest that increased biodiversity can allow (or speed up) the adaptation of individual plants to changing environmental conditions. This could be due to some kind of microevolution of the population, increased amounts of functional diversity (as proposed by [5]), or some other unknown mechanism. We proceed using this observation as an empirical rule in our modeling, and make simplifying assumptions in order to extrapolate it to general systems.

1.1 Assumptions

We make the following assumptions:

1. We assume that there are a set number of species, who interact only through competition and possible adaptation effects.

2. We consider only competition for water, and assume that this is the limiting resource for plant growth.

3. We assume that intraspecies competition is stronger than interspecies competition, and that interspecies competition does not depend on the relative species. For simplicity, we also assume that competition is symmetric; i.e., $a_{ij} = a_{ji}$ (see section 2.1).

4. There are seasonal variations in water availability, as well as random droughts that occur. We model the droughts as effects that add on to a consistent seasonal variation, which likely is not true for real weather.

5. We also only consider two traits for species: general fitness (carrying capacity) and the impact of water on the fitness (water susceptibility).

6. That the adaptation effect occurs for any set of species, and is not dependent on their traits.

7. The key metric for a plant ecosystem is the total population, as a proxy for total biomass. We are particularly interested in its year-to-year stability and the effects from droughts

8. In a spatial representation (the cellular automaton model), the resources are constant across the whole area.

1.2 Variables

Continuous model:

t	Time in years
p_i	Population of species i
r_i	Inherent growth rate for species i
a_{ij}	Competition between species i and j, with $a_{ii} = 1$.
K_i	The carrying capacity of species i
b_i	The measure of inverse water susceptibility
$W(t)$	The amount of water at time t
$D(t)$	The drought effects at time t
$B(\vec{p})$	The biodiversity of ecosystem with populations $\vec{p}$

Cellular automaton model:

RpF	The reproduction factor for a given plant cell
I	Inherent value (i.e., fitness) for a plant species
N_s	The number of neighbors that are the same species as the plant cell
N_d	The number of neighbors that are a different species than the plant cell
C	Competition for resources of a plant cell
R	The total resources (water) in reach of a cell

1.3 Definitions

Continuous model	
carrying capacity	the maximum population supported by an ecosystem
water susceptibility	the impact of water on the carrying capacity of a species
Cellular automaton model	
neighbor	One of the eight surrounding cells to a given cell
neighborhood	Relating to the nine cell squared with a given cell as the center

2 Continuous model methods

The continuous models of the ecosystems, based on systems of first-order coupled differential equations, were all simulated computationally using the Scipy library (the "odeint" function) in Python; the default integration method was used in all cases.

2.1 Population dynamics

Our mathematical modeling is based on the competitive Lotka-Volterra equations, which model populations p_i competing with each other [2,3]. The equations are

$$\dot{p}_i = r_i p_i \left(1 - \frac{\sum_j a_{ij} p_j}{K_i} \right), \tag{1}$$

where r_i is the intrinsic per capita growth rate (births minus deaths), $a_{ij} = a_{ji} \in [0,1]$ is the competition factor between p_j and p_i, and K_i is the carrying capacity of the environment for population p_i. The carrying capacity here is directly related to fitness; if all competition factors are equal (e.g., $a_{ij} = 1 \ \forall i, j$), the species with the highest carrying capacity will eventually dominate the system. Using this equation we can include the effects of amount of water $W(t)$ on the carrying capacity with a function $K_i(W)$, varying between species.

Note that the competition factors are a direct measure of niche efficiency, where we set $a_{ii} = 1$ by definition (intraspecies competition). If $a_{ij} = 1$ for all pair i, j, then species compete for exactly the same resources (interspecies and intraspecies competition are the same), while if $a_{ij} < 1$ the species occupy different niches (and interspecies competition is less than intraspecies). If $a_{ij} = 0$ then j does not compete for i's resources at all. For simplicity, we assume $a_{ij} = a_{ji}$ for all of our modeling.

This equation can be written conveniently as a vector equation (using column vectors):

$$\dot{\vec{p}} = \vec{r} \odot \vec{p} \left(\mathbb{1} - \frac{A\vec{p}}{\vec{K}} \right), \tag{2}$$

where $\odot$ represents element-wise multiplication and division represents element-wise division. The matrix A and vectors $\vec{K}$ and $\vec{r}$ contain the same information as in eq. (1), but this form is convenient for computational purposes and notational. From this we can immediately find

the equilibrium for constant $\vec{K}$ by setting $\dot{\vec{p}} = \vec{0}$:

$$A\vec{p}_{eq.} = \vec{K} \implies \vec{p}_{eq.} = A^{-1}\vec{K}$$

2.2   Species variation

In order to create variation between species (apart from overall fitness), we use the function

$$K_i(W) = K_{i0}\left(\frac{1 + b_i}{b_i}\right)\frac{b_i W}{1 + b_i W}, \tag{3}$$

which is shown below in Figure 1. This function (based on a Type II functional response from mathematical ecology [3]) allows b_i to function as a kind of inverse water susceptibility factor, where larger b_i reduces the importance of water on the fitness of a species. This can be beneficial in dry weather, but harmful in wet conditions (when the species cannot make use of the water available). Conversely, small b_i allows a species to grow in wet seasons while making the species less fit in dry seasons. This balancing, while simplistic, allows us to separate the overall fitness from the varying effects of water on a particular species.

A final feature of this function is its asymptotic behavior. This allows us to increase b without limit (see section 2.1.5), while keeping the effect on the system bounded.
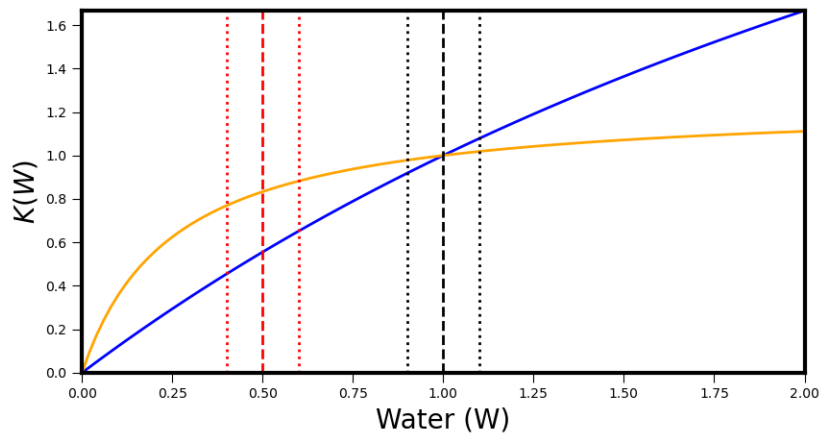

Figure 1: The water susceptibility for $b = 4$ (orange) and $b = \frac{1}{4}$ (blue). The blue curve represents a plant that can outperform in wet conditions and the orange curve represents a plant that can perform about the same for a variety of conditions. The vertical black lines represent examples of the mean rainfall (dashed) and the seasonal variation (dotted), and the red lines represent the same variation but in drought conditions.

2.3 Weather variation

Finally, we can model the amount of water available with

$$W(t) = 1 + W_0 \sin(2\pi t) + D(t), \tag{4}$$

where t is in years, W_0 is the amplitude of variation, and $D(t)$ describes any other weather effects that may occur (including droughts). First we implemented a step function for droughts, but we shifted to a version of an inverse parabola to make the effect smoother:

$$D(t) = \begin{cases} A - \frac{2A}{1 + \left(\frac{2}{T}(t - t_0)\right)^2} & \text{if } t \in [C - \frac{T}{2}, C + \frac{T}{2}] \\ 0 & \text{else} \end{cases} \tag{5}$$
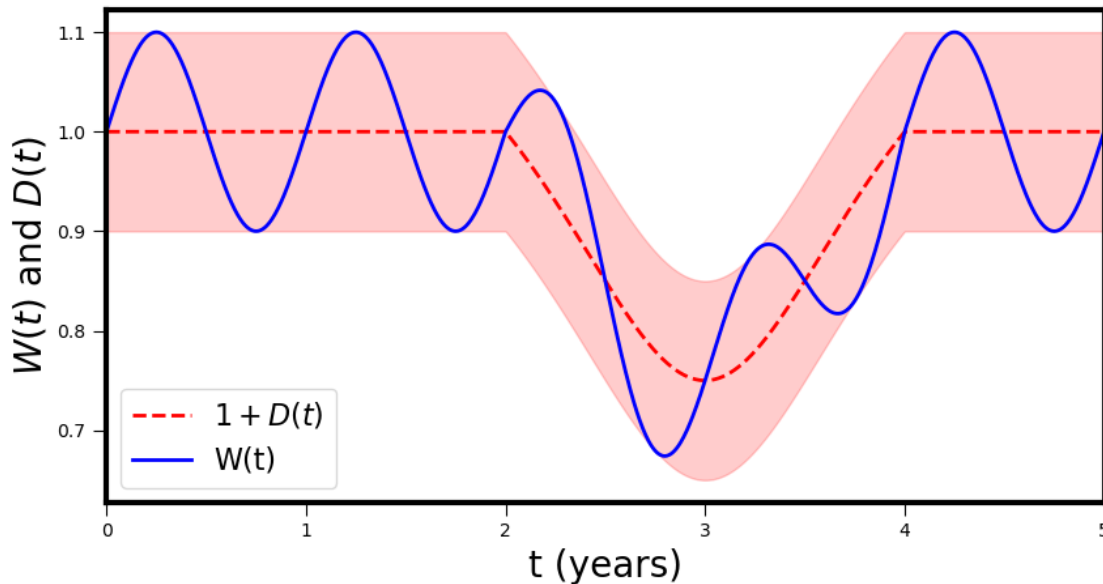

Figure 2: The seasonal variation in water over 5 years, with a drought occurring between years 2 and 4. The red shading shows the envelope of seasonal variation around the drought effects.

2.4 Parameter tuning and phase-effects

These functions, while based on physical mechanisms, are hard to connect to specific parameter values without any specific plant population or weather condition to study. Instead of choosing one specific population to base our parameters on, we instead examined the

dynamics of eq. (1) under various sets of parameters to choose values that exhibited various forms of realistic behavior, which we hope allows our model to address a range of ecosystems.

To do this we ran a simple two species (p_1 and p_2) simulation, varying the interspecies competition a_{12} and the inherent growth rates (r_1 and r_2). The two species have equal carrying capacity $K_{10} = K_{20} = 1$ (and thus equal fitness at average water conditions), but different water susceptibilities $b_1 = \frac{1}{4}$ and $b_2 = 4$. The equilibrium seasonal oscillations are shown in Figure 3 (below).
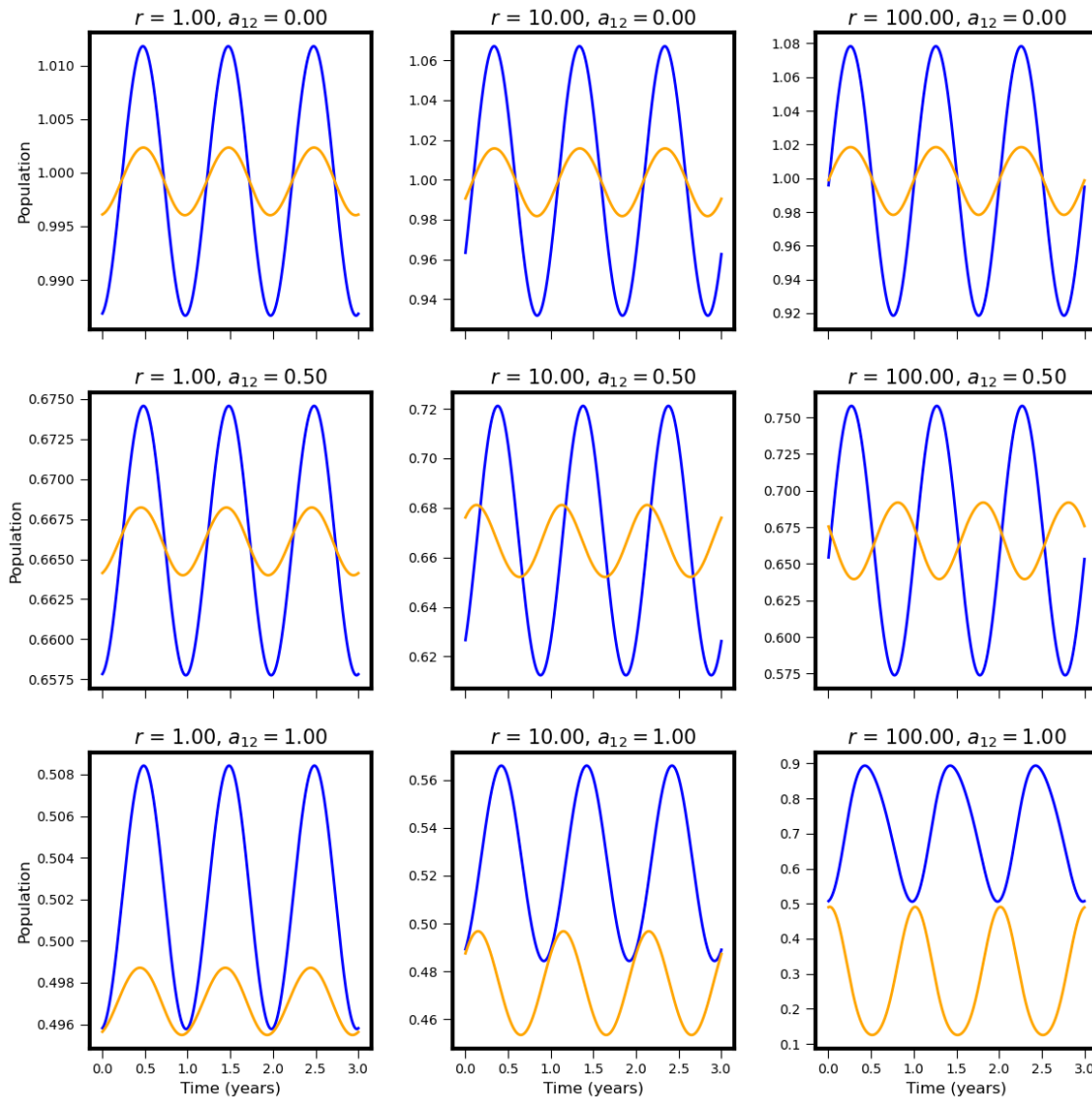

Figure 3: The populations of plants with two different water susceptibilities, $b = 4$ (orange) and $b = 1/4$ (blue), across 4 years with varying growth and competition rates. Note that $a_{12} = 1$ means inter- and intraspecies competition is identical, and $a_{12} = 0$ means there is no interspecies competition.

For no competition $a_{12} = 0$ (top row, Fig. 3), we can see that the growth rate only affects the amplitude of oscillation. For moderate and high interspecies competition $a_{12} = 0.5, 1$ (middle and bottom rows, Fig. 3), the growth rate significantly affects the results. Low growth results causes in-phase oscillations and high growth causes anti-phase; we decided to use the intermediate growth rate $r = 10$ since we expect both that population variation would lag behind the water by some degree and that peak population would occur at different times for the two species.

Note that the wet plants seem to perform better than the dry plants, despite having the same average fitness ($K_{i0} = 1$). We initially thought this was due to minor asymmetries in $K(W)$ near 1 (see Figure 1), since the function is not perfectly linear; i.e., maybe the net amount of performance increase tends to be higher than the net amount for dry plants. However, after changing to a linear function we still observed the same effect. This effect, and the exact nature of the variation in phase due to growth rate, are features of the system of ODEs we did not have time to investigate fully.

2.5 Adaption due to biodiversity

Taking the COMAP observations of adaptation as an empirical rule, we can add an additional equation to the population dynamics. We assume that the relative density of other species (not the total amount) is the factor determining the rate of adaption; one hundred plants of another species may be significant may have significant effects on an ecosystems of one thousand plants, but not in one of one million plants. We also assume that the traits of the species in the ecosystem do not affect the rate of adaptation; this most likely would not be true if this adaptation process was due to an interbreeding effect, since traits would be inherited. From these assumptions, use the following equation to measure the biodiversity of an ecosystem of plant species

$$B(\vec{p}) = -\frac{\vec{p}}{|\vec{p}|} \cdot \ln\left(\frac{\vec{p}}{|\vec{p}|}\right), \tag{6}$$

which is the entropy of the distribution of plant species. This function has the advantage of being maximized when all species occur in equal amounts (i.e. maximum diversity) and being strictly positive. We also want the traits to be altered only in times of drought, so

there should be a dependence on the current amount of water present. Based on these considerations, we propose the following rule for altering the traits of species:

$$\dot{b}_i = s(1 - W)B(\vec{p})^2 \frac{\sum_{j \neq i} p_i}{|\vec{p}|}. \tag{7}$$

where s is some constant of proportionality. This formula has the advantage of allowing adaptation in both directions: if there is excess water, $\dot{b} < 0$ and the species would adapt to wet conditions.

The dependence on the density of other species $(\frac{\sum_{j \neq i} p_i}{|\vec{p}|})$ can be rationalized by the fact that a species should adapt faster if it is in an ecosystem full of other species. We square the entropy purely for empirical reasons, as the dependence on the total number of species is too low when we use a linear dependence. If time permitted, we would have liked to develop a mechanistic theory of the observed phenomena to allow a more motivated equation.

3   Continuous model results

Based on our research on the known role that biodiversity plays in an ecosystem, we decided it would be valuable to first compare the dynamics of an ecosystem without trait adaptation since we know there should be effects due purely to niche efficiency and the insurance hypothesis, without the observed generational adaptation.

3.1   The dynamics of a two species ecosystem without adaptation

We first ran a simulation of two species experiencing a single drought event to observe how the system was altered and returned to equilibrium, the results of which are shown below.
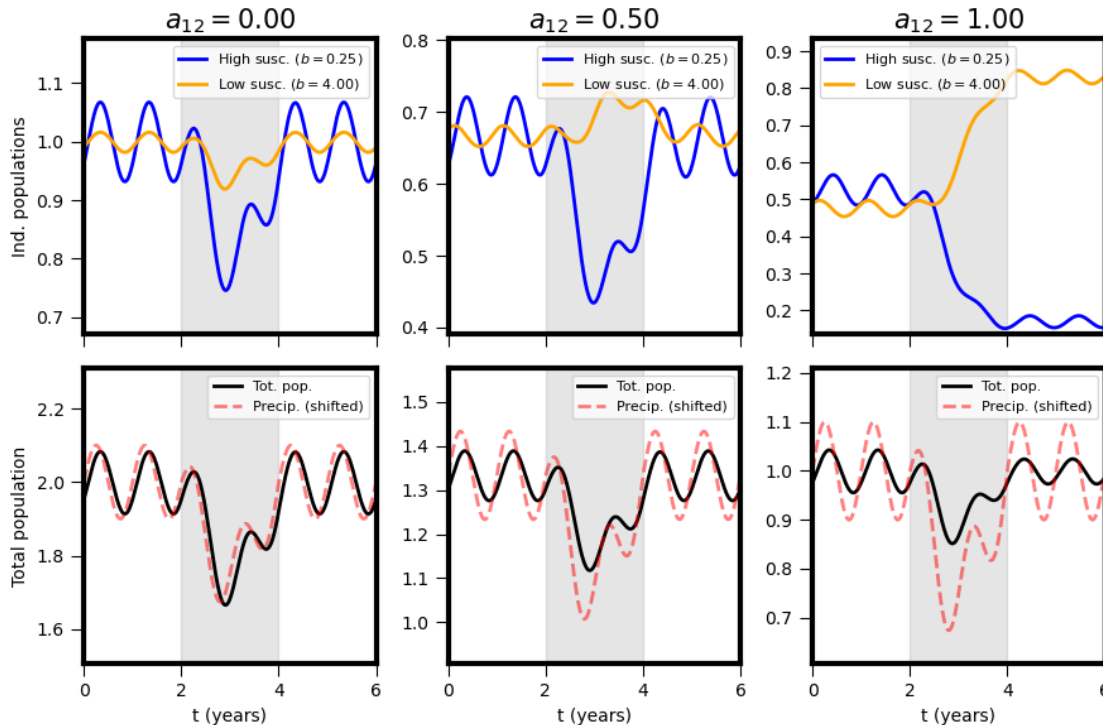

Figure 4: Top row: the populations of plants with varying water susceptibilities, $b = 4$ (orange) and $b = 1/4$ (blue), across 6 years with a drought occurring from year 2 to year 4 (gray shading) for varying levels of interspecies competition (a_{12}). Bottom row: the total population and precipitation for the ecosystem.

These results show that while noncompeting species (left column) have the highest total population, they suffer the largest decrease in times of drought, both in net decrease and fractional decrease ($\approx 17\%$ decrease). Competing species mitigate both the net and fractional

decrease ($\approx 16\%$ and 15% for the middle and right columns, respectively), while having lower net biomass on average. These results, even without any species adaptation, show having competing species with different traits can mitigate ecosystem fluctuations. It is worth noting as well that the maximum competition caused a massive, seemingly permanent decline the in the high water susceptible pop. These results indicate that a moderate amount of competition between species results in the most stable system, both at the ecosystem and species level.

3.2 Growing the number of species without adaptation

First, we examined the effect of adding species without the adaptation rule; our rationale was to compare the inherent effects of a diverse ecosystem, based on niche efficiency and the insurance hypothesis. We loosely followed the methods of [8] by generating 250 species of plants with varying water susceptibilities (b_i, ranging from 2^{-5} to 2^5), randomly selected fitness (carrying capacity K_i, ranging from 0.95 to 1.05), and fixing interspecies competition to be half as strong as intraspecies competition ($a_{ij} = \frac{1}{2}$ if $i \neq j$), based on the results in section 3.1. For each number of species, 25 randomly selected ecosystems were generated.
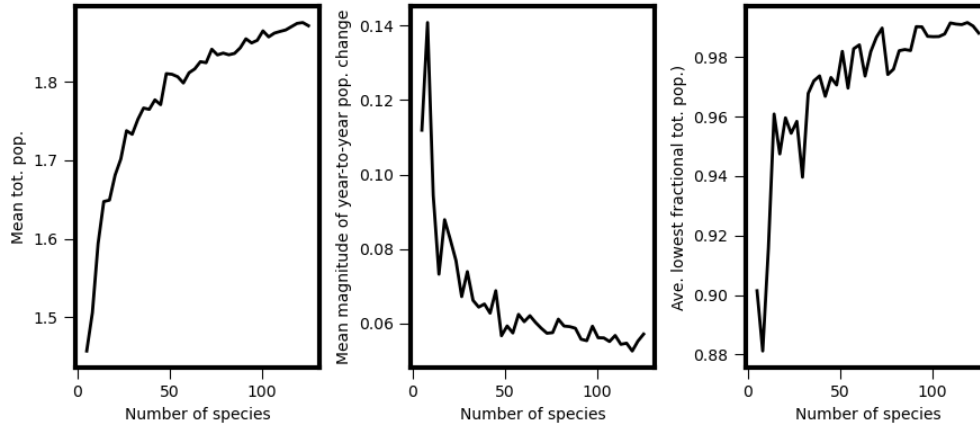

Figure 5: The mean total population (left), the mean magnitude of the population change between years (middle), and the lowest fraction of the mean population that the yearly population drops to (right), as a function of the number of species.

We varied weather conditions by adding 20 droughts of varying intensity and duration over 50 years, then examined the yearly mean total population for all of the ecosystems, the results of which are shown in Figure 5.

Increasing the number of species tends to increase the total population, reduce the year-to-year variability in total population, and reduces amount that the population drops (as a fraction of the total population) (see Figure 5, above and Figure 6, below). While our experiment involved adding species to a system, this result has implications for removing species from an ecosystem; we can see that holding all else constant, removing species tends to decrease productivity and system stability. However, adding species produces diminishing returns to both of these effects.
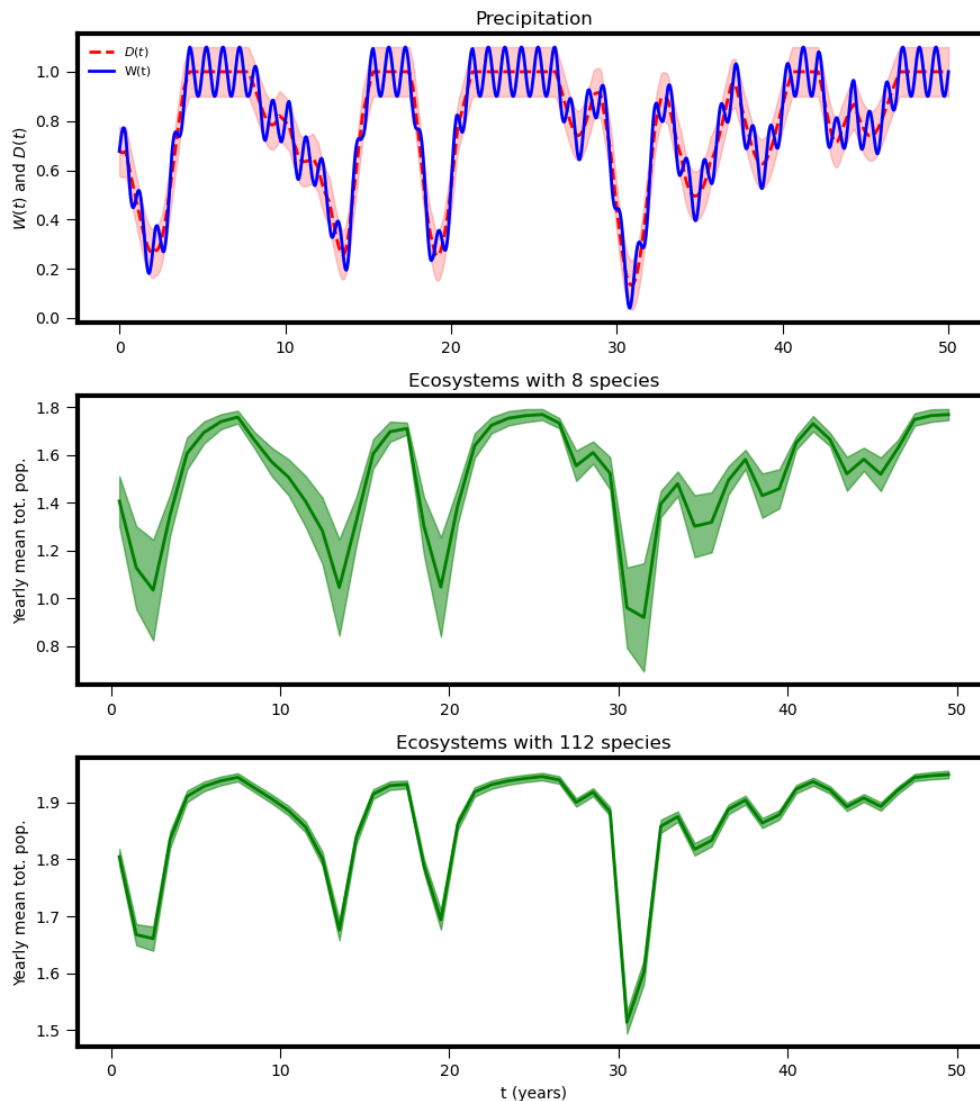

Figure 6: The precipitation over the 50 year period, as well as the year-to-year population for the 8-species ecosystems and the 112-species ecosystems (displaying the mean plus or minus one standard deviation across ecosystem replicates). Notice the increased population and reduced year-to-year change with increased population.

3.3   The dynamics of a two species ecosystem with adaptation

Now, we consider the effects of allowing biodiversity-dependent trait adaptation in the case of two species. The effects are small for only a single drought event, which is to be expected since adaption occurs only for subsequent generations. Thus we plot the effects for a sequence of drought events, using $s = 10$ (the adaptation rate constant).
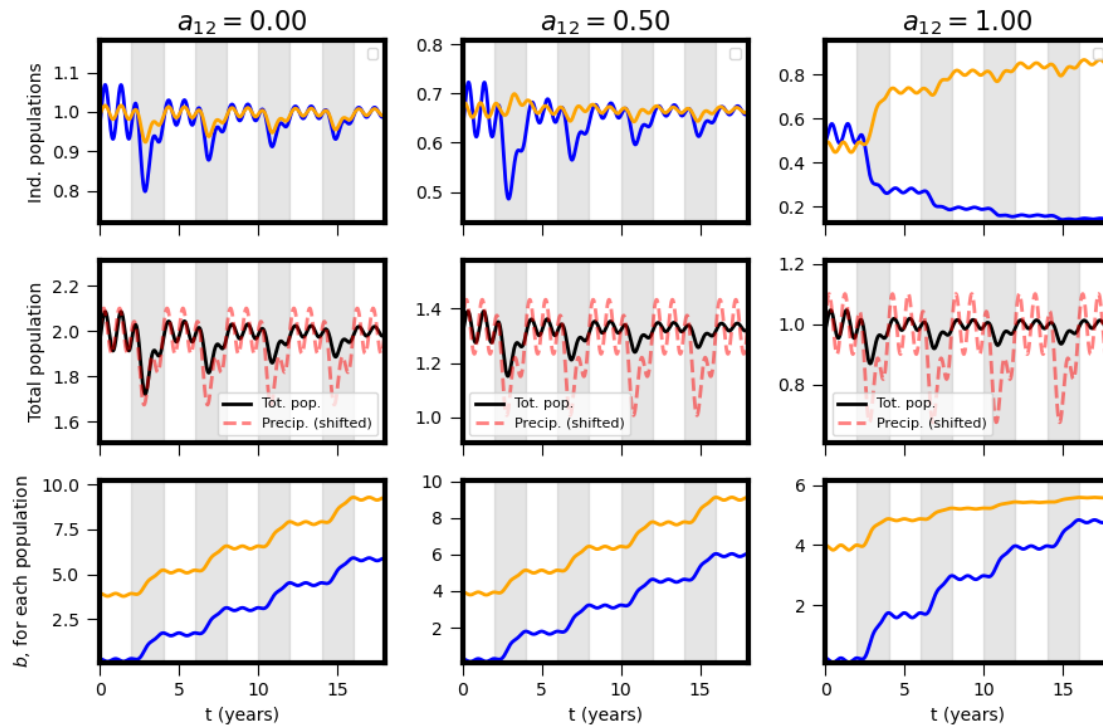

Figure 7: Top row: the populations of plants with varying water susceptibilities, $b = 4$ (orange) and $b = 1/4$ (blue), across 18 years with a drought occurring every 4 years (gray shading) for varying levels of interspecies competition (a_{12}). Middle row: the total population and precipitation for the ecosystem. Bottom row: the value of b for each species over time. Increasing b demonstrates adaptation to drought conditions.

The results demonstrate that our model allows species to adapt in times of drought, and shows increasingly decreased reduction in population over each subsequent drought. Using $s = 10$ here is a bit extreme; perhaps we should not expect such a strong effect for a system with only 2 species. However, this high value of s allows the effects of the adaptation to be observed relatively quickly on a small system.

3.4 Growing the number of species with adaptation

Now we repeat the simulation in section 3.2, but this time allowing for the biodiversity dependent adaptation. We decrease the value of s to 1 to reflect more reasonable (in our opinion) rates of adaptation, and all other parameters are identical to section 3.2.
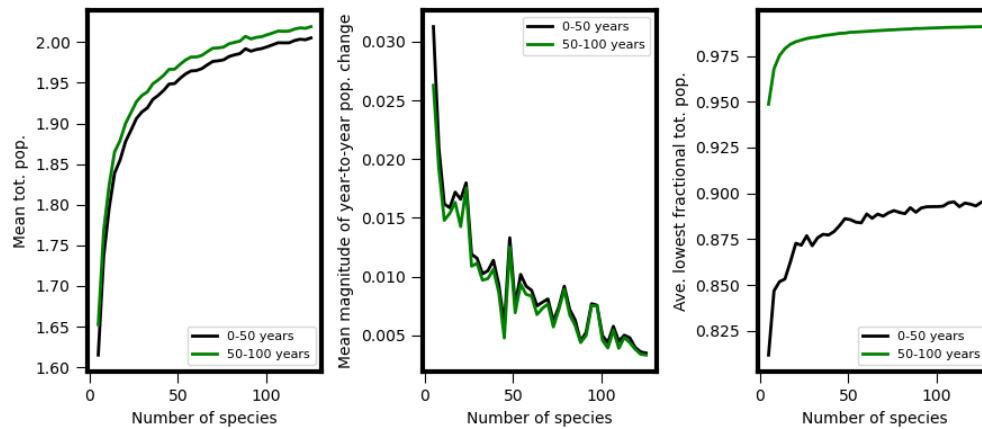

Figure 8: The mean total population (left), the mean magnitude of the population change between years (middle), and the lowest fraction of the mean population that the yearly population drops to (right), as a function of the number of species. Statistics for the first and last 50 years are computed separately to show the effect of adaptation over time.

Immediately, we observe that the adaptation has a significant positive effect on both the total population (Fig. 8, left) and on the decreasing the severity of drought effects (Fig. 8, right), with not a clear effect on the year-to-year variation (Fig. 8, center). In addition, we see an increasing benefit to a larger number of species over time. In section 4.2, we concluded that the number of species gave only diminishing benefits as more are added, demonstrated by the asymptotic curve. However, in this simulation for the total population we can see that the effects of higher numbers of species adaptation actually increase after there are ≈ 10 or more species. This roughly corresponds to the study done by [Tilman grass] which also found an increasing benefit to biodiversity over time in grass populations, which may suggest that his mechanism (species becoming increasingly complementary) could be a potential cause for the observations provided by COMAP.
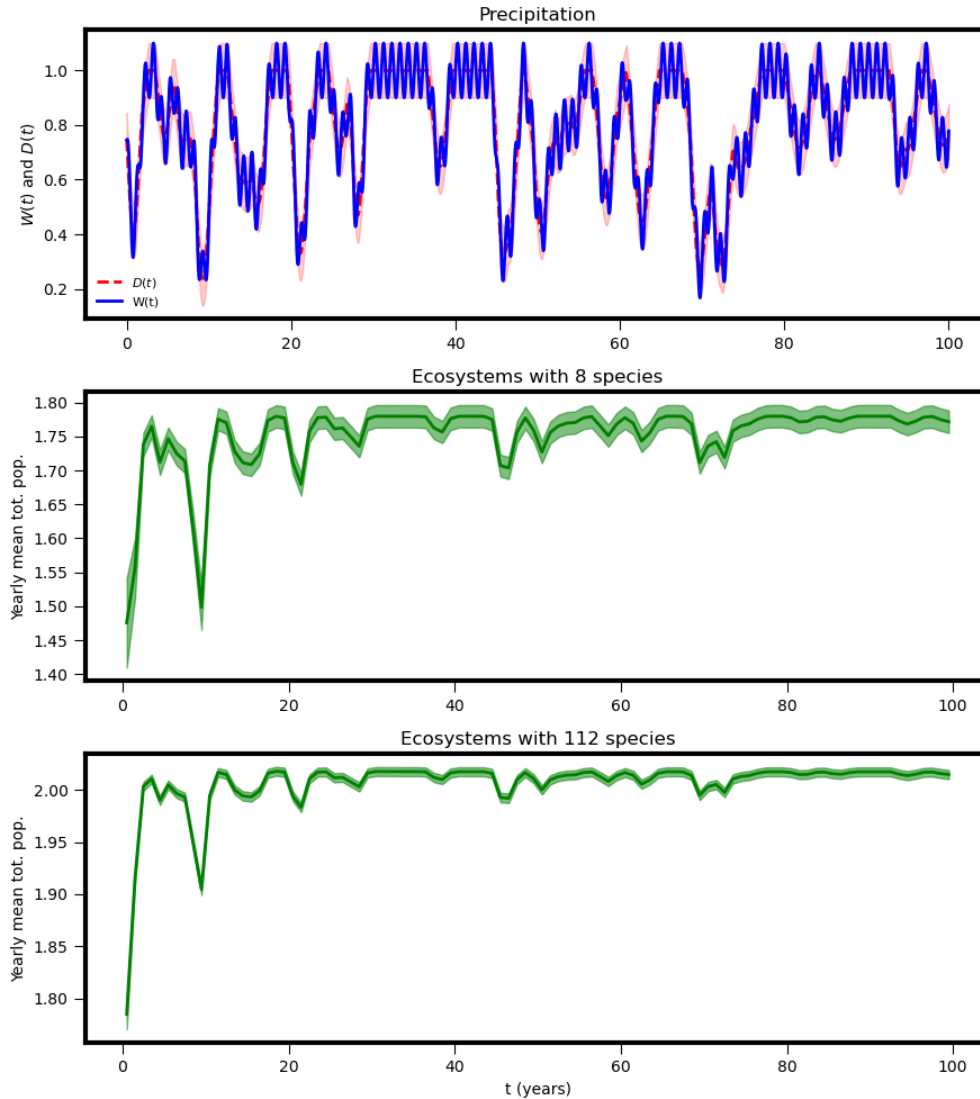
Figure 9: The precipitation over 100 years, as well as the year-to-year population for the 8-species ecosystems and the 112-species ecosystems which have drought adaptation effects ($s = 1$). Notice in particular the reduced effect of droughts in later years of the simulation.

4 Cellular automaton model methods

In addition to the continuous modeling, we worked on a complementary discrete spatial model which could describe the complex spatial relationships that would occur in a diverse ecosystem, also implemented in Python. We were able to implement the effects of niche complementary and insurance hypothesis, but were not able to implement the adaptability.

4.1 Model requirements and implementation

A cellular automaton (CA) model is a collection of cells that evolve according to some set of rules. We used this method to model a plant ecosystem, where the grid of square cells describes the plant population and the update rules reflect the growth, spread, and death of individual plants in the ecosystem. Each cell can contain either no plant or a plant of some species. Each cell is also assigned a resource value R, which in this case represents the amount of water available (other resources could be added in future models) which fluctuates seasonally and according to drought conditions.

To determine the behavior of each plant, we want to calculate a value that represents the resources the plant has available in relation to the resources it requires. We implement this by defining the RpF (reproduction factor) of the plant cell, given by

$$RpF(cell) = R(1 - C) * I, \tag{8}$$

where C represents the net competition for the resources and I is the inherent efficiency (i.e., fitness) of the plant. The cell is then modified each time-step according to

$$\begin{cases} RpF < K_1 \implies & \text{Cell dies} \\ K_1 \leq RpF < K_2 \implies & \text{No change} \\ K_2 \leq RpF \implies & \text{Cell spreads,} \end{cases}$$

where K_1 and K_2 are constants representing how the model behaves, and if the cell spreads $(K_2 \leq RpF)$ it will spread towards a neighbor with the lowest RpF.

The next important aspect of plant ecosystems to be simulated is the competition, where we again assume (following niche efficiency) that intraspecies competition is stronger than interspecies competition. Let N_s be the number of same-species neighbors and N_d be the number of different-species neighbors. Following the approximate ratio used in section 3.1, we calculate the competition as

$$C = N_s + N_d/2. \tag{9}$$

Finally, the resource value R is calculated

$$R = (R_{\text{seasonal}} - D) * 9 \tag{10}$$

where R_{seasonal} represents the seasonal variations in weather conditions, and D represent the drought conditions at a given point in time, and the equation is multiplied by 9 to scale by the size of the cells neighborhood.

The basic algorithm is outlined below.

Def. *Update* function:

Given an initial state matrix G and resource state R:

1. Construct matrices N (next) and S (spread).

2. For each (i, j), calculate $RpF(G, R)$ for the cell:

    (a) $RpF < C_1 \implies$ Cell dies next iteration ($N_{ij} \leftarrow 0$)

    (b) $C_1 <= RpF < C_2 \implies$ No change ($N_{ij} \leftarrow G_{ij}$).

    (c) $RpF >= C_2 \implies$ Cell spreads to lowest RpF neighbor, (l, k) ($S_{lk} \leftarrow G_{ij}$).

3. For each (i, j):

    • Update next state with spreading ($S_{ij} > 0 \implies N_{ij} \leftarrow S_{ij}$).

4. return N

Then for each time-step:

1. $G = \text{update}(G)$

2. Calculate R based on time of year and drought conditions.

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5   Cellular automaton model results

Some representative results for running the model are shown in Figure 10. The matrix representing the ecosystem is shown at two points in time, where the color of each cell represents a plant of some species or the lack of a plant (black). A plot summarizing the species and total populations are shown, as well as the water level at that time (here fluctuating only due to seasonal variation).
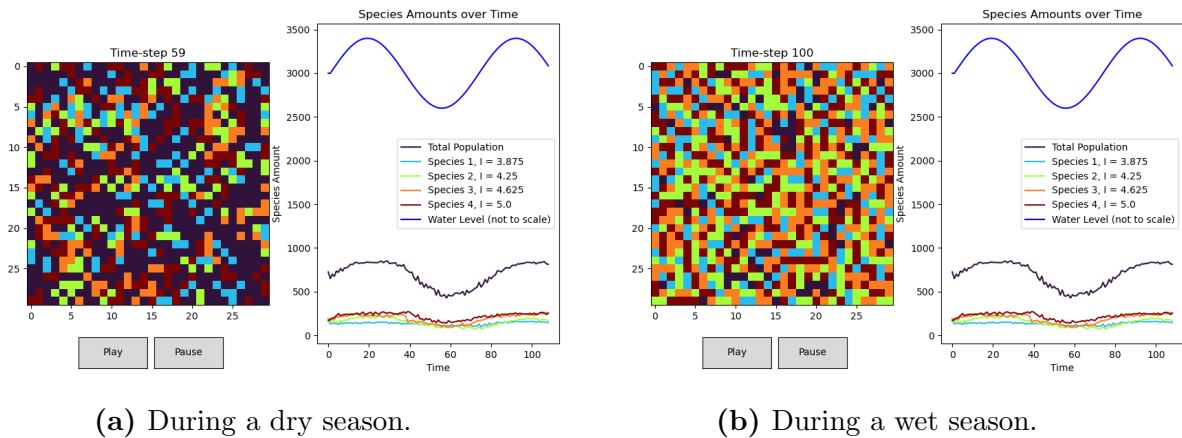
(a) During a dry season.

(b) During a wet season.

Figure 10: A 30x30 grid simulation paused at differing seasonal conditions.

5.1 Biodiversity effects on populations

We first tested the simulation on two species of differing fitness (represented by I), and the results are shown in Figure 11.
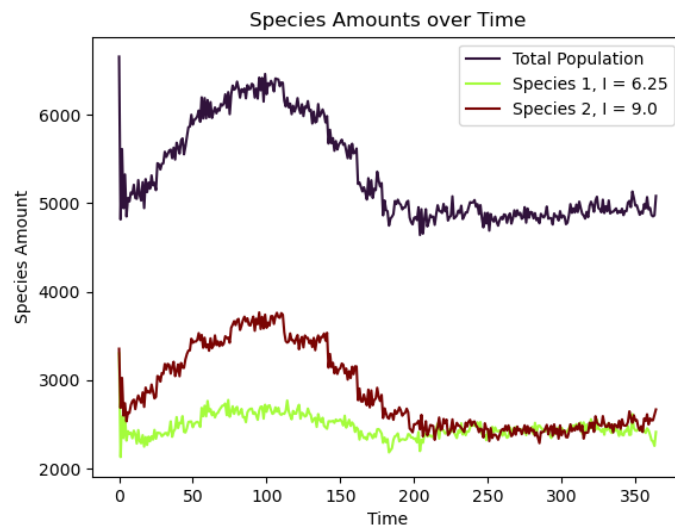

Figure 11: The plot over one seasonal cycle for two species. The higher I value species require less resources which means that it is in higher quantities during the wet season. During the dry season, however, biodiversity is much more important than the fitness of the species, and thus the two species converge in populations.

In wet conditions - when there is plenty of resources, the species separate in population due to fitness, but they do not in dry conditions. This can be explained in part by niche

efficiency, since when less resources are available biodiversity (which increases efficiency) is more important for keeping an ecosystem alive. This holds for increased numbers of species (see the start and end of Figure 12), and impacts the effect of droughts.
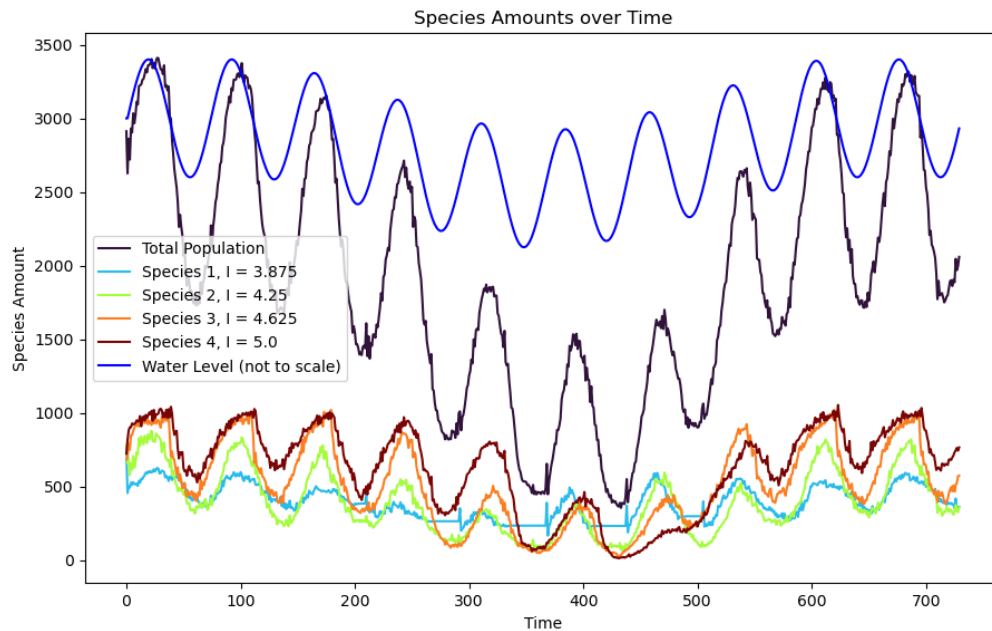

Figure 12: A 4 species simulation with a drought in the middle third of the simulation. The blue line represents the total water level, which decreases due to the drought. The plant populations decrease dramatically, but they recover over a few seasonal cycles following the drought.

This model can also simulate a drought (Figure 12). The normal seasonal cycle will still occur, but a severe drought can shock a plant population. Notice how various species are impacted differently, demonstrating qualitatively that biodiversity can ensure some degree of stability for the ecosystem as a whole, since all species do not change simultaneously.

5.2   Biodiversity effects on production

We also tested the effects of biodiversity loss from a drought, and ran a simulation where 2 species were killed off during a drought event (see Figure 13). We find that even when weak species are lost, the total productivity of the system is impacted due to the loss of biodiversity. This means that even the plants that survived (which would be the strongest

and most resilient ones), will make up a lower total population since they are competing more with their own species and not with others.
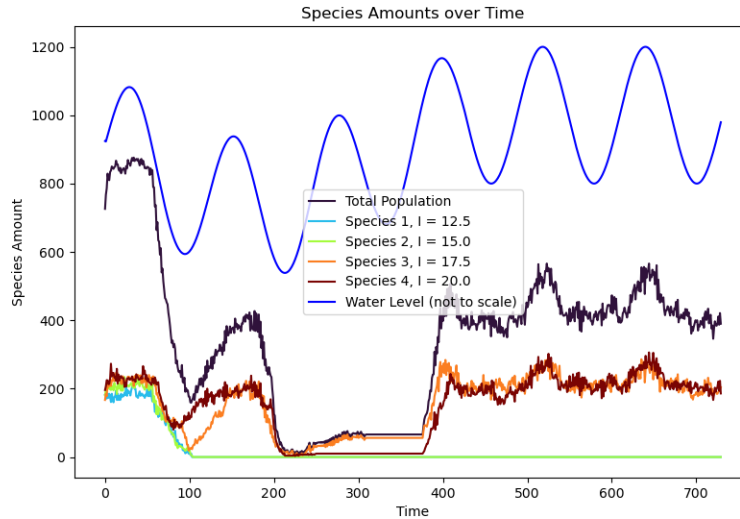

Figure 13: A drought in the first cycle kills off two of the four species. Even after the populations settle, the total production (estimated by the total population) decreases. This shows that the strongest plants by themselves are worse off than having more species with lower fitness values.

5.3 Differences in fitness

We next tested variations in the distribution of fitness across the ecosystem, shown in Figure 14). We found that the relative fitness played only a significant role in wet seasons, when resources were abundant. Here the fitter species tends to follow a large amplitude sinusoidal curve, with high maximums and low minimums, while the less fit species remained relatively constant. With less difference in fitness, this effect is diminished, and in dry seasons the fitness seems to have no effect on the population since biodiversity is the controlling factor.

Finally, we tested the effects of varying numbers of species (all with different fitness values) on the total production of the ecosystem. We found that adding more species does increase the total plant population, and thus the ecosystem's efficiency, but it does carry diminishing returns (see Figure 15). Even adding species of relatively low fitness can contribute to the total production by adding biodiversity to the system, and so we find fitness-independent total product increases.
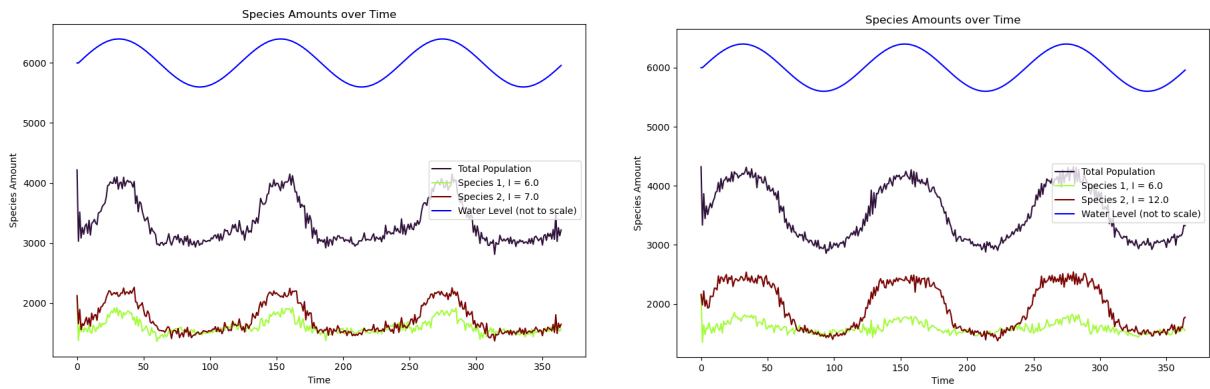
(a) Very similar fitness values between the two species.

(b) A large difference in the fitness values of the two species.
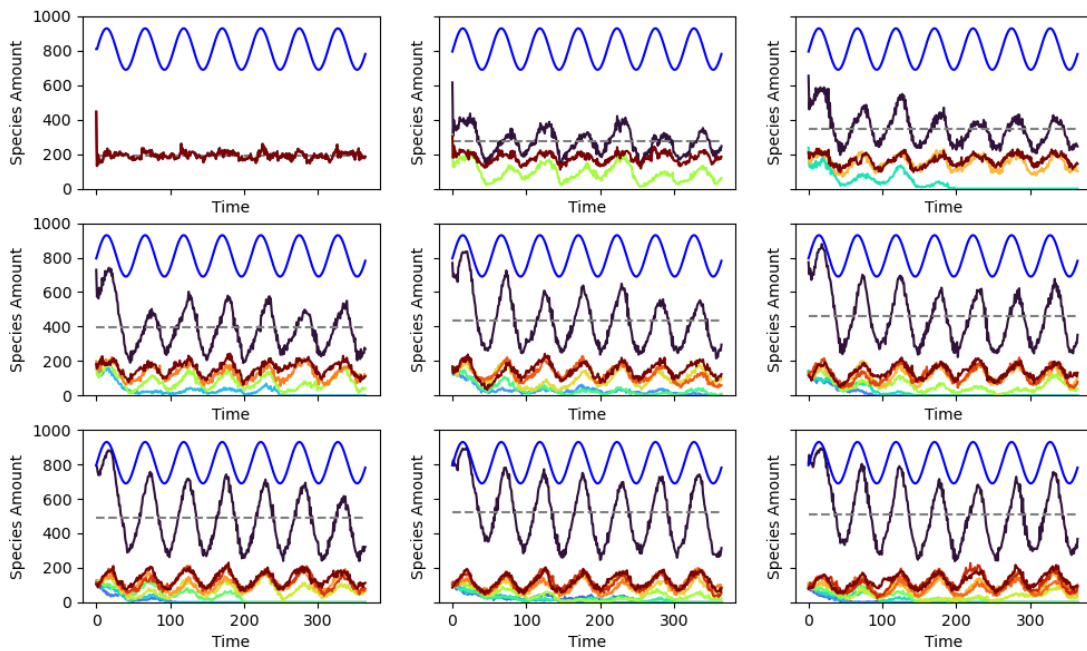
Figure 14: The effects

Figure 15: Multiple simulations where the top left plot has one species and the bottom right has nine. The dashed gray line on each plot represents the average species population over the simulation. Notice how it increases as you add more species, but the return diminishes with greater biodiversity.

6   Conclusion

The goals of this project were to understand and model how biodiversity affects plant ecosystems times of climate uncertainty, particularly drought conditions. We considered three main effects of biodiversity on an ecosystem (niche efficiency, the insurance hypothesis, increased adaptation) and constructed two complementary models to study them. We focused on the dynamics of the total population, since this represents the biomass essential to the rest of the ecosystem, and were interested in its stability through varying weather conditions.

The first was a continuous model derived from the competitive Lotka-Volterra equations. This was adapted to include a dependence on water and the ability to vary the traits of species. The second model was a cellular automaton model, which modeled the interactions between individual plants in an ecosystem as a function of the weather conditions and plant traits. These models both show that biodiversity increases productivity and stability of ecosystems in drought conditions, although generally with diminishing returns. The implications of these diminishing returns may be that changes to the number of species in an ecosystem produce a drastic effect only as the total number becomes small, which means that effects to ecosystem health could drastically change even with a steady decrease in biodiversity. Our current results indicate that a large number of species may act as a sort of buffer, reducing the effects of small reductions to biodiversity in an ecosystem.

When we implemented generational adaption into the continuous model, we found that the effects of biodiversity were both stronger and grew over time, suggesting that biodiversity plays an even more important role in the long-term stability of an ecosystem if this adaptation process occurs.

There are countless interacting components we did not consider in our model of plant ecosystems, including animal predation, human deforestation and pollution, other natural disasters, and more. We also did not consider resources other than water, which would greatly complicate our modeling of resource competition. Despite the simplicity of our models, they demonstrate that the effects of biodiversity can have a relatively large impact on the overall health of an ecosystem. In future work, these models can be extended to include more factors and produce more conclusive results on the effects of biodiversity.

7   References

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