Effects of Disturbance and Conspecific Negative Density Dependence on Forest Composition and Diversity: A Simulation-Based Approach

David M. Chan
*Virginia Commonwealth University*, dmchan@vcu.edu

Benjamin S. Ramage
*Randolph-Macon College*, BenjaminRamage@rmc.edu

Matthew E. Mills
*Virginia Commonwealth University*, millsme37@gmail.com

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Effects of Disturbance and Conspecific Negative Density Dependence on Forest Composition and Diversity: A Simulation-Based Approach

Matthew Erik Mills¹, David M. Chan¹,*, Benjamin S. Ramage²

1 Introduction

Biodiversity is a critical component of ecosystem health and a strong predictor of the ecological services provided to humans [44]. These services include crop pollination, pest control, carbon sequestration, and provision of materials for industries ranging from construction to pharmaceutical research. Biodiversity conservation is a major concern in our rapidly changing world, especially in forests, which are among the most diverse and complex ecosystems. However, conservation efforts are hindered by the fact that the underlying causes of forest biodiversity remain obscure [17].

Two of the most important drivers of forest diversity and composition appear to be (i) conspecific negative density dependence (CNDD) and (ii) disturbance. Previous studies suggest most, if not all, forests are affected by both processes. CNDD, a form of species-specific negative feedback, refers to a reduction in survival and/or growth rates when conspecific (“same species”) densities are high, typically owing to the local accumulation of species-specific natural enemies (e.g., pathogens, insects) [10, 21]. Thus, CNDD provides an advantage to rare species and serves to maintain local diversity. Disturbances, discrete events that kill or remove biomass and change abiotic conditions, can be natural or anthropogenic (e.g., hurricane or timber harvest), abiotic or biotic (e.g., wildfire or disease outbreak), and highly variable in a wide range of parameters [34]. Biotic disturbances and CNDD may overlap in certain contexts (e.g., host-specific pest outbreaks), but disturbances are by definition abrupt and episodic, while CNDD is usually gradual and continuous [13, 47].

CNDD prevents or reduces local dominance by one or a few species, increasing alpha diversity (i.e., local diversity), and these local impacts may also influence regional diversity patterns [23, 21]. For instance, the Janzen-Connell Hypothesis asserts that tropical forest diversity is maintained by strong CNDD [11, 22]. However, conspecific inhibition does not necessarily explain diversity beyond very local scales, and thus it can be an important driver of compositional patterns even in temperate systems with low regional species diversity [53, 15, 53].

Disturbance effects are typically much more obvious than those associated with CNDD. Due to their inherent variability, disturbances almost always increase spatial heterogeneity and beta diversity (compositional turnover across space) [47]. Disturbances may also increase alpha diversity (e.g., by reducing densities of a dominant com-
petitor), but the opposite can occur if the disturbance homogenizes local species composition (e.g., by eliminating fire-sensitive species in high-intensity burn patches; [24]). In addition to these direct mortality-driven effects on diversity, disturbances indirectly influence compositional dynamics by altering a wide range of environmental conditions (e.g., light and soil moisture), creating an environment that is more favorable for some species and less favorable for others.

To investigate processes that span vast areas and/or long time periods, ecologists are increasingly turning to simulations. The ability to quickly change parameters allows researchers to consider topics ranging from optimal timber yield to the effects of climate change on large landscapes [14]. Complex forest simulation models are also used to model fluctuations over time, and to investigate factors that may alter compositional trajectories and outcomes.

Numerous empirical and simulation-based studies have investigated disturbance and CNDD independently, but little is known about how these two processes interact. As global change accelerates, disturbances are likely to become more frequent and intense [32], and interactions between disturbance and CNDD may become increasingly important drivers of forest composition and diversity. Here we address this research gap via a flexible, agent-based simulation model that allows for interactive effects of variable CNDD strength and disturbance type. We explore a range of scenarios, modeled over a simulated 500-year period, and present the resulting compositional dynamics and diversity outcomes.

2 Model

2.1 Introduction to forest simulations

There have been many models developed to simulate forest dynamics, some successfully measuring species composition and growth dynamics as early as the 1970s [26, 4]. These models vary in many different aspects, including their mechanics, desired data input and output, and ultimate purpose. Current models do not generally integrate both aspects of abiotic disturbance and CNDD in such a way that the interactions of these effects can be easily quantified. Our conceived model demonstrates and measures the effects of the interactions between CNDD and these different types of disturbances.

Since the commercialization of computing, simulations have become essential tools in many areas of study that are based on mathematical models. In ecology and biology, agent-based models, statistical distribution models, and the integration of differential questions using discrete time steps have become popular topics for computation [3, 9]. Of particular relevance to forest simulations, there are spatial models which are based on individuals, unit cells, or polygons in a landscape, and also distribution models which are based on statistical distributions of species, tree sizes, and other parameters of trees [13, 8, 14]. These simulations have become common ways to gain insight into forest management techniques, the drivers of biodiversity, and the effects of climate change and disturbances on forests [14, 35, 32, 12, 16, 25, 30, 11, 33, 15, 8].

Two of the best known and most used forest simulation models are LANDIS and SORTIE [15, 8], both of which are spatially explicit models that capture stand dynamics on a unit cell level and simulate disturbances, light levels, and use multiple species [13]. While they satisfy many of our needs, some calculations are done at a coarser spatial scale than is necessary for our investigation.

2.2 The agent-based model

To capture the interaction between conspecific density dependency and disturbances, we created an agent-based model embedded in a flat toroidal landscape. The model follows three steps each year: 1) mortality (including background, resource-driven, and disturbance-induced), 2) seed production and dissemination, and 3) growth.

The primary mechanism that drives these interactions is a two dimensional mesh over the landscape that tracks the amount of available resources, referred to as “the resource surface.” The calculation of this surface depends on the proximity of individuals in the landscape and their diameter at breast height (DBH). Each species has a slightly different impact on the surface. The resource surface is used when calculating the growth, establishment, and mortality of individuals in the landscape. The influence of each species type on the resource surface is further used to calculate the species-specific influence in the landscape.

Disturbances are introduced into the simulation at defined intervals, and act strictly on the individual trees in the simulation by increasing mortality. We focus on large wind events like hurricanes that affect trees with large DBH, forest fires that affect trees with small DBH, and spatial block effects like clear cutting. These disturbances affect the species-specific effects since a disturbance removes individuals from the landscape thereby changing the resource surface, which impacts how the forest develops locally. If one species is removed at a higher rate, for instance, this can result in a decrease in that species’ influence in the landscape.

2.2.1 Species

We use this model to assess how compositional dynamics are affected by different disturbances with different
strengths of CNDD. Four species were chosen to represent forests in the middle Atlantic region of the United States. This allowed for sufficient variation in species characteristics to cover pioneer species, late successional species, and both shade tolerant and shade intolerant species.

Black cherry (Prunus serotina) represents early successional trees in the middle Atlantic. It has pioneering characteristics such as a large seed spreading radius on account of transport by animals, fast maturity, and quick proliferation of fruit. Black cherry has a smaller mature DBH and height, which coupled with an extreme shade intolerance, makes it less competitive to late successional species in older landscapes. Black cherry responds well to disturbance because as gaps are created in the landscape, the availability of resources will provide places for it to grow.

Yellow poplar (Liriodendron tulipifera) represents longer living pioneers in the middle Atlantic. It is the largest species and it has the fastest growth rate of the four species in the simulation. It also has decent seed spreading capability because its samaras, which are the seed carrying fruit of the species, are carried by wind. Yellow poplar is a shade intolerant species, however, its quick growth rate and colossal size make it competitive in older landscapes especially when compared to the frailty of black cherry.

White oak (Quercus alba) is a middle successional species. It is slower growing than black cherry and yellow poplar, and because its acorns fall largely under the limbs of the adult trees, it is less capable of establishing in new areas. Along with these characteristics that make White oak slower to spread, it is much more shade tolerant than black cherry and yellow poplar, allowing individuals of the species to dwell in the understory of a landscape for longer periods of time.

American beech (Fagus grandifolia) represents a late successional species in the middle Atlantic. It is a medium size species that is highly shade tolerant and slow-growing. The nuts that the species produces fall below the limbs of adult trees, and can follow a seed crop pattern of two to eight years. American beech is capable of living in the understory of a landscape for extended periods of time as a smaller seedling or sapling. When larger trees neighboring these smaller individuals die, these seedlings and saplings will be provided with an opportunity to grow.

Table 1 shows the particular parameter values used in the simulation. These values were derived from information found in The United States Department of Agriculture Forest Service Agricultural Handbook - Silvics of North America. We then modified these values until the DBH histograms were right skewed showing sufficient replacement and approximately 8,000 to 10,000 individuals to hectare near steady state. A sustainable forest will have a diameter at breast height (DBH) distribution that is right skewed because there must be many more smaller individuals to replace dying mature individuals to maintain a population of adults in the forest.

The values in Table 1 are parameters that guide the dynamics of each agent by the species of that agent. The maximum DBH of each individual is the point at which a species’ mortality rate increases to simulate death from old age. This is not a true maximum. The maximum height corresponds to the maximum DBH, and is used to calculate the curves in Figure 5. The maximum growth rate in DBH is true maximum growth rate. The maximum seed count is related to the number of seeds an individual would produce at a high DBH. These values help guide the curves in Figure 5. The seed dispersal radius is the value used for the standard deviation in the seed dispersal kernels shown in Figure 6. These values are much higher for the pioneers. The influence radius of each species dictates each species’ usage of resources in Figure 7. The shade tolerance power estimates the shape of the curves (i.e., how sharp the sigmoidal curve appears) in Figure 8. Finally, the mortality rates for each species guide the curves in Figures 2 and 4. The mortality rates for the late successional species are much less than in the pioneers.

### 2.3 Yearly dynamics

This model considers a one hectare square landscape (Figure 1), simulated with toroidal boundary conditions to avoid edge effects, a common approach in forest simulation models. Each tree or agent in the model has an associated location, species, DBH, height, and age. Each individual is classified into one of three classes that include:

- **Seedlings** – individuals with a height less than 1.37 meters (and thus a non-existent DBH),
- **Saplings** – individuals with a height greater than 1.37 meters and a DBH between 0 and 10 cm,
- **Adults** – individuals with a height greater than 1.37 meters and a DBH above 10 cm.

In the initialization of the landscape, each species makes up an equal proportion of the community. A right skewed Beta distribution is used for the DBH distribution, with small trees present in high numbers and trees with increasing DBH steadily declining in abundance, matching patterns frequently observed in natural forests. The locations of each individual are chosen using a uniform random distribution, and then individuals which are spaced too close together are given new locations until a minimum spacing of 0.75 meters between all trees is found.
Table 1: Demographic values for each species.

<table>
<thead>
<tr>
<th></th>
<th>Black Cherry</th>
<th>Yellow Poplar</th>
<th>White Oak</th>
<th>American Beech</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum DBH (cm)</td>
<td>70</td>
<td>220</td>
<td>125</td>
<td>135</td>
</tr>
<tr>
<td>Maximum DBH Growth (cm/yr)</td>
<td>1.1</td>
<td>2.0</td>
<td>1.0</td>
<td>0.8</td>
</tr>
<tr>
<td>Maximum Height (m)</td>
<td>12.5</td>
<td>45</td>
<td>25</td>
<td>30</td>
</tr>
<tr>
<td>Maximum Seedling Growth (cm/yr)</td>
<td>1.0</td>
<td>1.5</td>
<td>0.9</td>
<td>0.75</td>
</tr>
<tr>
<td>Maximum Seed Count (#)</td>
<td>75</td>
<td>180</td>
<td>95</td>
<td>70</td>
</tr>
<tr>
<td>Seed Dispersal Radius (m)</td>
<td>75.0</td>
<td>52.5</td>
<td>6.25</td>
<td>7.5</td>
</tr>
<tr>
<td>Influence Radius at 50 cm DBH (m)</td>
<td>4.9</td>
<td>4.7</td>
<td>5.1</td>
<td>6.6</td>
</tr>
<tr>
<td>Shade Tolerance Power (unitless)</td>
<td>1.6</td>
<td>1.45</td>
<td>0.75</td>
<td>0.5</td>
</tr>
<tr>
<td>Maximum Seedling Mortality Rate (%)</td>
<td>70</td>
<td>40</td>
<td>25</td>
<td>15</td>
</tr>
<tr>
<td>Maximum Adult Mortality Rate (%)</td>
<td>20</td>
<td>10</td>
<td>5</td>
<td>3</td>
</tr>
</tbody>
</table>

Each year is based loosely on the seasons from the beginning of autumn to the end of summer of the next year, with the following steps occurring sequentially: 1) mortality (including background, resource-driven, and disturbance-induced), 2) seed production and dissemination, and 3) growth.

2.3.1 Mortality

For an individual $i$, to estimate the mortality of that individual, $M(i)$, an exponential decay function based on growth rate was used in the form

$$M(i) = \alpha \exp(-\beta G(i)) + \gamma,$$

where $G$ is the growth of the individual that can be measured in either changes in height or DBH, $\alpha$ and $\beta$ are species-specific and produce the decline in death probability based on height of the individual, and $\gamma$ is a minimum background death rate. With the mortality rate a function of growth rate, the faster an individual grows, the less likely it is to die, a pattern that is well-documented in the forest ecology literature [48].

Mortality curves are similar for all size classes, but rates are highest for seedlings (Figure 2), intermediate for saplings (Figure 3) and lowest for adult trees (Figure 4). Seedling mortality rates are highest because they are much more susceptible to death from lack of light, biotic effects such as pathogens or pests, and competition with other individuals [10, 13, 20]. Across all size classes, the same species-specific differences apply, matching the ecology of these species [6]. Black cherry has high mortality rates when not in optimal, high-growth situations, American beech can persist while growing very slowly, and the other two species exhibit intermediate sensitivities.

When a seedling dies, its remains have very little impact on the surrounding environment compared to the remains of an adult tree because they are small in comparison. However, when an adult dies, the remains may im-
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Figure 2: Seedling Mortality Probability as a Function of Growth Rate.

Figure 3: Sapling Mortality Probability as a Function of Growth Rate.

Figure 4: Adult Mortality Probability as a Function of Growth Rate.

2.3.2 Seed production and dissemination

Next we examine the proliferation of seeds from surviving individuals, and the calculation of whether or not these seeds establish themselves. In general, the number of seeds that an adult tree produces depends on the maturity of the individual. In this model, the maturity of a tree is measured by its DBH. A logistic growth function was used to correlate the number of seeds that an individual produces with its DBH for each species, which is given by

\[ O(i) = \frac{S_i}{1 + \beta_s \times \exp(-\gamma_s \times DBH(i))} \]  

(2)

where \( O(i) \) is the number of seeds that individual \( i \) produces, \( S_i \) represents the total number of seeds possible, \( \beta_s \) and \( \gamma_s \) control the shape of the seed curve, and DBH(\( i \)) is the DBH of individual \( i \). Figure 5 shows the functions which were created. The plots each start at zero seeds for an individual which is at zero DBH, and the seed count plateaus and follows the maximum seed count to beyond the maximum allowed DBH for each species.

Black cherry trees are an early reproducing species and thus very quickly achieve their maximum ability to produce seeds. Although black cherry has a high mortality rate, it is still prevalent in the iterations of the model because of its ability to produce seeds in a short life span. Also, transport from other forest locations can occur from the digestion of cherry seeds by animals. This is modeled by including a small amount of cherry seeds spread throughout the landscape no matter the condition of the cherry population in the landscape, presumed to be from outside the modeled landscape.

Yellow Poplar has the quickest growth rates and largest DBH capabilities of all of the species in the model, and thus has a corresponding largest amount of seeds it can produce. White oak and American beech produce a moderate amount of seeds later in their lives, which is reflected in the Figure 5. American beech follows a seed crop pattern, referred to as masting, with a 25% chance to produce many seeds and a 75% chance to produce few seeds, making its establishment of seedlings very high about one quarter of the years in the model. The displayed value in Figure 5 is a weighted average of the two possibilities.

After the seeds have been produced, a location for each of the seeds is created by following a Gaussian distribution around the parent tree. This distribution depends on the species of the tree. The probability distribution is

\[ \text{probability} = \frac{1}{\sigma \sqrt{2\pi}} \exp\left(-\frac{(x-u)^2}{2\sigma^2}\right) \]

where \( u \) is the center of the distribution, \( \sigma \) is the standard deviation, and \( x \) is the distance from the center.

This is modeled by allowing the agent to persist for some time, during which its effect on the resource surface will slowly diminish to zero over several years, following the equation given in Equation 4, which is discussed later.

2.3.2.2 Transport of seeds

Transport of seeds is modeled by allowing the agent to persist for some time, during which its effect on the resource surface will slowly diminish to zero over several years, following the equation given in Equation 4, which is discussed later.

2.3.2.3 Germination and growth

Germination and growth of seeds is modeled by allowing the agent to persist for some time, during which its effect on the resource surface will slowly diminish to zero over several years, following the equation given in Equation 4, which is discussed later.

2.3.2.4 Seedling mortality

Seedling mortality is modeled by allowing the agent to persist for some time, during which its effect on the resource surface will slowly diminish to zero over several years, following the equation given in Equation 4, which is discussed later.

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displayed in Figure 6 for each species. This distribution has a deviation that is proportional to the height of the tree. White oak and American beech have a small scaling factor, while yellow poplar has a slightly larger scaling factor because its seeds spread further than the acorns and nuts produced by white oak and American beech. Finally, black cherry does not follow this height scaling of the Gaussian distribution because, in reality, cherries produce by the individuals are often transported via animals in the landscape to far locations [6]. The probability density function for black cherry which is presented in Figure 6 is valid for any height individual.

Each seed’s location is assessed to determine the likelihood of the seed’s survival. A calculation of the resource surface at its location is made in order to evaluate its probability of surviving to become a seedling. Based on the available resources at a given location, a seed is found to either survive or not by using a binomial calculation given its probability of survival.

2.3.3 Growth

Growth in this model is found by considering the level of influence of neighboring individuals of the individual of interest. If there is sufficient crowding around an area in the landscape, then individuals in that area grow less than individuals which inhabit more open locations. If there are large trees neighboring one another, then they inhibit growth of others at a higher level than smaller trees in the area. These ideas are captured in the model by allowing agents in the landscape to impact a resource surface of which the severity is based on their DBH and species. Each agent creates an impact in the local resource surface similar to Figure 7. This impact follows the equation,

\[ S_{i,j}(x_i, y_i, x_j, y_j) = \frac{((x_i - x_j)^2 + (y_i - y_j)^2)^{n/2} + f(t)c}{((x_i - x_j)^2 + (y_i - y_j)^2)^{n/2} + c} \]  

(3)

where \( S_{i,j} \) is the impact of individual \( j \) at the location of individual \( i \), \( (x_i, y_i) \) is the location of individual \( i \), \( (x_j, y_j) \) is the location of individual \( j \), \( n \) and \( c \) are species-specific parameters of individual \( j \), and \( f(t) \) is a term which controls the decay of the individual \( j \) when it dies. The function \( f(t) \) is zero when an individual is alive, and increases linearly to one when the individual dies, and is given by

\[ f(t) = \min(1, t_g/4) \]  

(4)

where \( t_g \) is the number of years the individual has been dead. When \( f(t) \) is one, the individual no longer impacts the resource surface, and is considered entirely decomposed.

![Figure 5: Number of Seeds Produced Vs. Diameter at Breast Height.](image5.png)

![Figure 6: Seed Distribution Kernels by Species.](image6.png)

![Figure 7: Two Dimensional Representation of Resource Surface Impact.](image7.png)
Overlapping effects from agents provide a multiplicative effect, given by

\[ R_i = \prod_{j \in J} S_{i,j} \]  

(5)

where \( R_i \) is the resource value at individual \( i \), \( J \) is the index set of all neighboring individuals, and \( S_{i,j} \) is the impact of individual \( j \) at individual \( i \)’s location, which follows Equation 3. Using a multiplicative effect insures that \( R_i \) will stay a measure between 0 and 1 where using an additive effect would not in certain circumstances. Neighboring individuals are those within 10 meters of each other. This equation captures the effects on resource availability due to local crowding. This value, \( R_i \), will vary between 0 and 1, with 0 representing a total absence of resources, and 1 representing an abundance of resources, which results when there are no neighbors. An example of the combined effects from several individuals is shown in Figure 7. A very large tree is near the origin imparting a large effect, while a seedling is located toward the top of the image and imparting a small effect. The resource value for any individual or seed, along with that individual’s tolerance level, creates a value which is used to calculate its growth. The equation is given by

\[ G(i) = (R_i)^\alpha \]  

(6)

where \( G(i) \) is the growth percentage of individual \( i \), \( R_i \) is the resource value at individual \( i \)’s location, and \( \alpha \) is a parameter which describes the shade tolerance of each species.

Finally, in order to find the level of growth for the individual, the growth percentage variable is scaled by the maximum growth by species. The growth of individual \( i \), \( Gr(i) \) is given by

\[ Gr(i) = G(i) \times MGR(i) \]  

(7)

where \( G(i) \) is the percentage growth of individual \( i \) and \( MGR(i) \) is the maximum growth rate of individual \( i \). Table 1 displays the values of shade tolerance power, \( \alpha \), and the maximum growth for each species. A graphical representation of Equation 6 can be found in Figure 8. It shows for each species, that depending on the available resource level, individuals of that species will grow at different rates. American beech has the highest tolerance and thus the best percentage growth per resource, while black cherry is the most shade intolerant and thus has the worst growth per available resource.

Seedlings first follow the growth percentage calculation from Equation 7 and then if the individual reaches a height of 1.37 meters a calculation is made to find its DBH using a three parameter Weibull Function given by

\[ H(DBH(i)) = \alpha_H \left(1 - \exp\left(-\frac{DBH(i)}{\beta_H}\right)^\gamma_H\right) \]  

(8)

where \( H(DBH(i)) \) is the height of individual \( i \) and \( \alpha_H, \beta_H, \) and \( \gamma_H \) are parameters based on the species of individual \( i \). The Weibull function was chosen because of its ability to closely represent empirical data 27. The value for DBH is found by solving the inverse of Equation 8. This function is displayed graphically by species in Figure 9.

Saplings and adults in the model follow a similar set of calculations where the DBH is found first, and then the height is adjusted using Equation 8. A value is found for the resource surface at the individual’s location, which is the altered by the shade tolerance of the species to find a percentage of the maximum growth. This maximum growth percentage is then applied to the maximum growth in DBH, which can be found in Table 1 in order to find the growth in DBH of the individual. After the growth in DBH is found, a calculation following Equation 8 is made to find the corresponding change in height.

2.4 Disturbance

Disturbance is a crucial component to shaping the overall biodiversity in a landscape 2. 35. 10. 13. The effects of gaps created by trees falling in a hurricane or underbrush cleared by a forest fire create growth opportunities, and disturbances with different characteristics can favor different species. Disturbances influence species composition indirectly via changes to the understory environment, thereby affecting subsequent recruitment, as well as directly via mortality. Some disturbances concentrate mortality in higher DBH individuals (e.g., hurricanes and other wind events) whereas others primarily impact lower DBH individuals (e.g., fires).

The following formula was used to model disturbance to higher DBH individuals or overstory disturbance. The chance of mortality of individual \( i \), \( M(i) \), is given by

\[ M(i) = \frac{\beta_h}{1 + \exp(\gamma_h(DBH(i) - \alpha_h))} \]  

(9)

where \( \alpha_h \) and \( \beta_h \) are assumed to be positive. This is a logarithmic growth function from low mortality at low DBH to high mortality at high DBH. The effective cutoff point in DBH is selected using the term \( \alpha_h \), the death rate is chosen by \( \beta_h \), and the parameter \( \gamma_h \) controls the sharpness of the transition between what is considered to be a low or high DBH individual.

The following formula was used to model disturbances that are more likely to affect smaller DBH individuals or understory disturbance. Here \( M(i) \) is given by

\[ M(i) = \beta_l \exp(-\alpha_l(DBH(i)). \]  

(10)

These disturbances were modeled using a decaying exponential from high mortality at low DBH to low mortality.
at high DBH. The effective cutoff point in DBH is denoted by \( \alpha_l \), and a death rate by \( \beta_l \).

In addition, some disturbances are not biased towards small or large trees, but rather have severe effects in localized patches (e.g., tornadoes, clearcut timber harvest). When modeling these disturbances, or \textit{block} disturbance, the landscape is first broken into individual cells and an initial cell is chosen to be affected by the disturbance. These disturbances spread to neighboring cells in a random fashion until the user defined number of cells is met. Then for each selected cell, the individuals are tested for removal based on percentage rate of removal. For example, Figure 10 shows an image of five affected areas in a twenty-five cell block disturbance.

2.5 Species interactions

A crucial part of this model is the implementation of species-specific interactions. Complex species-specific interactions can result from a variety of factors including belowground competition and damage resulting from pests and pathogens. Root systems can be highly competitive (if rooting depths and nutrients needs are similar) or complementary (if rooting depths and nutrient needs differ). Pest and pathogen effects are controlled by the extent to which the natural enemies present are generalists that attack both species or specialists that attack only one.

In order to capture the different dynamics, an \( N \times N \) matrix is created that describes the impact of species \( i \) on individual of species \( j \) for \( 1 \leq i, j \leq N \). The matrix is given by

\[
SIM = \begin{bmatrix}
    a_{11} & a_{12} & \ldots & a_{1n} \\
    a_{21} & a_{22} & \vdots & \vdots \\
    \vdots & \vdots & \ddots & \vdots \\
    a_{n1} & \ldots & \ldots & a_{nn}
\end{bmatrix}
\]  

where \( SIM \) represents the species interaction matrix and entry \( a_{ij} \) is taken to be the influence of species \( i \) on species \( j \). In order to find the level of species-specific influence on an individual \( i \) in the landscape, a species-specific interaction value, \( V(i) \), is found which is a scalar quantity that represents the level of influence of neighboring individuals, \( j \). This calculation uses the species interaction matrix by first calculating the weight, \( W(p) \), of each species type, \( p \), from the resource curve. The weight around individual \( i \) by species \( p \) is found by considering the complement of their influence on the resource curve, which is given by

\[
W(p) = 1 - \prod_{j \in p} S_{ij},
\]

where \( S_{ij} \) is the resource impact of individual \( j \) at the location of individual \( i \), and \( p \) is the species of interest.
The calculations for each species are then combined into a row vector:

\[ W(P) = \langle W(p) \rangle, \quad p \in P, \quad (13) \]

with \( P \) being the set of all species.

Given the species of individual \( i \), the species interaction matrix can be combined with the species weighting around individual \( i \) by considering the \( P_i \) column of the species interaction matrix. \( \text{SIM}_P \) gives the level of influence of each species on the species of interest, and is a column vector extracted from the total species interaction matrix. The product of this vector with the weight of each species type gives a scalar, \( V(i) \), which describes the severity of species interaction influences on individual \( i \), and is given by

\[ V(i) = W(P) \ast \text{SIM}_P. \quad (14) \]

After the calculation of the species specific effect on each individual, \( V(i) \), it can be used in the calculation of both the growth and mortality rate. When \( V(i) \) is used to alter the mortality rate, it adds an additional chance of death for the individual which is proportional to \( V(i) \). This equation is a modification of Equation \( 1 \) and is given by

\[ \text{MM}(i) = M(i) + \delta_m(i) \ast V(i) \]

where \( \text{MM}(i) \) is the modified mortality rate of individual \( i \), \( M(i) \) is the original mortality rate of individual \( i \), and \( \delta_m(i) \) is a factor which controls the severity of the effect, which depends on the species of individual \( i \).

When the species interaction value is used to alter the growth rate, it lowers the growth percentage for the individual which is proportional to \( V(i) \). This equation is a modification of Equation \( 2 \) and is given by

\[ \text{MG}(i) = G(i) - \delta_g(i) \ast V(i) \]

where \( \text{MG}(i) \) is the modified growth percentage of individual \( i \), \( G(i) \) is the original growth percentage of individual \( i \), and \( \delta_g(i) \) is a factor which controls the severity of the effect and depends on the species of individual \( i \).

Species-specific effects can vary considerably. Here we examine the extremes. Consider the case with weak conspecific effects, where species affect one another similarly, and another case with strong conspecific effects, where each species strongly impacts itself. To examine these cases, two different species interaction matrices are considered. For a \textit{weak} conspecific interaction, the matrix is given by

\[ \text{SIM}(\text{weak}) = \begin{bmatrix} 0.5 & 0.5 & 0.5 & 0.5 \\ 0.5 & 0.5 & 0.5 & 0.5 \\ 0.5 & 0.5 & 0.5 & 0.5 \\ 0.5 & 0.5 & 0.5 & 0.5 \end{bmatrix}. \quad (17) \]

\[ \text{SIM}(\text{weak}) \] indicates an inter-species interaction in which the effects are equal for conspecifics and heterospecifics.

At the other extreme, \textit{strong} conspecific interactions are modeled by the following species interaction matrix:

\[ \text{SIM}(\text{strong}) = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}. \quad (18) \]

In this case, \( \text{SIM}(\text{strong}) \) is indicative of a species interaction matrix in which there are only conspecific effects. The changes to the growth rates in the scenario were taken to be at most a 20% decrease to seedlings, a 5% decrease to saplings, and a near zero effect on adults. The changes to the mortality rates were taken to be at most a 35% increase to seedlings, a 10% increase to saplings, with near zero effect on adults. These values were selected because it is known that there is a high level of impact on seedlings when compared with adults [29].

The weak conspecific effect manifests in the scenario by forcing younger individuals to prefer additional separation from all individuals. In the scenarios that implement a strong conspecific effect, younger individuals prefer maximal separation from their parents and members of the same species.

### 2.6 Scenarios

We explored eight combinations of conspecific effect strength and disturbance type, while holding all other variables constant. These scenarios crossed two conspecific effect strengths (\textit{weak} or \textit{strong}) with four disturbance types (understory, overstory, block, and none).

Understory disturbances primarily target low-DBH individuals (< 2.5 cm DBH). Examples of this type of disturbance include low-intensity forest fires and pulses of predation from large herbivore herds. Overstory disturbances target primarily high-DBH individuals (> 20 cm DBH). Disturbances that mostly impact large trees include hurricanes and severe thunderstorms. Block disturbances impact spatially defined patches (3 out of 25 grid cells overlaid on the landscape) during each event, with the probability of mortality rate constant (0.75) across all size classes within each affected patch. Disturbances like this are usually of anthropogenic origin (e.g., timber harvest), but may also result from floods or tornadoes. Background mortality occurs in all cases and thus compositional turnover can occur between disturbances and in scenarios without disturbance, albeit at a slower pace.

As noted above, the two conspecific effect conditions (\textit{weak} or \textit{strong}) determine the extent to which established trees inhibit the growth and survival of conspecifics. For instance, with strong conspecific effects, a white oak seedling growing one meter from a large white oak tree...
has a low growth rate and chance of survival. With weak conspecific effects, this same white oak seedling is still negatively affected by the large white oak tree, but no more so than it would be by a similar heterospecific tree.

For each scenario, fifty simulations were conducted over the five-hundred-year period. These simulations were averaged to determine the basal area dynamics over the 500 years. We also conducted diversity calculations. Scenarios were run with varied initializations of the landscape, but these initial conditions did not impact dynamics and are not presented here.

2.7 Model measurements

During each run the number of individuals in each species, as well as the age, DBH, and height of each individual is recorded. This data is used to construct the basal area diagrams in the following section.

Additionally the diversity calculations which are used are those using Hill Numbers for \( (h = 2) \). The calculation is given by

\[
D^h = \left( \sum_{i=1}^{R} p_i^h \right)^{1/(1-h)} \tag{19}
\]

where \( D^h \) is the diversity calculation of Hill number \( h \), \( R \) is the number of species, and \( p_i \) is the proportion of species \( i \). In these simulations, there are four total species in these calculations. These calculation is made at the level of the entire landscape, called the gamma diversity, and also made inside twenty-five cells that divide the landscape, making a value for the alpha diversity. The gamma diversity gives a measurement of the overall diversity in a landscape, while the alpha diversity measure local diversity.

3 Results

The goal of this study is to investigate how different disturbance types interact with different species-specific interactions. We first describe species-level dynamics for each scenario, and then move on to a comparative summary of how emergent biodiversity patterns vary across scenarios.

3.1 Scenario A: no disturbance and weak conspecific effects

We first examined weak conspecific effects without disturbance. As can be seen in Figure 11, American beech quickly dominates and black cherry quickly loses volume in the landscape in favor of the other species. The yellow poplar and white oak persist in reasonable abundance for a few hundred years, but nevertheless dwindle until they are essentially removed from the landscape. Although white oak is a later successional species with greater shade tolerance than black cherry or yellow poplar, it too is outperformed by the American beech in this scenario. Although less shade tolerant than white oak, yellow poplar has a very fast growth rate and large maximum size, and this likely explains the roughly comparable performance of these two species.

3.2 Scenario B: no disturbance and strong conspecific effects

Next we consider strong conspecific effects without disturbance. In a comparison of the basal area by species between the weak and strong conspecific effects scenarios, it is clear that the addition of stronger conspecific effects creates much different dynamics in the simulations. Rather than slowly disappearing like in Scenario A, Figure 12 shows that yellow poplar and white oak persist, and appear to nearly stabilize by about 400 years. This is likely because beech begins to inhibit its own seedlings and saplings when it is extremely abundant, allowing other species to persist despite the fact that beech is the species best adapted to a disturbance-free landscape. Also of note in this scenario is that white oak seems to do better than yellow poplar, which was not the case in the disturbance-free scenarios, we first examine the case in which conspecific effects are weak. Again we see that beech dominates the landscape and black cherry does not fare well, but the other two species, and especially yellow poplar, benefit tremendously from understory disturbance see Figure 13.

Like Scenario A, Scenario C has weak conspecific effects, so the differences in species composition can be attributed solely to the inclusion of understory disturbance. Yellow poplar’s large size and fast growth rate should allow it to more quickly grow out of the DBH danger zone. In addition, the relatively shade-intolerant seedlings of yellow poplar likely benefit from the additional light that reaches the forest floor when the lower canopy is thinned or removed. As such, it makes sense that yellow poplar performs especially well with understory disturbance.
### 3.4 Scenario D: understory disturbance and strong conspecific Effects

The next scenario is one in which understory disturbance occurs in the presence of strong conspecific effects. We have seen previously that yellow poplar and white oak benefit from both understory disturbance and strong conspecific effects when these conditions are applied separately. Thus, it is not surprising that when both are present simultaneously, yellow poplar and white oak achieve even greater dominance, see Figure 14. In fact, yellow poplar's basal area even approaches that of beech, and it would be fair to characterize the resulting forest as one that is co-dominated by American beech and yellow poplar along with a respectable component of white oak too.

### 3.5 Scenario E: overstory disturbance and weak conspecific effects

We now begin to consider the effects of overstory disturbance, first in conjunction with weak conspecific effects. This type of disturbance targets high DBH trees and is most analogous to a high wind event like a hurricane or severe thunderstorm. The compositional trends produced by this scenario shown in Figure 15 are very similar to those produced by Scenario A (weak conspecific effects without disturbance). This is likely because the removal of large overstory trees increases the light and resources available to subcanopy trees, allowing them to quickly grow into the upper canopy, but does not meaningfully increase forest floor light levels due to the continued presence of small and medium-sized trees. The only notable distinction from Scenario A is that the current condition leads to a steeper decline of yellow poplar, with its effective disappearance occurring over 100 years earlier. This is probably because, as the fastest and largest growing species, yellow poplar is especially susceptible to disturbances that target large trees.

### 3.6 Scenario F: overstory disturbance and strong conspecific effects

Now that the scenario with weak conspecific effects and overstory disturbance has been explored, it is time to consider overstory disturbance with strong conspecific effects. Yet again, the inclusion of strong conspecific effects lead to a major change in compositional trends as shown in Figure 16. Comparing these results to Scenario E, we see that yellow poplar and white oak benefit substantially from strong conspecific effects, undoubtedly because the dominant beech trees begin to exhibit self-inhibition.

Overall, the current scenario looks very similar to Scenario B (no disturbance and strong conspecific effects),
but with some minor differences in the white oak and yellow poplar trajectories. In the presence of strong conspecific effects, yellow poplar does slightly better with no disturbance than with overstory disturbance, likely because, as noted previously, its large size and fast growth rate makes it disproportionately subject to mortality. White oak, in contrast, does slightly better with overstory disturbance, appearing to benefit from the yellow poplar mortality. Meanwhile, beech remains dominant throughout, and cherry is still unable to persist.

3.7 Scenario G: block disturbance and weak conspecific effects

Now that both understory and overstory disturbances have been explored, the last type of disturbance is one which impacts the landscape in discrete patches (i.e., blocks), causing uniform mortality (0.75 probability) across all size classes within the affected area. Examples of this type of disturbance include tornadoes, floods, and clearcut timber harvest.

As usual, we first consider block disturbance in the presence of weak conspecific effects. Compositional trajectories for this scenario, see Figure 17, are most similar to Scenario C (understory disturbance with weak conspecific effects), but yellow poplar does even better in the current context, with abundance that is comparable to beech through the entire 500 years. Even without strong conspecific effects to force self-inhibition of ultra-abundant species (i.e., beech), yellow poplar appears to benefit substantially from periodic disturbances that remove 75 percent of all trees within discrete patches. This makes sense given that yellow poplar is fast-growing and shade-intolerant, with far-dispersing seeds that are likely to blanket all disturbed patches. White oak, in contrast, does not disperse as far or grow as fast, and this likely explains why it does not benefit much from block disturbance, despite needing more light than beech. It does however do slightly better than in Scenario A (no disturbance and weak conspecific effects), probably because of the increased light availability at patch edges, and because some mature white oak trees inevitably survive within disturbed blocks.

3.8 Scenario H: block disturbance and strong conspecific effects

The final scenario we examined is one in which block disturbance is coupled with strong conspecific effects. Here we see, yet again, that strong conspecific effects benefit both yellow poplar and white oak, and especially the latter, Figure 18. With block disturbance and weak conspecific effects, the landscape was already co-dominated by beech and yellow poplar, and thus yellow poplar’s boost
here is marginal. In contrast, mirroring the trend we have seen for all disturbance conditions (including the no disturbance scenarios), white oak does dramatically better when conspecific effects are strong. While white oak is equally subjected to these effects, the actualized self-inhibition is much greater for beech simply because of beech’s greater abundance.

3.9 Diversity across scenarios

Now that we have completed our examination of compositional trajectories over time for each scenario, we turn to a comparison of the emergent diversity values (see Equation [19]). Here we consider the final (year 500) diversity values across all eight scenarios.

In all cases, we found that diversity was higher when conspecific effects were more strongly negative, see Table 2. This pattern held across all disturbance types, including the absence of disturbance, and manifested for both alpha (local) and gamma (landscape-level) diversity. This makes sense given that strong conspecific effects inhibit the formation of large mono-specific patches, thereby preventing a single species from dominating some or all of the landscape. The influence of conspecific effect strength was most pronounced in the understory disturbance scenario, least pronounced in the no disturbance scenario, and intermediate in the overstory and block disturbance scenarios.

Understory and block disturbances yielded the greatest diversity overall, and this was true with either weak or strong conspecific effects. Diversity was low without disturbance and with overstory disturbance, as these landscapes were heavily dominated by beech. However, in the presence of strong conspecific effects, diversity was slightly higher with overstory disturbance than with no disturbance. These patterns were qualitatively identical for both alpha and gamma diversity.

4 Discussion

Our results revealed clear interactions between disturbance and CNDD strength. In all scenarios, beech dominated and cherry comprised a very small fraction of basal area, but there was considerable variation in the performance of yellow poplar and white oak, and these differences appear to account for the diversity results described above.

Without disturbance, and with weak conspecific effects, beech eventually achieved near total dominance as the other three species were driven close to local extinction. This is ecologically plausible given that beech is highly shade-tolerant, capable of regenerating in the deep shade beneath its own canopies, and sometimes found in monospecific stands where major disturbances have not

<table>
<thead>
<tr>
<th>Conspecific Effects</th>
<th>Weak</th>
<th>Strong</th>
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<tbody>
<tr>
<td>Alpha Diversity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No Disturbance</td>
<td>1.0</td>
<td>1.2</td>
</tr>
<tr>
<td>Understory Disturbance</td>
<td>1.3</td>
<td>2.0</td>
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<td>Overstory Disturbance</td>
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</tr>
<tr>
<td>Block Disturbance</td>
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<td>1.7</td>
</tr>
<tr>
<td>Gamma Diversity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No Disturbance</td>
<td>1.0</td>
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Table 2: Alpha and Gamma diversity numbers (Hill 2) after 500 years.
occurred for a century or more. With strong conspecific effects, yellow poplar and white oak were able to persist in reasonable numbers. The stronger inhibition of beech seedlings by beech adults seems to have allowed white oak and yellow poplar to persist even in the absence of disturbance. However, white oak clearly outperformed yellow poplar, likely because white oak is more shade-tolerant. In real ecosystems, conspecific effect strength may vary across stands [7][30], depending on the local prevalence of species-specific pests and other factors, so both scenarios are plausible, and indeed beech does not always dominate undisturbed areas in which it occurs [1][36].

When disturbances were concentrated in the understory (mostly affecting small trees), conspecific effect strength had a major impact on relative abundances, with white oak proving to be most sensitive. White oak numbers fell dangerously low when conspecific effects were weak, but remained at robust levels when conspecific effects were strong. This may seem odd given that white oak seeds (acorns) disperse very short-distances, falling mostly near conspecifics (the parent tree). However, in a stand dominated by beech and yellow poplar, any seed, regardless of dispersal pattern, has a good chance of being close to an adult of one of these species. Thus, the positive net effect of increased conspecific effect strength (for all species) on white oak is likely due to the fact that white oak never surpasses yellow poplar (or beech) in abundance. Yellow poplar also benefitted slightly from stronger conspecific effect strength, but did reasonably well in both conditions, and fared much better overall, compared to the disturbance-free scenarios. This was almost certainly due to the much higher understory light levels. Despite the fact that large overstory trees were not disturbed in these scenarios, subcanopy trees and saplings intercept a substantial fraction of the light that would otherwise reach the forest floor, and thus disturbances concentrated in the understory can substantially benefit shade-intolerant seedlings like those of yellow poplar. In addition, as a very fast-growing tree, young yellow poplar trees should have a better chance of surviving the next understory disturbance, as compared to the other species we modeled.

Overstory disturbance yielded results that were similar to the no disturbance scenarios. When conspecific effects were weak, beech achieved near total dominance. With strong conspecific effects, white oak maintained moderate abundance, and yellow poplar persisted (but not comfortably). The similarity of the overstory and no disturbance scenarios suggests that overstory tree mortality, without accompanying mortality of subcanopy trees and saplings, did not appreciatively increase forest floor light levels. In these conditions, highly shade-tolerant beech is a formidable competitor, and the deep shade persisting even after overstory mortality is created primarily by thicket of beech saplings and small trees. As such, a strong conspecific effect (beech self-inhibition) is necessary to allow for the establishment of other species, particularly moderately shade-tolerant white oak.

Results from the block disturbance scenarios were similar to those produced by the understory disturbance scenarios, which is again related to the prevalence of beech thickets in the understory/subcanopy layers. Understory disturbance thins these thicket throughout the landscape, while block disturbance decimates them, as well as overstory canopy trees, in local areas. In both cases, white oak and yellow poplar benefit considerably. However, yellow poplar achieves slightly greater abundance with block disturbance. This makes sense given that, compared to white oak, yellow poplar is less shade-tolerant (and faster growing in high light) and has farther dispersing seeds. As such, when there are local patches where both the understory and overstory have been decimated, yellow poplar is more likely to arrive and also able to grow faster.

Forest simulations are necessarily extreme simplifications of the real world. As such, our objective in this study was not to predict likely outcomes for any particular forest, but rather to explore and demonstrate what could happen, given a fairly limited and reasonable set of assumptions. Most importantly, our results suggest that composition and diversity may be influenced by interactions between disturbance and CNDD. Accordingly, to accurately predict outcomes and/or understand mechanisms, empirical ecologists may need to consider both of these factors simultaneously.

These conclusions broadly dovetail with an emerging body of empirical literature focused on potential context-dependency of CNDD strength and CNDD-driven dynamics. For instance, several studies have shown that CNDD can vary across space as a function of light availability and local soil conditions [5][19][23][32]. In addition, CNDD can fluctuate from year to year with variation in temperature and precipitation [50], and similar experimental work has shown that artificially induced drought can alter conspecific effects [49].

Conspecific effect strength can also vary across species [12], and even within species [51]. We considered experimenting with these sources of variation but soon realized that the potential parameter space would quickly explode to unmanageable levels. As such, we opted to explore how different types of disturbance interact with different CNDD strengths, applied consistently across all species in each scenario, but varied across scenarios. Our results demonstrate that interactions between disturbance and CNDD can have important implications even in a highly simplified, species-poor situation. In conclusion, as a complement to recent empirical studies, our simulation-based findings strengthen the evidence that CNDD is not
an isolated phenomenon, but rather a process that can yield different outcomes in different contexts.

Author Contributions
Mills contributed to the model creation, model coding, model simulation, interpretation of results, and manuscript editing. Chan contributed to the model creation, model coding, interpretation of results, and manuscript writing. Ramage contributed to the problem creation, model creation, interpretation of results, and manuscript writing.

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