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ARTICLE

Mechanisms regulating understory plant diversity in three forest types: a simulation study

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ABSTRACT

Understory plant communities play a crucial role in forest ecosystems, significantly contributing to nutrient cycling, providing habitats, and supporting forest restoration. While light penetration and soil quality are known drivers of these communities, the mechanistic role of the canopy structure remains understudied. This paper examines how different canopy characteristics, specifically canopy percentage and the canopy effect intensity, affect plant diversity in the understory layer through a lattice simulation model. Based on the lattice Lotka-Volterra competition model with microhabitat locality (Tubay and Yoshimura 2018), we simulated understory population dynamics across three forest types: evergreen, deciduous, and mixed. Our results reveal that the canopy structure acts as a critical biological filter for the understory plant species, identifying a tipping point in evergreen forests where species diversity collapses once canopy cover exceeds 80%. In contrast, we show that seasonal leaf shedding in deciduous forests acts as a *temporal buffer*, preventing competitive exclusion and maintaining high diversity even under high canopy cover and high canopy effect. These findings demonstrate that temporal variations in canopy cover are as vital as spatial heterogeneity in maintaining forest biodiversity. By providing novel simulation-based evidence for these mechanisms, this study offers a mechanistic framework that can help inform forest management and conservation strategies, particularly regarding the potential impact of canopy density thresholds on understory biodiversity.

INTRODUCTION

Forests consist of several interacting layers, including the canopy, understory, and forest floor. One key interaction is between the canopy and the understory plant community. The understory—shrubs, grasses, mosses, lichens, and tree saplings and seedlings (Land for Wildlife 2016)—helps stabilize the soil surface and supports nutrient cycling and energy flow (Land for Wildlife 2016; Pisek 2017; Pan et al. 2013). It also influences forest survival and regeneration by shaping seedling dynamics in higher layers (Gilliam 2007; Deng et al. 2023). The canopy, the uppermost vegetation layer, is structurally complex and ecologically critical (Nadkarni et al. 2004). It regulates abiotic conditions—such as precipitation, sunlight, and airflow—reaching lower layers and contributes nutrients via leaf litter (Mestre et al. 2017; Dormann et al. 2020; Hou et al. 2024). Together, these canopy-driven conditions create heterogeneous microhabitats that strongly influence understory species diversity (Deng et al. 2023).

Understanding the plant diversity of forest ecosystems supports forest preservation and management. The plant diversity of the forest flora, specifically in the understory, has been studied due to its role on plant biodiversity and forest restoration and survival (Chavez and Macdonald 2012; McLachlan and Bazely 2001; De Steven *et al.* 2015). The species diversity is commonly measured through the total number of species in the community, called the species richness, and the abundance of each species, called the species evenness (Moore 2013). There are limited studies that explore the relationship between the canopy layer and the understory layer in a general forest setting (Deng *et al.* 2023). Most empirical work relies on plot-based sampling followed by diversity indices and statistical analyses to relate understory diversity to environmental drivers (Barnett et al. 2019; Brosofske et al. 2001; Dormann et al. 2020; Toledo et al. 2014). Reported drivers include soil moisture and temperature, leaf-off light availability, nutrient availability, litter depth/intensity, and management regime (Chavez and Macdonald 2010; Gazol and Ibañez 2010; Deng et al. 2023). Several studies report higher understory diversity under lower canopy cover (Zangy et al. 2021; Helbach et al. 2022), and higher diversity in deciduous and mixed forests than in evergreen forests (Babier et al. 2008; Chavez and Macdonald 2010; Fourrier et al. 2015; Jobidon et al. 2004; Mestre et al. 2017). The goal of

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this study is to provide more general results on the effect of various canopy characteristics on the population dynamics in the understory plant communities using mathematical simulations.

Several mathematical models have been introduced to understand the diversity of plant communities. These approaches range from gap dynamics models, which simulate succession based on individual tree growth and competition for light (Botkin *et al.* 1972; Shugart 1984), to matrix population models that analyze demographic transitions between growth stages (Usher 1966). Spatially explicit lattice models have also been widely used to investigate how local interactions drive community patterns (e.g., Yoshimura *et al.* 2004; Tubay *et al.* 2018). In this context, Takenaka (2006) studied coexistence among seedlings and tree species in a forest using a tree-based simulation model. He considered a 40 × 40 lattice wherein 40 species, each with 40 trees, were randomly placed in each cell. The simulation ran for 1500 hypothetical years and was repeated 10 times for each parameter variation. In the control simulations, the results showed that the number of species with lower fecundity decreased sooner than those with higher fecundity. Moreover, extinction was also observed when reproduction was lower, but the rate of extinction was slower. The results also showed that coexistence among species was influenced by the seedling establishment rate and the mortality rate under the canopy in the forest-floor seedbank (Takenaka 2006).

The lattice Lotka-Volterra model used in this study is defined as a Markov chain process wherein a lattice site is occupied or vacated by a species (Matsuda *et al.* 1992). This model helps explain different interactions of species, such as competition, mutualism, and predation (Bunin 2017; Matsuda *et al.* 1992). Additionally, incorporating the lattice structure of the model accounts for spatial heterogeneity, which is essential for plant communities where local interactions and spatial distribution affect population dynamics (Bunin 2017; Dopson and Emary 2024; Matsuda *et al.* 1992). The lattice Lotka-Volterra model has been widely used to understand the population dynamics of plant ecosystems (Cammarano 2011; Matsuda *et al.* 1992; Tainaka 1988; Tubay *et al.* 2015; Tubay and Yoshimura 2018; Yoshimura *et al.* 2004). Tubay *et al.* (2015) used the lattice Lotka-Volterra competition model to determine the multi-species coexistence in a terrestrial plant community. In their paper, they introduced differences in the soil microhabitats between species by assigning random settlement rates of species over the lattice. Results showed that multi-species coexistence is possible with site-specific and species-specific birth rates. Moreover, diversity was also promoted when species-specific variability in mortality was introduced in their model. Cammarano (2011) extended Lotka–Volterra models to examine light competition among co-dominant temperate-forest species, suggesting that coexistence is facilitated when understory performance depends on canopy composition via differences in light transmissivity.
The primary objective of this study is to explain the mechanisms by which canopy structure regulates understory diversity. Building upon the lattice Lotka-Volterra model with microhabitat locality (Tubay *et al.* 2015; Tubay and Yoshimura 2018), which primarily focused on soil heterogeneity, this study introduces the canopy layer as a dynamic environmental filter. Specifically, we incorporate canopy phenology, such as seasonal shedding and canopy effect intensity as distinct variables to simulate their differential effects on understory fecundity and mortality. By doing so, this study provides a novel mechanistic framework to explain how canopy structure regulates the coexistence among plant species in the understory. However, it is important to note that this model only utilizes simplified parameters to represent complex climatic variables and assumes constant interaction coefficients. These simplifications were intentionally chosen specifically isolate the influence of canopy structure on population dynamics. By excluding stochastic environmental noise, we can more clearly attribute observed shifts in diversity to the varying spatial and temporal constraints of the three forest types.

MATERIALS AND METHODS

The mathematical model used in this study was adopted from Tubay *et al.* (2015) and Tubay and Yoshimura (2018), with additional parameters incorporating the canopy characteristics into the model. This simulation study aims to describe the species diversity of understory plant communities under the canopy layer.

Multiple Contact Process

A two-dimensional lattice system was considered with N number of species. Each site was either vacant (O) or occupied (X_i) by a single individual of species i. Moreover, each vacant site can be occupied by an offspring of species i from a neigboring occupied site X_i at rate of b_i (birth rate), while each occupied site X_i was being emptied at a rate of m_i(mortality rate). The resulting birth-death dynamics (multiple contact process are defined by Eqs. (1)-(2).

$$X_i + O \rightarrow X_i + X_i \text{ , rate of } b_i \tag{1}$$

$$X_i \rightarrow O, \text{rate of } m_i \tag{2}$$

Microhabitat Locality

The birth rate of species is affected by a random species- and site-specific parameters that represents the microhabitat locality denoted by $\epsilon_i[m,n] \in [0,1]$. This represents how the water, soil nutrients, and other microhabitat-specific factors at site $[m,n]$ influence the fecundity of species i. By this, the birth rate b_i was given by

$$b_i = B_i \cdot \epsilon_i[m,n] \tag{3}$$

where B_i is the basal fecundity of species i.

The variation in the basal fecundity B_i is given by $B_i = B - (i-1)s$ for $i = 1,2,\cdots,N$ where the minimum difference in the fecundity rate is $s = \frac{p}{N}$ and p is the maximum birth rate difference. With this, B is the birth rate of the most fecund species. Note that B_i was the species-specific fecundity and $\epsilon_i[m,n]$ could also be interpreted as the local settlement rate of species i at site $[m,n]$ which follows a uniform distribution in [0,1].

Moreover, another version of the model was used in which the mortality rate of species i was affected by the microhabitat locality. A random parameter $\mu_i[m,n]$ was also introduced into the mortality rate, which was given by

$$m_i = M + h\mu_i[m,n] \tag{4}$$

where M was the lowest mortality rate among species, h was the range of mortality differences, and $\mu_i[m,n] \in [0,1]$ was a random parameter that represents the site- and species-specificity of species i at site $[m,n]$ similar to $\epsilon_i[m,n]$. Also, $\mu_i[m,n]$ followed a uniform distribution in $[0,1]$.

Canopy Effect Intensity

The canopy effect intensity represents the environmental filtering caused by the canopy layer on the understory compared to open canopy. This is denoted by $\alpha \in [0,1]$, representing the maximum intensity of canopy effects understory plants and is used to modify fecundity or mortality depending on the model variant.

In the Birth Model, this parameter reduces the reproductive potential of species i. The modified birth rate is given by modifying the baseline Eq. (3) as follows

$$b_i = \begin{cases} B_i \cdot \epsilon_i[m,n] \cdot \alpha_i \text{ , if site [m, n] is covered by the canopy} \\ B_i \cdot \epsilon_i[m,n] \text{, otherwise.} \end{cases} \tag{5}$$

In this model, the mortality rate remains determined by the baseline Eq. (4).

In the Mortality Model, the canopy effect intensity increases the death rate of species i, simulating stress. The modified mortality rate is defined by modifying the baseline Eq. (4) as follows

$$m_i = \begin{cases} M + h_1\epsilon_i[m,n] + h_2\alpha_i \text{, if site [m, n] is covered by the canopy} \\ M + h_1\epsilon_i[m,n] \text{, otherwise} \end{cases} \tag{6}$$

where h_1 and h_2 are constants that weight the influence of microhabitat locality ($\epsilon_i[m,n]$) and the canopy effect intensity (α_i) on mortality, respectively. In this study, both h_1 and h_2 were set to 0.05 to ensure the combined mortality contribution does not exceed 0.2, which is considered a high mortality rate for plant species (Condit *et al.* 1995, Lutz and Halpern 2006). The birth rate remains determined by the baseline Eq. (3).

Simulation

Three forest types were considered in this study: evergreen, deciduous, and mixed forests. These distinctions serve as representations for different climatic regimes. Evergreen forests, representing stable climatic conditions with no significant seasonal variation, were modeled as multi-story forests with dense vegetation maintained throughout the year. On the other hand, deciduous forests represented regions with distinct seasonality, consisting mostly of plant species that shed their leaves during a specific season (Dreiss and Volin 2014). The mixed forests were a combination of evergreen and deciduous trees. For simplicity, the mixed forest considered in this study was approximately half evergreen and half deciduous. To simulate these environmentally-driven events, the canopy cover for the evergreen forest was maintained throughout the simulation, while for the deciduous forest, the canopy cover was removed every four time-steps. In this model, one time step corresponds to a single season; thus, this four-step interval mimics the periodic annual leaf shedding driven by seasonal climatic changes.

A lattice with size 100×100 is used in the simulations. Depending on the preset canopy percentage, the canopy cover is randomly laid out on the lattice. An initial population P_i for each species i is randomly distributed throughout the lattice. In this study, the number of species (N) was set to 20. The initial population P_i was set to 50 for each species i, resulting in a total initial population of 1000 individuals. The parameters for microhabitat locality $\epsilon_i[m,n]$ and canopy effect intensity α_i are randomly generated for each species i. It is important to note that the canopy percentage (spatial extent) and the canopy effect intensity (α_i) are modeled as independent parameters in this study. This independence allows for the separate evaluation of spatial constraints versus physiological stress factors on understory dynamics, ensuring that the results disentangle the effects of habitat availability from environmental filtering strength. Population density (or lattice occupancy) was calculated as the ratio of the number of occupied sites (surviving individuals) to the total number of lattice sites (100×100). Finally, to ensure robustness, all results and figures presented in this study represent the average of ten independent simulation runs.

Birth and Death Processes

Only two processes were involved in this system: the birth and death.

Birth Process – A local birth process was considered in this study. Two neighboring sites are considered. If the randomly chosen sites are occupied or both are vacant, then no reproduction would occur. However, if one of the two sites that are randomly chosen is occupied by a species i and the other site is vacant, then the species i could reproduce in the vacant site with a birth rate of b_i.

Death Process – In this process, if the randomly selected site $[m,n]$ is occupied by an individual of species i then the individual could die at a rate of m_i.

These processes were performed for 10,000 time-steps, and each simulation is repeated ten times for stability and robustness. To ensure comparability across the different forest types, a controlled parameter set was used: the intrinsic species characteristics (including basal birth rates B, mortality rates M, and microhabitat responses ϵ) were held constant across all forest type scenarios. Consequently, any observed differences in community dynamics can be directly attributed to the variation in forest structure (canopy phenology) and the canopy effect intensity (α_i).

Parameters

The parameters used in this study were summarized and described in Table 1. The default values of the parameters and their references are also indicated in the table.

Table 1: Description of parameters used in the simulations

Parameters	Description	Default Value	Reference
L	Lattice dimension	100	(Tubay *et al.*, 2015, Tubay and Yoshimura 2018)
N	Total number of species in the lattice	20	(Tubay *et al.*, 2015, Tubay and Yoshimura 2018)
P_i	Initial population of species i	50	(Tubay *et al.*, 2015, Tubay and Yoshimura 2018)
b_i	Effective birth rate of species i	(0,1]	(Tubay *et al.*, 2015, Tubay and Yoshimura 2018)
B_i	Basal Fecundity of species i	Formula-based	
B	Maximum birth rate	[0.5,0.8]	(Tubay *et al.* 2015, Tubay and Yoshimura 2018)

p	Maximum birth rate difference	0.4	(Tubay *et al.* 2015, Tubay and Yoshimura 2018)
$\epsilon_i[m,n]$	Microhabitat locality of species i at site $[m,n]$ about birth process	[0,1]	(Tubay *et al.*, 2015, Tubay and Yoshimura 2018)
m_i	Death rate process i	Formula-based	
M	Minimum death rate	0.1	(Condit *et al.* 1996, Lutz and Halpern 2006)
$\mu_i[m,n]$	Microhabitat locality of species i at site $[m,n]$ about death process	[0,1]	(Tubay *et al.*, 2015, Tubay and Yoshimura 2018)
α	Maximum canopy effect intensity	[0,1]	Varying
α_i	Canopy effect intensity on species i	$[0,\alpha]$	Varying
can_per	Canopy cover percentage	[0,100]	Varying

RESULTS

The simulation study focused on the species diversity of the understory plant community with varying canopy characteristics, such as canopy percentage and canopy effect intensity. The parameters considered were the canopy percentage, the effect of the canopy on different life processes of plants, basal fecundity, and basal mortality rate. This section was divided into three parts: when (1) canopy characteristics, (2) basal fecundity, and (3) mortality rate were varied. Unless stated otherwise, **Figures 1** to **4** use a constant basal fecundity rate (B) of 0.8 and a constant mortality rate (M) of 0.1. **Figures 5** and **6** are the results of modifying the values of the basal fecundity (B), canopy effect intensity (α), and canopy percentage in the Birth Model. On the other hand, **Figures 7 to 9** show the results of changing the canopy effect intensity and canopy percentages in the Mortality Model.

Species Diversity and Varying Canopy Characteristics

The comparison of the plant species diversity in different forest types is exhibited in **Figure 1**. The lattices in **Figure 1** show the species diversity at $10,000$ generations. In deciduous and mixed forests, few species dominate in areas under the canopy cover, while more species compete in the areas without the canopy cover. In evergreen forests, the results showed that more species thrive under the canopy cover compared to deciduous and mixed forests.

The population dynamics were also observed over time, as shown in **Figure 2.** In the long run, approximately six species experienced an increase in population density in evergreen forests, while the populations of other species declined. Five of the six species had population densities between 10% and 20%. In the deciduous forest, only two species showed an increase in population density above 20% while the population density of other species declined over time. In mixed forests, five species exhibited growth in their population densities. However, only two species maintained a population density between 20% and 30% . Overall, the populations of all 20 species stabilized in all forest types. Additionally, population densities of species in evergreen forests were found to be lower compared to those in deciduous and mixed forests.

The diversity of the plant species in different forest types with varying canopy percentages is shown in **Figure 3**. The plant species diversity in the understory was observed to be lower in evergreen forests than in deciduous and mixed forests. Moreover, the number of surviving species decreases as the canopy percentage increases.

The species diversity and the total population density in different forest types with varying canopy percentages and maximum canopy effect intensity (α) were observed and the results were summarized in **Figure 4.** The heatmap illustrates the average number of surviving species at the end of the simulations. Specifically, the shading represents species diversity (where darker shades indicate a higher number of surviving species), while the numerical values inside each cell represent the total population density (calculated as the lattice occupancy percentage), regardless of species type. As the number of surviving species increases, the shade on the heatmap darkens.

In evergreen forests, varying the maximum canopy effect intensity (α) had little to no effect on species diversity when the fixed percentage of canopy cover is within the range of 0% and 50%. The results indicated that there was high species diversity, regardless of the maximum intensity of the canopy effect intensity (α). However, when the canopy percentage was higher with a lower α, the number of surviving species declined. Additionally, when the lattice was fully covered by a high canopy, and the canopy effect intensity was high, then a significant number of surviving populations dropped to approximately less than five.

Similarly, in deciduous forests, when the canopy percentage is lower, there is little to no effect on species diversity. That is, the plant community had high species diversity on varying values of canopy effect intensity on lower canopy percentages. Species diversity was also observed to be at its lowest when there was full canopy coverage, and the value of the canopy effect intensity was very small. Lastly, in mixed forests, the species diversity is also high even with varying α when the canopy percentage is lower. Moreover, the species diversity is lower when there is a 100% canopy coverage on any value of the canopy effect intensity α.

Figure 3 illustrates a gradual decrease in surviving species between 0% and 75% canopy cover, followed by a distinct tipping point at approximately 80%, leading to a sharp decline in diversity. Even under a strong inhibitory canopy effect ($\alpha \in [0,0.1]$) and closed canopy, coexistence persists, albeit with a reduced number of surviving species. Furthermore, these results indicate that regardless of the canopy effect intensity, the number of surviving species consistently decreases as canopy percentage increases.

Species Diversity and Varying Basal Fecundity

The diversity of plant species in the understory was also observed when the maximum basal fecundity (B) was varied. The values considered were based on the study of Tubay *et al.* (2015) which are 0.5, 0.6, 0.7, and 0.8. The results of these simulations are presented in **Figure 5.** As the value of maximum basal fecundity increases, the number of surviving species increases slightly in each forest type. Moreover, regardless of the maximum basal fecundity, mixed forests have the highest understory diversity, while evergreen forests have the lowest among forest types.

The species diversity and the total population density were observed when both the canopy effect intensity and basal fecundity were varied. The results of the simulations were summarized in

Figure 6. It showed that species diversity was highest in evergreen forests when the maximum basal fecundity was 0.8 and canopy effect intensity (α) was 0.3. The species diversity was higher when the maximum basal fecundity and the canopy effect intensity were higher. It could be observed that there was a low population density when the canopy percentage and canopy effect intensity were both high. Additionally, a high species diversity was observed in the deciduous forest when the maximum basal fecundity was 0.8, except in lowest intensity canopy effect intensity ($\alpha = 1$), and when the basal fecundity was $B = 0.7$ and the canopy effect intensity is relatively higher ($\alpha = 0.2$). However, no pattern could be observed regarding the species diversity in deciduous forests with varying canopy characteristics. On the other hand, in mixed forests, the number of thriving species is higher when the maximum basal fecundity is 0.8. Moreover, there was a higher number of surviving species when the canopy effect intensity was lower and the basal fecundity was higher.

Species Diversity and Mortality Rate

The influence of varying canopy characteristics incorporated in the Mortality Model on the diversity of plant species in the understory was also observed. Moreover, it was important to note that unlike in the previous subsection, if the values of α were closer to 1, then the canopy effect intensity was considered higher in the Mortality Model.

The species diversity in different forest types was compared when the maximum canopy effect intensity (α) is 1, and the results were shown in **Figure 7.** A relatively lower species diversity in all forest types was observed due to a high basal mortality rate and a high canopy effect intensity. It can also be observed that as the canopy percentage increases, the number of surviving species decreases. This trend is also similar to the results in the Birth Model from the previous subsection. Moreover, the number of surviving species also generally declines as the canopy percentage increases.

The diversity of plant species in different forest types was observed when both the canopy effect intensity and canopy percentage were modified in the Mortality Model. The results are displayed in **Figures 8** and **9.** It can be observed that with varying canopy effect intensity, understory coexistence persists in all forest types with an estimated six species surviving at most on average. Additionally, the graph also showed erratic behavior in the species diversity with varying values of canopy effect intensity and cover percentage. However, it can be seen that when the canopy effect intensity is at the minimum, that is $\alpha = 0.1$, the number of surviving species is highest across varying canopy percentages in both deciduous and mixed forests.

Simulation results also showed in **Figure 9** that there are fewer species in the long run at all forest types when both the canopy percentage and canopy effect intensity are high. In both evergreen and deciduous forests, it is more evident that there is a lower species diversity when the canopy effect intensity was higher ($\alpha \in [0.5, 1]$ at maximum canopy coverage. Moreover, when the community was not under canopy, high species diversity in all forest types was observed as well.

DISCUSSION AND CONCLUSION

The lattice Lotka-Volterra model has been used to understand the population dynamics of plant communities (Tainaka 1988; Matsuda, 1992; Tubay *et al.* 2015; Tubay and Yoshimura 2018; Yoshimura *et al.* 2004). In this study, we extended the lattice Lotka-Volterra model with microhabitat locality developed by Tubay *et al.* (2015). While previous iterations focused primarily on soil heterogeneity, our framework introduces the canopy as a dynamic environmental filter. By incorporating canopy phenology, specifically temporal shedding, we move beyond simple spatial models to demonstrate how the timing of environmental stress is as crucial as its intensity in regulating understory coexistence.

To provide a clearer overview of the simulation outcomes, we summarized the key findings in Table 2. This table categorizes the results into verifications of existing ecological theories and new predictions specific to the mechanistic interactions modeled in this study.

Table 2: Summary of simulation results across forest types, distinguishing between verifications of empirical patterns and new model predictions.

Category	Forest Type	Key Simulation Result	Implication / Context
Verification of Empirical Results	**All Types**	Species diversity generally decreases as **canopy percentage** increases.	Consistent with light limitation studies (Chavez and Macdonald, 2010) confirming that the canopy acts as an environmental filter
	Deciduous & Mixed	Higher species diversity observed compared to evergreen forests.	Verifiesempirical observations that seasonal leaf shedding allows for temporal niche differentiation (Babier *et al.* 2008; Mestre *et al.* 2017; Lee *et al.* 2024).
	All Types	Coexistence is maintained through spatial heterogeneity (microhabitat locality).	Confirms the baseline Lattice Lotka-Volterra theory (Tubay *et al.* 2015) that site-specificity promotes diversity.
New Model Predictions	**Evergreen**	**Threshold Effect:** Diversity remains stable up to 75% canopy cover but drops significantly once canopy cover exceeds **80%** with a high canopy effect intensity (α)	Predicts a specific "tipping point" for evergreen canopy ecosystems where canopy cover becomes detrimental to understory diversity.
	Deciduous	Diversity remains high even with varying canopy effect intensity (α) provided canopy percentage is low (<50%).	Suggests that the seasonal absence of canopy (shedding) buffers the understory against high stress factors like canopy covers (Lee *et al.* 2024)
	Mortality Model	High Canopy Percentage + High Canopy effect intensity = **Erratic/Unstable** diversity trends.	Predicts that when canopy stress directly increases mortality (rather than just limiting birth), the community becomes less stable compared to resource-limited systems.

The results in **Figure 1** showed that coexistence among different species persists in different forest types. However, fewer species thrive under the canopy cover. This supports a combination of environmental filtering theory and niche differentiation theory in ecology. In environmental filtering, some conditions act as a filter to determine which species can survive (Kraft *et al.*, 2014; Mestre *et al.*, 2017). In this case, the filter is the influence of the canopy cover on the plant species in the understory. On the other hand, the niche theory suggests that limited resources, such as light and precipitation, create a niche in which only certain species can survive (Sun *et al.* 2022). In this study, the few species that survived under the canopy can be seen as those with traits that can adapt easily in low-light environments. The population density of each species stabilized over time, as exhibited in **Figure 2**. This also supports niche differentiation, where the species' population stabilizes over time as they occupy certain niches in the understory community (Kang 2020; Stigall 2014).

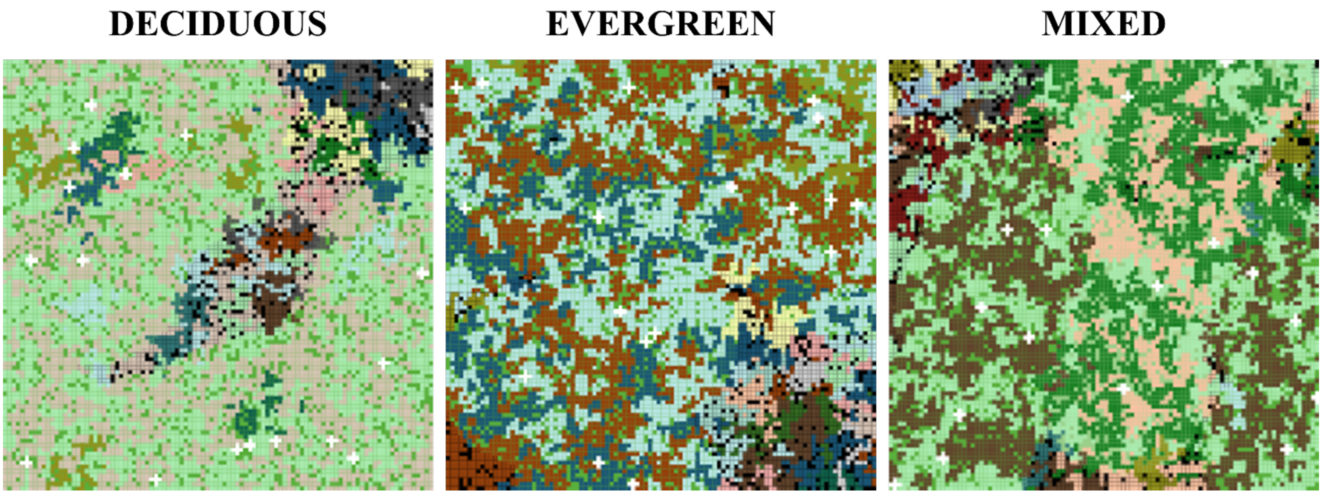


Figure 1: Lattice comparison of species diversity in different forest types. Simulation results of a 20-species lattice Lotka-Volterra competition model of different forest types. The light green cells represent the canopy cover, while the various other colors correspond to individuals of the different plant species. Simulation parameters: lattice size $\mathbf{100} \times \mathbf{100}$, fixed canopy effect intensity for each species $\boldsymbol{i}$ ($\boldsymbol{\alpha_i} \in [\mathbf{0}, \mathbf{1}]$), canopy percentage ($\mathbf{80}\%$), basal fecundity ($\boldsymbol{B} = \mathbf{0.8}$), and mortality rate ($\boldsymbol{M} = \mathbf{0.1}$)

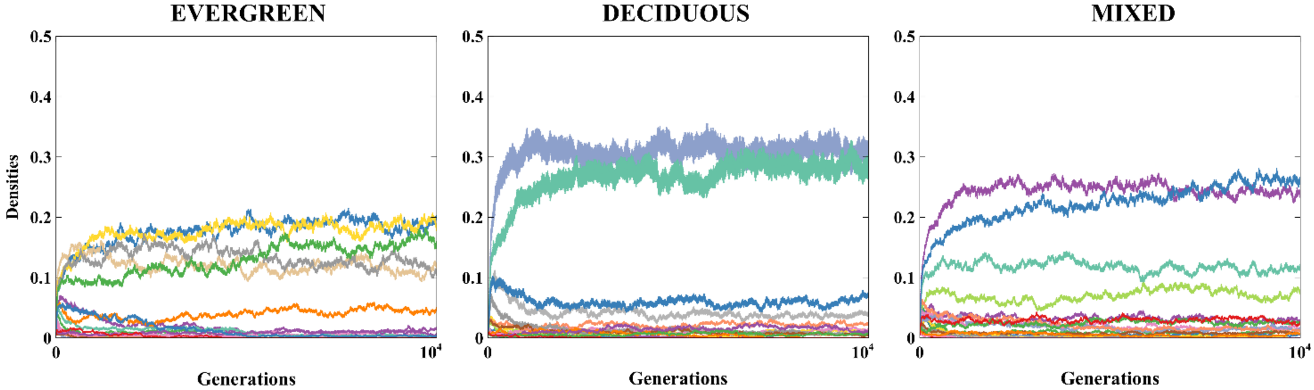


Figure 2: Temporal density dynamics in different forest types. Simulation results of a 20-species lattice Lotka-Volterra competition model with lattice size $\mathbf{100} \times \mathbf{100}$, fixed canopy effect intensity for each species $\boldsymbol{i}$ ($\boldsymbol{\alpha_i} \in [\mathbf{0}, \mathbf{1}]$), canopy percentage ($\mathbf{80}\%$), basal fecundity ($\boldsymbol{B} = \mathbf{0.8}$) , and mortality rate ($\boldsymbol{M} = \mathbf{0.1}$)

Generally, there was a higher species diversity in mixed and deciduous forests than in evergreen forests, as exhibited in **Figure 3**. In evergreen forests, there is canopy cover throughout the year. With this, the species compete for limited resources the entire time. In deciduous and mixed forests where the canopy sheds, additional litter from the canopy shedding increased the soil nutrients received by the plants (Giweta 2020). This result supported different studies (Mestre *et al.* 2017; Babier *et al.* 2008; Jobidon *et al.* 2004; Chavez and Macdonald 2012; Fourrier *et al.* 2015), where they observed that species diversity was higher in both deciduous and mixed forests than in evergreen forests. Moreover, the results in **Figure 3** showed that as the canopy cover percentage increases, the number of surviving species decreases. This showed that with the lesser canopy cover, more light penetrated the understory plant communities, and hence, this increased the survivability of the plant species. The results supported the study of Helbach *et al.* (2022), which showed that light availability influenced species diversity.

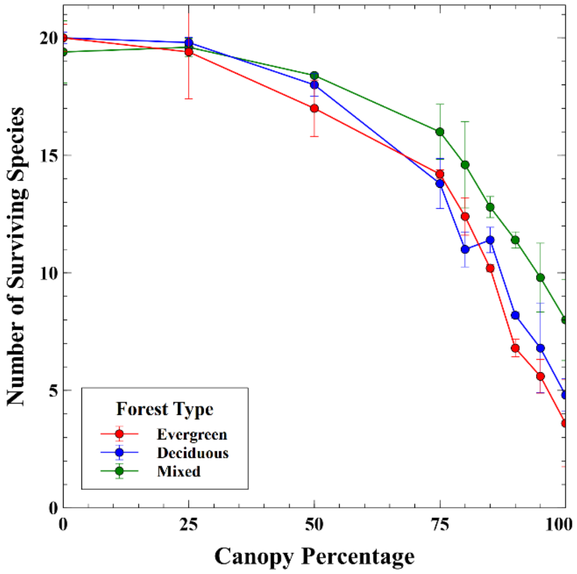
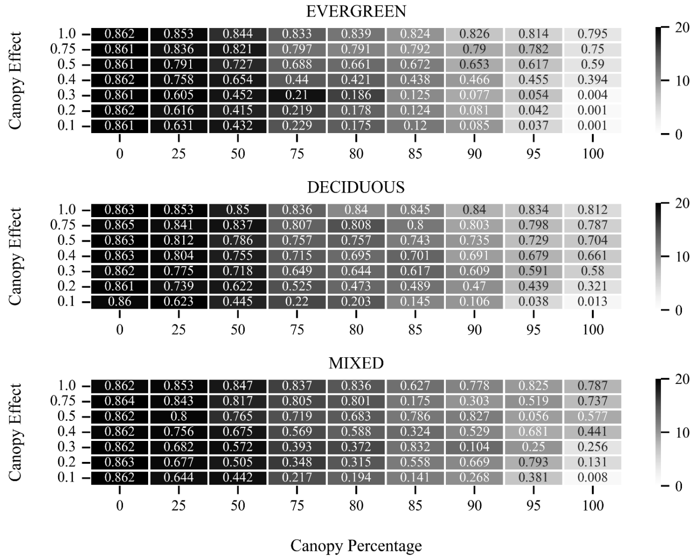


Figure 3: Species diversity in different forest types with varying canopy percentages. Simulation results of a 20-species lattice Lotka-Volterra mode with lattice size $\mathbf{100} \times \mathbf{100}$, fixed canopy effect intensity ($\boldsymbol{\alpha_i} \in [\mathbf{0}, \mathbf{1}]$), basal fecundity ($\boldsymbol{B} = \mathbf{0.8}$), mortality rate ($\boldsymbol{M} = \mathbf{0.1}$) and varying canopy percentage (average of $\mathbf{10}$ runs of $\mathbf{10,000}$ generations with the corresponding standard deviations and error bars.)

The canopy effect intensity α was varied to demonstrate that coexistence in understory plant communities persists regardless of species' shade tolerance (**Figure 4**). While coexistence was maintained, we observed that species diversity consistently declined as the canopy cover percentage increased, a trend that held across all forest types (**Figure 3**). Furthermore, population density decreased as both the canopy percentage and the canopy effect intensity increased most notably in evergreen forests. Additionally, the evergreen forests showed lower population densities compared to other forest types when both canopy cover and canopy effect intensity were high. In this specific scenario, the combination of extensive canopy coverage and a strong inhibitory effect significantly lowered the reproduction rate of plant species, confirming that the dynamics of the plant species in the understory are driven by the interplay between the spatial extent of the canopy and the intensity of its effect.



EVERGREEN

Canopy Effect	0	25	50	75	80	85	90	95	100
1.0	0.862	0.853	0.844	0.833	0.839	0.824	0.826	0.814	0.795
0.75	0.861	0.836	0.821	0.797	0.791	0.792	0.79	0.782	0.75
0.5	0.861	0.791	0.727	0.688	0.661	0.672	0.653	0.617	0.59
0.4	0.862	0.758	0.654	0.44	0.421	0.438	0.466	0.455	0.394
0.3	0.861	0.605	0.452	0.21	0.186	0.125	0.077	0.054	0.004
0.2	0.862	0.616	0.415	0.219	0.178	0.124	0.081	0.042	0.001
0.1	0.861	0.631	0.432	0.229	0.175	0.12	0.085	0.037	0.001

DECIDUOUS

Canopy Effect	0	25	50	75	80	85	90	95	100
1.0	0.863	0.853	0.85	0.836	0.84	0.845	0.84	0.834	0.812
0.75	0.865	0.841	0.837	0.807	0.808	0.8	0.803	0.798	0.787
0.5	0.863	0.812	0.786	0.757	0.757	0.743	0.735	0.729	0.704
0.4	0.863	0.804	0.755	0.715	0.695	0.701	0.691	0.679	0.661
0.3	0.862	0.775	0.718	0.649	0.644	0.617	0.609	0.591	0.58
0.2	0.861	0.739	0.622	0.525	0.473	0.489	0.47	0.439	0.321
0.1	0.86	0.623	0.445	0.22	0.203	0.145	0.106	0.038	0.013

MIXED

Canopy Effect	0	25	50	75	80	85	90	95	100
1.0	0.862	0.853	0.847	0.837	0.836	0.627	0.778	0.825	0.787
0.75	0.864	0.843	0.817	0.805	0.801	0.175	0.303	0.519	0.737
0.5	0.862	0.8	0.765	0.719	0.683	0.786	0.827	0.056	0.577
0.4	0.862	0.756	0.675	0.569	0.588	0.324	0.529	0.681	0.441
0.3	0.862	0.682	0.572	0.393	0.372	0.832	0.104	0.25	0.256
0.2	0.863	0.677	0.505	0.348	0.315	0.558	0.669	0.793	0.131
0.1	0.862	0.644	0.442	0.217	0.194	0.141	0.268	0.381	0.008

Figure 4: Species diversity and lattice occupancy percentage in different forest types with varying canopy characteristics. Simulation results of a 20-species lattice Lotka-Volterra competition model with lattice size $\mathbf{100} \times \mathbf{100}$. The background shading corresponds to Species Diversity, while the numerical values inside each cell indicate the Lattice Occupancy Percentage. Parameters: fixed basal fecundity ($\boldsymbol{B} = \mathbf{0.8}$), and mortality rate ($\boldsymbol{M} = \mathbf{0.1}$). Data points represent the average of 10 independent runs of 10,000 generations.

Varying canopy characteristics were incorporated into the birth and death processes. Species diversity showed a slight increase as the maximum basal fecundity (B) increased, as shown in **Figure 5.** A lower canopy effect intensity resulted in lower effective birth rates, as derived from **Eq. 5**, leading to a lower population in the entire lattice. With this reduced population density, particularly evident when canopy percentage is increased, competition among species was lower, preventing competitive exclusion and resulting in high species diversity as exhibited in **Figures 3, 4 and 7.**

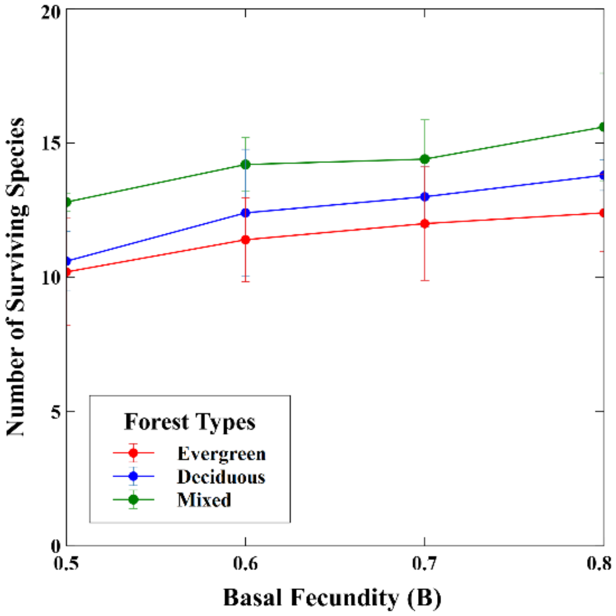


Figure 5: Species diversity in different forest types using the Birth Model with varying basal fecundity. Simulation results of a 20-species lattice Lotka-Volterra model with lattice size *100×100* and fixed mortality rate ($M = 0.1$), canopy percentage (80%) and canopy effect intensity ($i \in [0,1]$) (average of 10 runs of 10, 000 generations with the corresponding standard deviations and error bars.)

Moreover, regardless of the value of the maximum basal fecundity, species diversity was higher in mixed and deciduous forests compared to evergreen forests, as seen in **Figure 6**, where their heatmaps exhibit darker shades. This indicates that varying the basal fecundity did not alter the trend of which forest type supported the highest plant diversity. This result can be attributed to canopy shedding; species with high effective birth rates in open conditions experience a reproductive advantage after shedding events (Mestre *et al.* 2017; Lee *et al.* 2024). This dynamic neutralized the suppressive effect of the canopy on species diversity in deciduous forests.

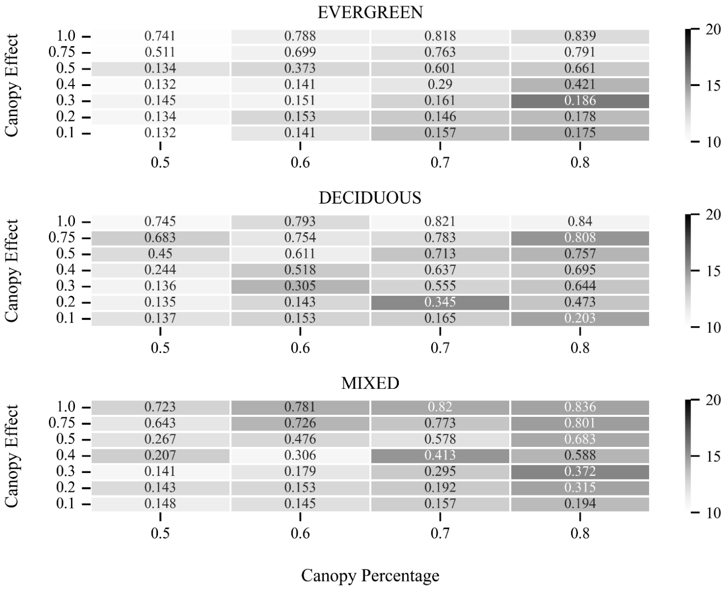


Figure 6: Species diversity and population density in different forest types using a Birth Model with varying basal fecundity (B) and canopy effect intensity (α). Heatmap shading represents species diversity (darker shading indicates higher diversity), while numerical values inside cells represent population density. Simulation results are from a 20-species lattice Lotka-Volterra model with lattice size (100×100), fixed canopy percentage (80%), and mortality rate ($M = 0.1$). Results show the average of 10 runs of 10,000 generations.

However, **Figure 6** also showed that while increasing the canopy effect intensity leads to increased population density, there is no obvious trend in its effect on species diversity, a distinction from the clear positive impact of increasing canopy percentage observed in **Figures 3, 4, and 7**. Unlike the canopy effect intensity, it can be seen in the same figure that, in general, increasing basal fecundity results in an increase in diversity, as darker shades are more evident as basal fecundity increases.

The canopy effect intensity was incorporated into the death process, and lower species diversity was observed in the three forest types, as shown in **Figure 7**. Specifically, there is a decreasing trend in the number of surviving species as the canopy percentage rises. This was caused by an increase in the effective mortality rate of all species. The mortality rate was expected to increase and the birth rate to decrease under the canopy because of the limited resources that are important to the survivability of different plant species. Incorporating varying canopy effect intensities in the Mortality Model showed no particular trend, as seen in the results in **Figures 8 and 9**. Low species diversity was expected when the canopy effect and the canopy percentage were both high. This was due to a higher effective mortality rate for each species. In both deciduous and mixed forests, higher species diversity was observed when there was no canopy cover and when the canopy effect intensity was low with a higher canopy cover.

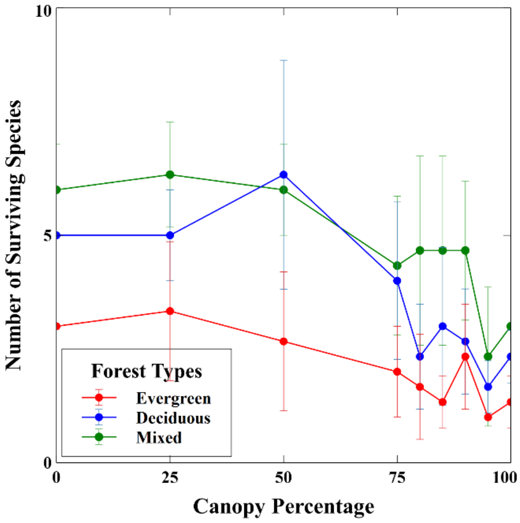


Figure 7: Species diversity in different forest types using Mortality Model with varying canopy percentage. Simulation results of a 20-species lattice Lotka-Volterra model with lattice size $\mathbf{100} \times \mathbf{100}$ and fixed basal fecundity rate ($\boldsymbol{B} = \mathbf{0.8}$) and canopy effect intensity ($\boldsymbol{i} \in [\mathbf{0}, \mathbf{1}]$) (average of 10 runs of 10,000 generations with the corresponding standard deviations and error bars.)

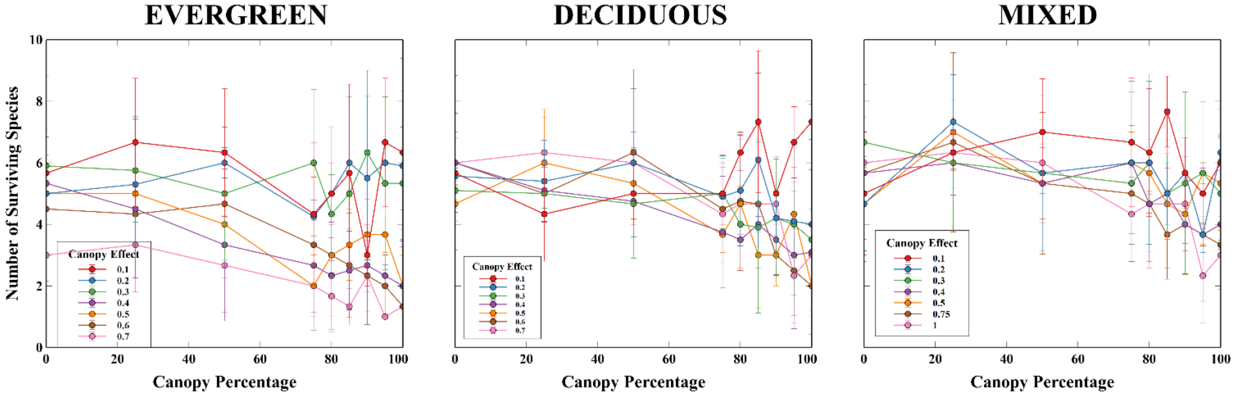


Figure 8: Species diversity in different forest types using Mortality Model with varying canopy percentage and canopy effect intensity $\boldsymbol{\alpha}$. Simulation results of a 20-species lattice Lotka-Volterra model and with lattice size $\mathbf{100} \times \mathbf{100}$ and fixed basal fecundity rate ($\boldsymbol{B} = \mathbf{0.8}$)and basal mortality rate ($\boldsymbol{M} = \mathbf{0.1}$) (average of 10 runs of 10,000 generations with the corresponding standard deviations and error bars.)

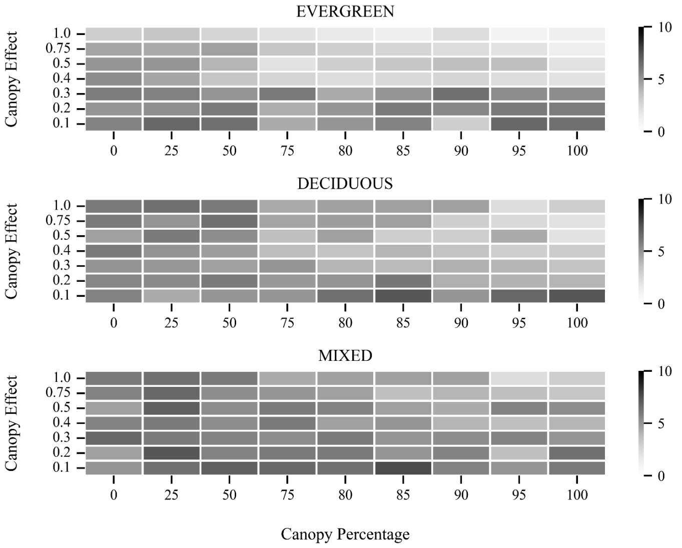


Figure 9: Species diversity in different forest types using Mortality Model with varying canopy percentage and canopy effect intensity ($\boldsymbol{\alpha}$). Heatmap shading represents species diversity (darker shading indicates higher diversity). Simulation results are from a 20-species lattice Lotka-Volterra model with lattice size ($\mathbf{100} \times \mathbf{100}$) and fixed maximum basal fecundity ($\boldsymbol{B} = \mathbf{0.8}$). Results show the average of 10 runs of 10,000 generations.

The previous results were caused by both sets of parameters resulting in a lower effective mortality rate.

These findings have direct implications for forest management and conservation. In particular, the 80% canopy-cover threshold predicted for evergreen forests suggests that silvicultural practices such as strategic thinning—aimed at maintaining canopy cover below this level—may help preserve understory biodiversity (Bragg et al. 2020). In managed evergreen plantations, such interventions could partially replicate the buffering effect that occurs naturally in deciduous and mixed forests, reducing competitive exclusion of sensitive understory species (Chavez and Macdonald 2012).

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

CONTRIBUTIONS OF INDIVIDUAL AUTHORS

Asst. Prof. Gamilla-Amorosa and Dr. Tubay conceived and designed the study. Asst. Prof. Gamilla-Amorosa developed the code and conducted the simulations. Both authors analyzed and interpreted the results. Asst. Prof. Gamilla-Amorosa drafted the manuscript under the supervision of Dr. Tubay.

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