Ensemble Behavior from Individual Dynamics in Multispecies Forest Populations

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This paper represents my own work in accordance with University regulations.

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Abstract

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MULTISPECIES FOREST POPULATIONS

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In this paper we present the derivation of macroscopic equations governing forest
populations and use these to explore and understand interspecies interactions.
Traditionally, complex numerical models have been used to to predict the be-
havior of forest populations from the behavior of individual trees. We explore
the possible consequences of interspecies interaction, including an analysis of
several mechanisms for coexistence of different species. Using the macroscopic
equations we also reproduce the process of ecological succession and demon-
strate how it can enable coexistence of different species whenever these species
differ by a minimum distance in trait-space.

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Chapter 1

Introduction

If this thesis appeared as a chapter in a physics textbook, it would be called the "Pacala forest" theory, in the same spirit that we refer to the theory of Fermi gases or Debye solids. In an ecology textbook it would go by the title "a simple model of light-competition in temperate forests" referred to thereafter by acronym only. Ignoring whatever this might imply about the psychology or ego of physicists and ecologists, we highlight the use of the words *theory* and *model*. By model, we imply that what follows is a simplification of the real world that tries to capture the same behavior. This work is about a model of a forest in the sense that it does not contain everything we know about real forests, but attempts to capture their interesting behavior in a simplified version. By theory we mean an explanation – probably mathematically based – that explains a set of observations. The Debye theory of solids refers to a set of assumptions we make about a solid that lets us determine certain properties and behaviors analytically. We don't need to believe these assumptions hold for real solids – they are merely approximations – yet we expect the resulting T^3 law to match pretty well at least for many solids (for a good discussion of this theory, see [9]). The Debye solid exists only in the ideal world of forms, yet its behavior closely matches that of real solids.

This is exactly what we hope to accomplish with the theory of Pacala forests.

The Pacala forest is also an ideal only approximately realized by real forests. Yet like the Debye solid, it is an object that we can investigate analytically, deriving properties we expect to hold true for the real world. The idealized object is our model, our approximation of the real thing. The manipulations we apply comprise the theory. What follows then, is a presentation of the theory of Pacala forests and how that theory can be applied to understand interactions between different species.

Few physics text-books spend much effort explaining what we mean by a solid, or why we want a theory of it. Perhaps that is supposed to be obvious. In any case, before we begin the theory of the Pacala forest, let us take a quick look at what we mean by forest and what we want to know about it.

1.1 Forest Populations

A forest is a composed of individual trees confined to some finite area. We distinguish between those variables which are properties and behaviors of the individual trees and those which are properties of the forest. Properties of the trees include the various things trees do: grow (in height and area), die, and reproduce and most importantly, compete for sunlight. Our definition of forest mentions a finite area. This may seem trivial, but it isn't really. If forests were not confined to finite area, trees would have no reason to grow tall, they could simply grow outwards. In a finite area, they can only grow up. All of this growing is about competition for sunlight. In order to get more sunlight, a tree needs to get out of the shade of its neighbors, and essentially everything a tree does is designed around this goal. Different species will attempt to do this in different ways, by practicing different *strategies*, some of which will become clear through our investigation. The properties of the forest will be determined by this competition. Forest properties include the densities of trees and distribution of tree heights. These variables change as the forest ages, starting from an open patch as a result of the growth, death, and competition of individual trees. The essence of this process is captured in Figure 1.1, where trees grow in height and

Figure 1.1: Forest growth from an open patch. Image courtesy of British Columbia Ministry of Forests and Range [20], reproduced with permission.

crown area and thin in density on a finite plot. The challenge of the theory is to derive these variables describing the forest from the variables describing individual trees.

The Debye solid consists of quantum harmonic oscillators on a finite lattice. The oscillators have their own set of properties: their mode or frequency of oscillation. The solid has properties such as specific heat, temperature, and so forth. The theory derives relations in these properties from the properties of the oscillators.

In Debye theory the oscillators are identical. We begin with this assumption for forests as well, which we refer to as a *monoculture*, indicating that all trees are from the same species. We are interested in understanding forests consisting of multiple different species. Clearly with higher degrees of freedom we have more interesting behavior to deal with. We will particularly be interested in temporal dynamics of this heterogeneous forest. Here the concept of tree competition becomes even more central. There are a few well known facts about interspecies

competition in forests that we hope to recreate, as well as answering questions about long-term forest behavior that cannot be easily observed. It will be useful to be familiar with these general phenomena before we explore further.

The two chief phenomena of interest go by the terms *succession* and *coexistence*. Succession refers to the predictable changes in an ecological community composition, where tree species that colonize open fields quickly are eventually replaced by more shade-tolerant species. Coexistence refers to separate species surviving in the same environment where neither one will ever out-compete the other. Though the two phenomena seem contradictory, they are both easily observed in nature. Part of our objective will be to understand how both of these can occur.

1.2   From Individual to Ensemble

1.2.1   Trees and Forests

Our first goal is to derive the behavior of the forest from the behavior of the individual trees; that is, to find the appropriate macroscopic equations of the forest as an ensemble. Later we will use these macroscopic equations to investigate interspecies interactions.

We choose to begin with individual trees rather than formulating a theory at the level of the forest directly for several reasons. Chief among these, the individual trees are much easier to understand than the whole forest, just as a single harmonic oscillator is much easier to understand than the entire solid. Additionally, the properties of an individual tree are much easier to *measure* than the properties of the entire forest. Lastly, existing models based on individual trees have proven very successful in the absence of models starting at the forest-level. Because an individual tree can be more easily measured and modeled, traditional approaches have involved entering these individual properties into a giant particle simulator, a computer program that calculates the growth, death, reproduction and so forth of each individual tree for each instant in time.

This process is analogous to simulating many harmonic oscillators to determine the properties of a solid. These simulations such as the TASS/SYLVER/TIPSY have been so successful as to be commercially available today for economic analysis and stand-level planning of real forests [13, 14].

Despite this success, the individual-based simulations have several drawbacks. Computational requirements make it impossible to simulate very large forests [16]. An analytic theory also allows insights that are obscured in the simulator. However, these non-linear spatial models in the simulations are notoriously intractable, and previous approximations attempting to describe the entire forest have either proven inadequate [19] or remain too complicated to be analytically tractable [15]. The Pacala forest escapes this by virtue of its key assumption, known as the perfect plasticity approximation. Like statistical mechanics, finding the right macroscopic equation is largely an issue of starting with the right approximations.

1.2.2   Atoms and Solids

Many aspects of statistical mechanics share the same basic structure to transition from individual states to macroscopic variables. Since we have made our analogy explicit to Debye theory, let us take a moment to revisit that derivation by way of example of this process in physics. Like much of statistical mechanics, Debye theory begins by assuming the ensemble (the solid) is made up of many little quantum harmonic oscillators, idealized entities which we can easily describe. For instance, their energy levels are integer multiples of $\hbar\omega$, where ω is the oscillation frequency. Our forest starts with the ideal tree for similar reasons.

When we put them in a cubic box of sides length L, the modes of oscillation are quantized, $\omega_n = n\pi v L$ where v is the speed of propagation in the solid. If these oscillations were photons in an empty cavity we would have $v = c$. In a solid we call them phonons. This finite space will also be crucial to the forest, though the it will be an area (or open box) rather than a volume.

Statistical mechanics proceeds by collecting the individual states together by means of a a partition function Z, the sum of Boltzmann factors $\exp(-\epsilon/\tau)$, effectively organizing them by energy τ. Our forest model will instead organize individual trees by common age, termed cohorts.

From the partition function we can calculate probability distributions and hence the expectation values of the macroscopic quantities we seek (such as energy or specific heat). What follows a quick reminder of how this derivation proceeds in the Debye case:

The partition function for the phonons is

$$Z = \sum_{s=0}^{\infty} \exp(-s\hbar\omega/\tau) \tag{1.1}$$

for fundamental temperature $\tau = k_B T$. With $x \equiv \exp(-\hbar\omega/\tau) < 1$, this has the form $\sum x^s$ and the sum converges:

$$\frac{1}{1 - \exp(-\hbar\omega/\tau)} \tag{1.2}$$

The probability that the system is in state s is given by:

$$P(s) = \frac{\exp(-s\hbar\omega/\tau)}{Z} \tag{1.3}$$

The thermal average value of s is then

$$\langle s \rangle = \sum_{s=0}^{\infty} sP(s) = Z^{-1} \sum s\exp(-s\hbar\omega/\tau) \tag{1.4}$$

Defining $y \equiv \hbar\omega/\tau$, observe

$$\sum s\exp(-sy) = -\frac{\mathrm{d}}{\mathrm{d}y} \sum \exp(-sy) =$$
$$-\frac{\mathrm{d}}{\mathrm{d}y}\left(\frac{1}{1 - \exp(-y)}\right) = \frac{\exp(-y)}{[1 - \exp(-y)]^2} \tag{1.5}$$

Multiplying by Z^{-1} from (1.4), we find

$$\langle s \rangle = \frac{1}{\exp(\hbar\omega/\tau) - 1} \tag{1.6}$$

which is known as the Planck distribution. We'll hang on to this, since we'll need it in a moment.

N atoms in a solid each have three degrees of freedom, one longitudinal and two transverse. We call these vibrations phonons, in analogy to photons in a free cavity which have only two degrees of freedom. Each vibrational mode n is composed of components n_x, n_y and n_z. Integrating over the volume element $dn_x dn_y dn_z$ for positive octant and multiplying by three for the degrees of freedom we have,

$$\frac{3}{8} \int_0^{n_D} 4\pi n dn = 3N \tag{1.7}$$

Where n_D is the maximum number of modes. Solving we find

$$\frac{1}{2}\pi n_D^3 = 3N; \qquad n_D = (6N/\pi)^{1/3} \tag{1.8}$$

The thermal energy U of the modes is (using the Planck distribution 1.6 for $\langle s_n \rangle$)

$$U = \sum \langle \epsilon_n \rangle = \sum \langle s_n \rangle \hbar\omega_n = \sum \frac{\hbar\omega_n}{\exp(\hbar\omega_n/\tau) - 1} \tag{1.9}$$

We can the replace the sum with the integral form, equation (1.7),

$$U = \frac{3}{8} \int_0^{n_D} 4\pi n^2 \frac{\hbar\omega_n}{\exp(\hbar\omega_n/\tau) - 1} dn \tag{1.10}$$

From the wave function of the phonons we have $\omega_n = \frac{n\pi v}{L}$ for velocity v in the solid. Then with $x \equiv \frac{n\pi v\hbar}{L\tau}$ we have

$$U = \frac{3L^3}{\pi^2\hbar^3 v^3}\tau^4 \int_0^{x_D} \frac{x^3}{\exp x - 1} dx \tag{1.11}$$

For low temperatures $x_D \equiv \frac{n_D\pi v\hbar}{L\tau} \gg 1$ and the integral term is effectively

independent of temperature ("low" requires that τ is much smaller than the numerator, a quantity known as the Debye temperature). Hence the energy scales as $U \sim \tau^4$. The specific heat C_V is simply the derivative of the energy at constant volume ($V = L^3$), which hence scales as $C_V \sim \tau^3$, hence the T^3 law.

The road ahead

We will now do the same for forest populations. To begin, we'll need to know a few things about the ideal tree. We will also need an assumption about our system to make the analytics possible, analogous to the low-temperature limit of Debye theory. We then combine individual trees into cohorts (where individuals share a common age rather than a common energy as they do in Z_N). Manipulating cohorts we can determine the macroscopic equations we need. With those equations we will be able to explore the interspecies interactions.

Chapter 2

An Analytic Model for Forests

2.1 Model Setup: the Ideal Tree

Trees are much more complicated than gas molecules or homogeneous solids, and ideal trees more complicated than ideal oscillators, but they are not as bad as one might think. Let's meet the ideal tree, Figure 2.1. The ideal tree consists of two parts: a stem or trunk and a crown. Its most important aspect is its height, z. Almost everything we will want to know about a tree can be determined by knowing its height from the size of its stem to the area of its crown. How it interacts with other trees will also depend most crucially on their relative height.

That said, we will generally find it easier to talk about the diameter of the stem D than the height of the tree. For one, this is more easily measured then the height, and as we have just observed, the two generally are connected by a simple allometric scaling relationship. Second, we will find that most parameters about the tree, such as its growth rates, can be most naturally expressed and measured in terms of diameter growth (think of tree rings). Our ideal trees

Growth of The Ideal Tree
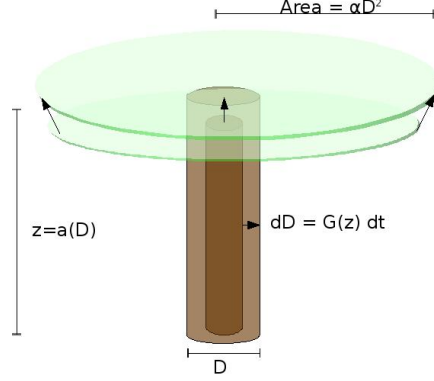
Figure 2.1: **The ideal tree**. The dimensions of the ideal tree can all be characterized by its diameter.

need not have constant diameter along the entire length of the stem, but only a standard height at which we will measure the diameter. Traditionally this has been diameter at breast height, dbh (we won't worry too much about where exactly we're measuring this height, merely observing that this can be a well-defined).

In addition to height z, and diameter D, our ideal tree has a certain crown area A. Generally, the crown of our ideal tree will be two-dimensional or flat-topped. Some common functions of three-dimensional crown shapes behave identically to the simpler flat-top assumption under this model. While we will make no assumptions about the particular shape of the flat-top, (indeed it need not even be continuous), we will generally assume its area scales with the area of the stem by a scale constant α.

The ideal tree grows at some rate G which we measure in terms of diameter growth. The corresponding growth in height is computed based on the tree's allometry $a(D)$. We will not specify a particular functional form for the allometry of the ideal tree, but two common forms are

$$z = H_2(1 - \exp\left(-\tfrac{H_1}{H_2}D\right)) \tag{2.1}$$

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symbol	definition
z	Tree height (length)
D	Diameter (length)
A	Canopy area of an individual tree (area)
G	Growth rate of an individual tree (length/time)
μ	Death rate of an individual tree (number/time)
f	Fecundity of an individual tree (number/time)
N	Number density (number/time)

Table 2.1: Symbols for common quantities

and a power-law:

$$z = \beta D^{\theta} \tag{2.2}$$

The exponential form has a maximum height H_2 and H_1 the slope at zero height, while under the power law trees grow continuously taller with increasing diameter growth.

The ideal tree does not live forever. It dies at a rate μ. It must also reproduce, at a rate f. While these can be thought of as continuous rates, it often makes sense to treat these as average annual values so we need not worry about particular seasons in the lifetime of the tree. As we have already mentioned, the ideal tree lives in a box or plot of finite total area. Seeds are dispersed uniformly throughout this area, and grow up in densities reasonably close to the average density N. We will tend to normalize the area of the entire plot to unity. These traits are summarized in Table 2.1.

2.2   Perfect Plasticity Approximation

A mean-field approximation

The perfect plasticity assumption (PPA) states that trees will always fill any gaps that open in the canopy. This means that if a large tree dies, opening some hole in the canopy, we will not need to know *where* the hole is located in the $x-y$ plane. Instead, the gap is simply filled from the trees immediately below it. This allows us to avoid spatial dependence in x and y, giving us only a single spatial

variable z to worry about. Essentially this allows us to successfully apply a mean-field approximation across any plane through the forest – we assume that the properties of the forest at any position (x, y) for a fixed height z and time t can be effectively approximated by their mean value across that plane.

Uniform canopy height

Another key consequence of this assumption is the observation that increased phototropism (plasticity of tree canopies) results in a decrease in the variance of crown join heights for three-dimensional crowns. Under the limit of perfect plasticity it is conjectured that all crowns will join at a single height in the canopy. This results in a well-defined height dividing the sunlit canopy trees from the shaded understory, providing a natural extension between the flat-top and three-dimensional crown model.

Motivation: choosing between extremes

This approximation was originally introduced by Pacala and colleagues to address one of the greatest weaknesses of the SORTIE individual-based forest simulator [18]. The original SORTIE model assumes that trees have perfectly rigid crowns. Real trees exhibit crown plasticity as a result of phototropism, as well as wind, and gravity, and the modular nature of crowns. Trees move to fill gaps both by leaning of the stem towards an opening and through individual branches growing into gaps [17]. The PPA is the opposite extreme of perfectly rigid crowns. Simulations built on this assumption are remarkably accurate [12, 13]. While it is certainly an oversimplification, the reality appears closer to this extreme than to the perfectly rigid crown extreme.

We consider the area of the crowns of each tree at height z, $A(z)$, listed in order from tallest to shortest. We will sum these areas from the tallest tree down until the total area of crowns equals the area of the plot of forest. The height at which we stop determines z^*. All trees below z^* are then completely shaded, and z^* effectively defines our canopy height. Forest models have suggested that

for a given species, crown area can be uniquely determined by tree height. Hence if $n(z)$ is the number of trees of height z in the plot, we have[1]

$$A_{\text{plot}} = \sum_{z>z^*} n(z)A(z) \qquad (2.3)$$

Dividing both sides by the area of the plot we can write this in terms of the density $N(z)$ of trees at height z,

$$1 = \sum_{z>z^*} N(z)A(z) \qquad (2.4)$$

In the limit of continuous size distribution and large number of trees this becomes:

$$1 = \int_{z^*}^{\infty} N(z)A(z)\mathrm{d}z \qquad (2.5)$$

Equation (2.5) defines the canopy height z^*, at which the sum of the crown areas fills the forest canopy. Under the perfect plasticity assumption the sunlight portion of each tree is simply $A(z)$, and all trees below z^* are consequently shaded. [2]

2.3   The Macroscopic Equation

We are now ready to derive our macroscopic equations – expressions for the population density and height structure of the forest – using only what we know about the ideal tree. Let the quantity $N_i(x, y, z, t)$ represent the number of trees of species i which have the center of mass of their crowns located within a three-dimensional box located at (x, y, z). We are interested in the average value over x and y for a large plot; that is, we are interested in predicting

---

[1]for a forest of multiple species, each $A(z)$ and $n(z)$ would have to be subscripted for the species it refers to, and the total area would have to result from the sum over all species as well.

[2]Contrast this to a rigid-crown approximation where gaps would always be available if crown shapes could not perfectly pack the plot area (i.e. in the case of rigid cylinder crowns). Hence the trees lying below have only partially illuminated crowns.

$N(z, t)$ the average population density for species i at height z. This describes the species distributions and height distributions of the forest.

2.3.1 Derivation

Consider the population inside a box at (x, y, z, t). After a time Δt, this population can change in the following three ways:

- Trees in the box can grow up out of the box, at rate $G(z, t)$

- Trees from below can grow up into the box at rate $G(z - \Delta z, t)$

- Trees in the box can die, at rate $\mu(z, t)$

We summarize these transitions respectively as follows:

$$\Delta N(z, t) = \Delta t G(z, t) N(z, t) - \Delta t G(z - \Delta z, t) N(z - \Delta z, t) - \mu(z, t) N(z, t) \quad (2.6)$$

In the limit of small Δt and small Δz, we can rewrite this as

$$\frac{\partial}{\partial t} N(z, t) = -\frac{\partial}{\partial z} [G(z, t) N(z, t)] - \mu(z, t) N(z, t) \quad (2.7)$$

giving us a partial differential equation (pde) for $N(z, t)$. To solve this, we need the boundary condition that the total population of the forest is conserved. We write this by stating that the seedling population N_0 at any time t must be over its life time produce N_0 seeds:

$$N(z_0, t) = \int_{z_0}^{\infty} \frac{f(z, t) N(z, t)}{G(z, t)} \mathrm{d}z \quad (2.8)$$

Here the function $f(z)$ gives the individual fecundity (offspring) of trees of height z. Given some initial condition $N(s, t = 0)$, equations (2.7) and (2.8) predict both transient and stationary regimes of a single-species forest. In the stationary regime, the initial size of each cohort is determined by the conservation of total area of the plot,

$$1 = \int_{z^*}^{\infty} N(z)A(z)\mathrm{d}z \qquad (2.9)$$

Equation (2.7) is an instance of the Von Foerster equation, common to size-structured populations [4,10]. Together with (2.8) and (2.9) these are our macroscopic equations. Before we put them to work we will solve the general equation for stationary states and then introduce several useful simplifications that will facilitate our subsequent analysis.

2.3.2 Stationary States

We can solve for the station state of this system. Setting (2.7) equal to zero and solving the resulting linear ordinary differential equation gives us

$$N(z) = N(z_0) \exp\left(-\int_{z_0}^{z} \frac{\mu(z') + \partial_z' G(z')}{G(z')}\mathrm{d}z'\right) \qquad (2.10)$$

Substituting (2.10) into (2.8) gives an implicit definition for the canopy height,

$$1 = \int_{z_0}^{\infty} \exp\left(-\int_{z_0}^{z} \frac{\mu(z') + \partial_z' G(z')}{G(z')}\mathrm{d}z'\right) \frac{f(z)}{G(z)}\mathrm{d}z \qquad (2.11)$$

While substituting into the area condition gives an equilibrium density for seedlings $N_0 \equiv N(z_0)$,

$$N_0 = \left(\int_{z^*}^{\infty} \exp\left(-\int_{z_0}^{z} \frac{\mu(z') + \partial_z' G(z')}{G(z')}\mathrm{d}z'\right) A(z)\mathrm{d}z\right)^{-1} \qquad (2.12)$$

2.3.3 Simplifying the Model

Most variables are chiefly functions of light intensity

Our macroscopic equations are a little unwieldy at the moment. We can simplify the model a little further by observing that functions such as the fecundity $f(z,t)$, growth rate $G(z,t)$, and death rate $\mu(z,t)$ are all essentially determined by the amount of light reaching the tree. Sunlight is the only resource in our model forest, required for carbon uptake via photosynthesis. A tree can spend

this resource to grow taller (and hence get more sunlight), to survive better (decrease death-rate μ through any of a number of strategies: making denser wood, making toxins to ward off herbivores or insects, and so forth), or invest that carbon in seeds, increasing fecundity. The dependence on height and time are really a consequence on the light intensity varying with z and t.

Light intensity is nearly a step function

We can take our simplification one step farther by first observing that light intensity is essentially a step function at the canopy. Above the canopy, trees experience direct sunlight, while below the canopy trees are in the shade. The difference between direct sunlight and shade is far greater than the different levels of shade that might exist under the canopy. Consequently, our functions $f(z)$, $G(z)$ and $\mu(z)$ can each be written as step functions with the step occurring at the canopy height z^*. Below the canopy the trees will then grow at a rate G_D (for growth in the dark) and at rate G_L for trees above the canopy.

Additionally, we observe that a tree's fecundity depends primarily on its carbon uptake, which is in turn proportional to the sunlight crown area, area, $f(z,t) = F \cdot A(z,t) \quad \forall z > z^*$ and zero otherwise. As we assume constant diameter growth instead of constant height growth, it will be useful to change our spatial variable to diameter rather than height. This change of variables is governed by the allometry of the tree, $D = a(z)$. Instead of the canopy height, we will keep track of the diameter at canopy height $D^* = a(z^*)$ to determine which trees are above or below the canopy, since for any tree of height z and diameter D, $D > D^*$ whenever $z > z^*$.

$$G(z) \begin{cases} G_D & D < D^* \\ G_L & D > D^* \end{cases} \tag{2.13}$$

We make the same assumptions regarding death rate $\mu(z)$ as discontinuous

step above and below the canopy,

$$
\mu(z) \begin{cases} \mu_D & D < D^* \\ \mu_L & D > D^* \end{cases} \tag{2.14}
$$

Our last assumption is that the area of the crown will also be determined from a simple allometry of the tree's diameter. This is based on a well-supported observation that tends to be independent of species, where a common rule of thumb is that the crown radius in meters is ten times the trunk diameter at breast height measured in centimeters. Maintaining generality we will assume the proportionality to be α, writing,

$$
A = \alpha D^2 \tag{2.15}
$$

The simplified macroscopic equations

Under these assumptions the equilibrium height distribution (2.10) becomes

$$
N(z) = \begin{cases} N(z_0)e^{-\mu_D D/G_D} & D < D^* \\ N(z_0)e^{-\mu_D \frac{D^*}{G_D}} \cdot e^{-\mu_L \frac{D-D^*}{G_L}} & D > D^* \end{cases} \tag{2.16}
$$

Similarly we can simplify the equilibrium seed density by (2.9) we have

$$
N_0 = F/G_L \tag{2.17}
$$

Equation 2.11 becomes:

$$
1 = \int_{D^*}^{\infty} \frac{F_L \alpha D^2}{G_L} \exp(-\mu_D \tfrac{D^*}{G_D}) \exp\left(-\mu_L \tfrac{D-D^*}{G_L}\right) dD \tag{2.18}
$$

symbol	definition
z^*	minimum height of a tree exposed to direct sunlight (canopy tree)
D^*	minimum diameter of a tree exposed to direct sunlight
α	Proportionality between stem area and canopy area of a tree
G_D	Growth rate of a tree in the dark, $z < z^*$
G_L	Growth rate of a tree in the light, $z \geq z^*$
μ_D	Death rate of a tree in the dark, $z < z^*$
μ_L	Death rate of a tree in the light, $z \geq z^*$
F	Fecundity of an individual tree exposed to direct sunlight

Table 2.2: Common parameters of simplified model.

2.4 Monoculture Predictions

We now have a workable model of a forest. Before we investigate the dynamics between species, we calculate a few properties of the monoculture forest that will come in very handy later.

2.4.1 Invasion of an Empty Habitat

When we refer to the ability of a species to invade, we mean whether that species can establish itself starting as a seedling on a landscape where it is not already present. To establish itself, this initial founding population N must have a positive deterministic growth rate, $\frac{\mathrm{d}N}{\mathrm{d}t} > 0$. Invasion of an empty habitat requires that an initial cohort of N trees can reproduce at least N offspring in its lifetime, growing in the light. That is,

$$N < \int_0^\infty N \exp(-\mu_L \tau) F \alpha (G_L \tau)^2 \mathrm{d}\tau \tag{2.19}$$

Where we have assumed the tree begins at negligible diameter.[3] Solving gives us the condition

$$1 < \frac{2 F \alpha G_L^2}{\mu_L^3} \tag{2.20}$$

---

[3]More generally the tree could start at some small diameter D_0, as its initial growth from seed to D_0 may instead be governed by resources stored in the seed and other environmental factors not accounted for in this light-competition model.

The expression on the right-hand side have a natural interpretation as the lifetime reproductive value of an individual. Each individual must on average do better than simply replacing itself (which would result in an equality).

2.4.2 Canopy Height

Integrating equation (2.18) we can determine the height of the forest canopy for a monoculture (single-species forest). Incidentally, this is easiest done by changing variables from space to time, integrating from the moment the cohort reaches the canopy $\tau = 0$ to infinity,

$$1 = \int_0^\infty \exp\left(-\mu_D \frac{D^*}{G_D}\right) e^{-\mu_L \tau} F\alpha (D^* + G_L \tau)^2 \mathrm{d}\tau \tag{2.21}$$

We now have three simple gamma integrals, which evaluate to:

$$\exp\left(\mu_D \frac{D^*}{G_D}\right) = \alpha F \left(\frac{D^{*2}}{\mu_L} + \frac{2 G_L D^*}{\mu_L^2} + \frac{2 G_L^2}{\mu_L^3}\right) \tag{2.22}$$

The ratio of growth rates to death rates is an order of magnitude greater than that of D^*, so the third term dominates. This gives an analytic expression for D^*

$$D^* = \frac{G_D}{\mu_D} \ln\left(\frac{2\alpha F G_L^2}{\mu_L^3}\right) \tag{2.23}$$

The canopy diameter and consequently the canopy height are then dominated by dynamics in the dark, while the effects of fecundity, growth and death in the light enter only weakly through the log term. Intuitively, higher growth rates, higher fecundity and lower death rates all increase canopy diameter (and consequently canopy height, as we will assume the height allometry to be monotonic increasing). We recognize the term in the logarithm as the lifetime reproductive value from equation (2.20). The earlier expression required this term to be greater than unity for the species to be able to invade an empty plot. Here we must satisfy that same inequality for D^* to be nonnegative.

It is important to observe that this is the *equilibrium* canopy height. The height of the closed canopy will evolve over time before relaxing to this steady state. This transient behavior is explored in 7.2, page 53. The stability of this solution has been demonstrated by Pacala and colleagues, [3]. Unless otherwise stated, we will use D^* to refer to the equilibrium canopy heights. We will usually treat this equilibrium value as a property of the species in consideration and the environment in consideration independent of time, and the reader must bare in mind that we are referring to the long-time equilibrium of a dynamical variable.

Chapter 3

Forest Competition

With our simplified macroscopic equations and the results from the monoculture forest in hand we are now ready to tackle the more interesting problems regarding long-term forest dynamics involving multiple species. As we mentioned when we first set out, our chief objectives are two-fold: to understand coexistence of different species and the process of succession, and hope to reconcile the two. In addition to dynamics that take place on an ecological scale – where species identity remains fixed – we will consider evolutionary dynamics where the phenotype of our trees is allowed to morph into new variants that will compete, invade, or die out. This topic will occupy us for the remainder of this investigation. This chapter will provide us with the basic tools to investigate interspecies interactions, which we will then explore in the following chapters.

3.1   Invasion Criterion

3.1.1   Terms and Notation

We begin by assuming our forest consists of a monoculture forest at equilibrium. We refer to this species as the *resident* and denote it by x. To explore interspecies interactions, we will generally begin by asking what happens when

we add some seeds of a different species to this forest. We refer to this species as the invader, which we usually denote as species y. For a species to invade, it must have a non-zero net growth rate in the environment set by the resident. Consequently a given cohort must survive to reach the canopy and more than replace its initial population. The effects of the other species can be felt by the trees below the resident's canopy, which may be different than the species would experience below its own canopy.

The parameters of the ideal tree, G, μ, F, α (for both light and dark) can vary between different species. In general these parameters will also depend on the environment the ideal tree finds itself in. As light is our only resource, this refers to the light environment. The light environment in turn is set by the characteristics of the canopy – particularly its transmittance. Transmittance is not an explicit parameter of the ideal tree, rather, it enters in the following way. We consider the species y. It has its own death rate in the dark, μ_D. This depends on the species y to which the ideal tree belongs, but also on the transmittance of the canopy. If the canopy consists of trees of type x, we denote the dependence of μ_D on that transmittance as $\mu_D(y, x)$. The first variable always lets us know which species we are considering, while the second variable lets us know what environment we are considering. For a monoculture x we would write $\mu_D(x, x)$. Though the transmittance does not get its own variable, it is still quantified. For instance if x casts a darker shade than y, we will have $\mu_D(y, y) < \mu_D(y, x)$ and $\mu_D(x, x) < \mu_D(x, y)$, that is, trees die faster under the canopy of x than under y. All other dark-based parameters are treated analogously.

Parameters describing the tree behavior under direct sunlight will not be influenced by the nature of the canopy below. Consequently, we do not denote μ_L as $\mu_L(y, y)$ but simply $\mu_L(y)$ indicating that it depends on species y alone.

3.1.2 Derivation of the Invasion Condition

We have two important diameters to worry about now for the invader species, y. The first is the diameter the invader must reach to be as tall as the resident's canopy, which we will denote $\tilde{D}^*(x, x)$. One can also think of this as the height of the resident canopy measured in the units of the invader, where the unit system is set by the allometry between height and diameter. For instance, if the trees follow identical allometries, they are using the same unit system, and $\tilde{D}^*(x, x) = D^*(x, x)$. More generally, if the resident species x follows the allometry $z = a_x(D)$ and the invader follows the allometry $z = a_y(D)$, then we define

$$\tilde{D}^*(x, x) \equiv a_y^{-1}\left(a_x\left(D^*(x, x)\right)\right) \tag{3.1}$$

Where a_y^{-1} is the functional inverse of a_y; $D = a_y^{-1}(z)$ is the diameter of a y species tree of height z. The second important D^* value is effectively the canopy diameter the invader would achieve growing in the shade of the resident, $D^*(y, x)$. It is not actually a steady state, (since y will either die out or cease to be rare) but rather more of a shorthand for the following expression:

$$D^*(y, x) \equiv \frac{G_D(y, x)}{\mu_D(y, x)} \ln\left(\frac{2\alpha(y)F(y)G_L^2(y)}{\mu_L^3(y)}\right) \tag{3.2}$$

For the invader to be successful, its initial population must more than replace itself when growing under the canopy of the invader. That is,

$$N_0 < \int_0^\infty N_0 \exp\left(-\mu_D(y, x)\frac{\tilde{D}^*(x,x)}{G_D(y,x)}\right) e^{-\mu_L \tau} F\alpha(\tilde{D}^*(x, x) + G_L\tau)^2 \mathrm{d}\tau \tag{3.3}$$

Evaluating the integral we recover,

$$\exp\left(\mu_D(y, x)\frac{\tilde{D}^*(x,x)}{G_D(y,x)}\right) < \alpha F\left(\frac{\tilde{D}^*(x, x)^2}{\mu_L} + \frac{2G_L\tilde{D}^*(x, x)}{\mu_L^2} + \frac{2G_L^2}{\mu_L^3}\right) \tag{3.4}$$

Making the same order of magnitude approximation as we had in (2.23), this simplifies:

$$\exp\left(\mu_D(y,x)\frac{\tilde{D}^*(x,x)}{G_D(y,x)}\right) < \frac{2\alpha F G_L^2}{\mu_L^3} \tag{3.5}$$

Isolating $\tilde{D}^*(x,x)$, we recover the condition,

$$\tilde{D}^*(x,x) < \frac{G_D(y,x)}{\mu_D(y,x)}\ln\left(\frac{2F\alpha G_L^2}{\mu_L^3}\right) \tag{3.6}$$

Which we can write as simply:

$$\boxed{\tilde{D}^*(x,x) < D^*(y,x)} \tag{3.7}$$

This invasion condition requires that the invader can over top the resident's canopy under the conditions set by the resident. Though the condition looks simple, it can have a wide variety of consequences, depending on how it is realized. Before we explore these further, we will need one more expression. It will be sometimes useful to rewrite the invasion condition as a comparison between the invader's performance under its own canopy and under the resident's. This is done as follows. From equation 3.5, the right-hand side can be rewritten using equation (2.23). Then taking the logarithms, we have the invasion condition,

$$\mu_D(y,x)\frac{\tilde{D}^*(x,x)}{G_D(y,x)} < \mu_D(y,y)\frac{D^*(y,y)}{G_D(y,y)} \tag{3.8}$$

This condition also has an intuitive interpretation: the invader y must do better in the resident's x setting than in its own. Since any species will simply accomplish steady replacement in its own equilibrium monoculture (by definition), it must do better than this to grow from a rare population under resident x.

3.2   Breaking down the invasion criterion

The invasion criterion (3.7) can be divided into two parts: one dealing with shading and the other with allometry. To investigate the significance of each of

these, we will hold one fixed independent of species and explore the consequences of variation between species in the other.

3.2.1 Identical Shading

Our first simplification assumes that the trees cast comparable levels of shade. In this case, $\mu_D(y, x) = \mu_D(y, y) = \mu_D(y)$ and $G_D(y, x) = G_D(y, y) = G_D(y)$; all growth and death parameters depend only on the species and not the environment. Consequently the diameters depend only on the species and not the environment set by the resident, which allows us to reduce them to functions of only the first variable, i.e $\tilde{D}^*(x, x) \rightarrow \tilde{D}^*(x)$ and $D^*(y, x) \rightarrow D^*(y)$ Equation (3.8) then simplifies:

$$\tilde{D}^*(x) < D^*(y) \tag{3.9}$$

Invasion now depends only on parameters we can measure in each species separately, we never need actually measure trees of the invader species growing in the environment of the resident. Instead, we need only equilibrium canopy heights of each species and the allometries of each species. By having a thinner allometry (taller trees for a given diameter), a species is more resistant to invasion. However, such a comparison is misleading, as thinner allometries will probably result in higher death rates, μ_D and μ_L. $D^*(x)$ depends linearly on inverse dark death rate μ_D, while most of the allometries will be less than linear, hence for larger trees it becomes harder and harder to make up in allometry what it loses in equilibrium D^* by thinning allometry. Consequently these trees would do better to focus on higher D^* than to attempt to raise actual height of the canopy at cost to the size of D^*.

Under this assumption of identical shade cast by both species, invasion can only be one way, (assuming allometries must be monotonically increasing). This may not be entirely obvious, particularly if one species has the higher allometry along a certain domain and the other has the higher allometry over another domain of diameters, as in Figure 3.1, so let us take a moment and prove it.
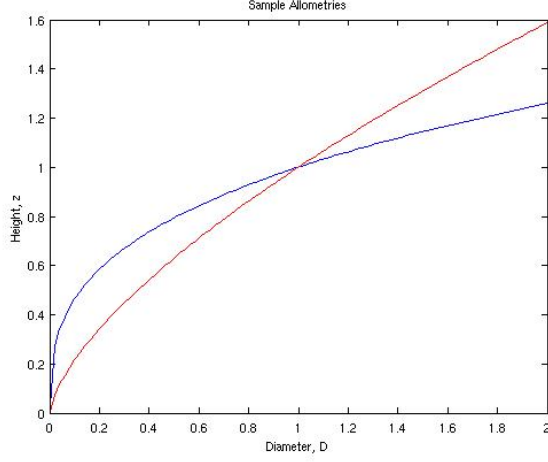
Figure 3.1: **Possible allometries.** Power laws with slightly differing exponents yield a different where each species is taller for a given height than the other one. However, as both allometries are still monotonic, it is impossible for these differing regions to enable coexistence of the two species.

Assume y can invade, $\tilde{D}^*(x) < D^*(y)$. Recall $\tilde{D}^*(x) = a_y^{-1}(a_x(D(x)))$. Then since the allometry a_y is monotonic

$$a_y(\tilde{D}^*(x)) < a_y(D^*(y)) \implies a_x(D(x) < a_y(D^*(y))$$

Since a_x (and its functional inverse) are also monotonic then,

$$a_x^{-1}(a_y(D^*(y))) > a_x^{-1}(a_x(D^*(x)) \implies \tilde{D}^*(y) > D^*(x)$$

Hence x cannot invade. This argument can be run backwards to demonstrate that if x cannot invade y, then y can invade x.

$D^*(y, x)$ is not a stable state, as if y can invade it will not remain rare forever. In the other limit we have demonstrated that once x becomes rare that it will not be able to re-invade, hence we can expect y to replace species x whenever (3.9) holds. By assuming that the shading cast be each species is identical, we are left with only very simple interspecies dynamics: only the

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tree with the higher canopy can invade. Differences in allometry between these make little difference in the possible dynamics – at most the difference becomes some corrective factor that lets us convert between units of diameter and height so that we can compare the two species. Consequently, we lose little if we assume all tree species to have the same allometry in this model: we can simply compare diameters directly without first converting to heights. If we want to take into account allometries, we can always go back and add this correction later without effecting the general result. Meanwhile, we have discovered that having all species cast identical shading results in only trivial interactions. Importantly, it does not allow for the coexistence of multiple species with differing canopy heights. We now change are simplification to ignore allometric differences and focus on differences is shading.

3.2.2 Identical Allometry

We return to the invasion criterion (3.8), and assume that the species have identical allometry, but possibly different shading. Essentially these means that we can remove the tilde ($\sim$) in the invasion criterion. The simplified invasion condition is:

$$\frac{\mu_D(y,x)}{G_D(y,x)}D^*(x,x) < \frac{\mu_D(y,y)}{G_D(y,y)}D^*(y,y) \tag{3.10}$$

We expand the diameter terms and re-arrange to have the condition explicitly in terms of the species-dependent parameters:

$$\frac{G_D(x,x)}{\mu_D(x,x)}\ln\left(\frac{2\alpha(x)F(x)G_L^2(x)}{\mu_L^3(x)}\right) < \frac{G_D(y,x)}{\mu_D(y,x)}\ln\left(\frac{2\alpha(y)F(y)G_L^2(y)}{\mu_L^3(y)}\right) \tag{3.11}$$

From this it is easy to see that an invader would do much better to try to out-compete the resident tree while in the dark, $G_D(y,x)\mu_D(y,x) > G_D(x,x)/\mu_D(x,x)$, than to beat out the resident by performing better in the light, for instance by increasing fecundity. Doubling its survival probability in the dark μ_D^{-1} is more effective then increasing fecundity F seven-fold. Unlike our previous case, the

story of this interspecies interaction does not end as soon as we know that y can invade x. Because the constant allometry assumption does not change the dimensionality of our functions, we will be able to capture the richness of the dynamics in (3.8) using the slightly simplified (3.10).

Chapter 4

Consequences of Invasion

To investigate possible interactions between two species y and x we ask two questions: Can y seedlings invade a resident monoculture x, and can x seedlings invade a resident monoculture y? The answer to each question is independent of the other, hence we have four possibilities enumerated in Table 4.1.

4.1 Dominance

Dominance is the simplest criterion to satisfy under Table 4.1. We have already seen one example of this by assuming shading is species independent. The invasion condition, (3.7), compares canopy diameters, each of which can be thought to consist of two parts, seen in expression (2.23). The first consists of the shade dependent terms: $G_D(y, x)/\mu_D(y, x)$, while the second involves the logarithm of the lifetime reproductive value, expression (2.20). While the shade-dependent terms depend both on the species y and the environment (canopy

	True	False
True	Coexistence	x Dominates
False	y Dominates	Founder Control

Table 4.1: Possible consequences of invasion

height) set by the resident x, the lifetime reproductive value depends on the species alone. With

$$\Lambda(y,x) \equiv G_D(y,x)/\mu_D(y,x) \qquad \phi(y) \equiv \ln\left(\frac{2F\alpha G_L(y)^3}{\mu_L(y)^3}\right) \qquad (4.1)$$

we can rewrite the invasion condition (3.7) (under identical allometry) and rearrange to obtain

$$\frac{\phi(x)}{\phi(y)} < \frac{\Lambda(y,x)}{\Lambda(x,x)} \qquad (4.2)$$

For y to be dominant we must also insist that x cannot invade once y determines the canopy,

$$\frac{\phi(y)}{\phi(x)} > \frac{\Lambda(x,y)}{\Lambda(y,y)} \qquad (4.3)$$

If shade tolerances are equal, dominance requires a higher lifetime reproductive value, while if lifetime reproductive values are the equal, dominance requires better performance in the shade. Recall that ϕ depends only on the logarithm of the light growth and death rates, while Λ depends linearly on this ratio, and consequently differences in shade are more likely to be responsible in determining the dynamics. Further, we can see that it is not enough for a species to cast deeper shade than the resident to invade, $\Lambda(\cdot,y) < \Lambda(\cdot,x)$, it must also be able to grow better in the shade, $\Lambda(y,\cdot) > \Lambda(x,\cdot)$. Finally, recall that if the species cast identical shade, the problem becomes one dimensional and we always have dominance of one species (ignoring the singular case of equality). In that case y is dominant if condition

$$\frac{\phi(y)}{\phi(x)} < \frac{\Lambda(x)}{\Lambda(y)} \qquad (4.4)$$

and otherwise x is dominant.

4.2 Founder Control

Founder control occurs when neither species can invade the other,

$$\frac{\phi(x)}{\phi(y)} > \frac{\Lambda(y,x)}{\Lambda(x,x)} \tag{4.5}$$

$$\frac{\phi(y)}{\phi(x)} > \frac{\Lambda(x,y)}{\Lambda(y,y)} \tag{4.6}$$

Using the notation we have just introduced, we can write this as

$$\frac{\phi(x)\Lambda(x,x)}{\phi(y)\Lambda(y,x)} > 1 > \frac{\phi(x)\Lambda(x,y)}{\phi(y)\Lambda(y,y)} \tag{4.7}$$

To satisfy this condition the two species must cast different levels of shade, since we have already shown that without this only dominance is possible. For founder control (4.7) the species that casts the darker shade must also be more shade-tolerant. That is, if $\Lambda(\cdot,y) < \Lambda(\cdot,x)$ then $\Lambda(y,y) > \Lambda(x,y)$. Similarly, the species casting the lighter shade must also be able to take advantage of that, $\Lambda(x,x) > \Lambda(y,x)$. This corresponds to the shade tolerant species having a less steep response in growth rate and mortality to differing light levels than the shade intolerant species. The shade intolerant species is opportunistic: able to take advantage of greater light availability but also more influenced by higher shade. This is equivalent to requiring that each species sets a higher canopy under its own shade (correcting for allometry; as the $\sim$ reminds us):

$$\frac{\tilde{D}^*(x,x)}{D^*(y,x)} > 1 > \frac{D^*(x,y)}{\tilde{D}^*(y,y)} \tag{4.8}$$

4.3   Coexistence

When each species can invade the other neither is competitively superior, resulting in ecological coexistence. The condition is easily derived as before,

$$\frac{\phi(x)\Lambda(x,x)}{\phi(y)\Lambda(y,x)} < 1 < \frac{\phi(x)\Lambda(x,y)}{\phi(y)\Lambda(y,y)} \tag{4.9}$$

To be able to satisfy both inequalities, the species need the same two sources

(a)	(b)
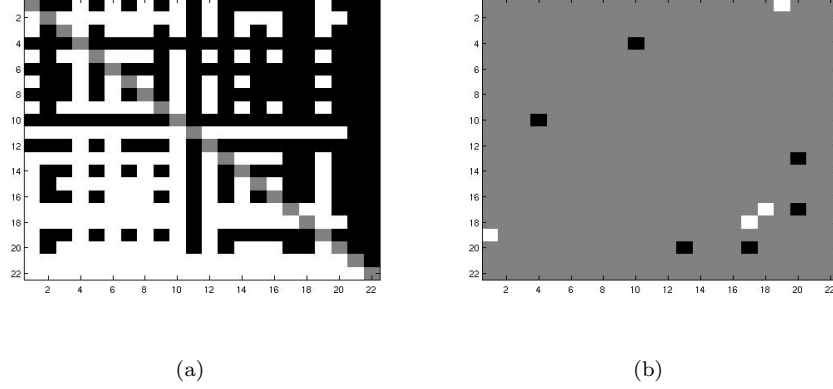
Figure 4.1: **Invasion Matrices**. (a) Invasion matrix for the 22 species in A based on model criterion. Rows represent invaders, while columns represent residents. Black means invasion is not possible. (b) Black means founder control (except along the diagonal which refers to a species against itself). Grey implies dominance, white implies coexistence.

of variation as in founder control:

- variation in transmittance of the canopy between species

- variation in shade tolerance between species

4.4   Invasion Matrix

Mutual invasibility is not easily satisfied. These conditions imply that each species must grow and survive less well under their own shade then under the shade of the other, which appears particularly implausible. Of all possible pairings of the 22 species in Appendix A, only two exhibit mutual invasibility. Figure 4.1(a) shows the invasion matrix for the 22 species [1, 21]. Listing species in columns represent the resident population, while the species in rows represents the invader. White denotes a value unity indicating invasion is possible, while black (zero) means it is not. The diagonal refers to species invading themselves. As we are not interested in this case we assign a half (gray) to the diagonal.

Adding this matrix to its transpose gives us the coexistence matrix 4.1(b). Here Gray has the value unity implying one species is dominant, black is zero implying the pair exhibit founder control, while white (two) corresponds to a coexistence pair.

The opposite shading strategy to coexistence – founder control – seems more logical: that a tree would cast such dark shade that only its own offspring could successfully grow [2]. Nevertheless only three of species pairs exhibit founder control. As this interpretation of coexistence is not very satisfactory, we return to our model to find what knobs we can turn to enable coexistence.

Chapter 5

Coexistence

In investigating interspecies interactions, we had two particular phenomena we wanted to explain: succession and coexistence. Succession we will see in the following chapter, though many of the components are already in place through our exploration of dominance. Meanwhile, coexistence appears more challenging to explain. We already have a simple theory of coexistence, based on (4.9). This requires a species to favor offspring of other species over that of its own, which seems a very unlikely evolutionary consequence and receives little support from known values of shade tolerance and shade cast for real species [1]. In this chapter we will modify the model directly to allow for coexistence by introducing a species that can reproduce in the dark, which we distinguish from other species by the appellation "shrub." The presence of the shrub not only influences the steady state of the tree, but can have important consequences to the forest stability.

5.1 Introducing a shrub

We consider such a shrub species which can reproduce in the shade of a tree canopy and form its own sub-canopy. For simplicity, the shrub will not produce under its own (darker) shade, but only under that of the canopy tree. Our

overhead canopy trees that only reproduces in the light, such as we have been describing. We adapt our notation to handle the three resulting regions, which we denote $_L$ above the tree canopy, $_D$ below the tree canopy but above the shrub canopy, and $_{DD}$ below the shrub canopy. We will also allow the parameters (growth rates, death rates, etc) in each of these regions to be species-dependent, which we will denote as the argument S for the shrub and T for the tree. We will not specify the environment, explicitly, as it will always be for both species being present. Proceeding as before, the diameter of the shrubs at the height of their (shaded) canopy will be

$$D^{**} \approx \frac{G_{DD}(S)}{\mu_{DD}(S)} \log \left(\frac{2F_D(S)\alpha(S)G_D(S)^2}{\mu_D^3(S)} \right) \tag{5.1}$$

Note that this will in general be different to shrubs growing in an open field unshaded by a tree canopy. The presence of the second canopy will reduce the canopy height attained by the tree canopy, (assuming the second canopy is darker and hence death-rates higher and/or growth rates less than they would be with no shrubs present). This correction will be proportional to the height of the shrub canopy, and can also be calculated in much the same manner:

$$D^*(T, S\&T) \approx D^*(T,T) - \left(\frac{\mu_{DD}(T)G_D(T)}{\mu_D(T)G_{DD}(T)} - 1 \right) D^{**} \tag{5.2}$$

Where the height of the tree canopy in the presence of the shrub $D^*(T, T\&S)$ is decreased from the height it would attain without the shrub by an amount proportional to the shrub height. For instance, if the tree dies twice as fast and grows twice as slowly under the shade of the shrub than under its own shade, its canopy is reduced by twice the height of the shrub canopy. To maintain stable coexistence in this model, a few intuitive criteria must be satisfied.

5.2 Survival of the tree species

For the tree canopy to over top the shrub canopy, its height independent of shrubs must exceed the height of the shrub canopy times the factor measuring the impact of the shrub:

$$D^*(T,T) > D^*(S, S\&T) \left(\frac{\mu_{DD}(T)G_D(T)}{\mu_D(T)G_{DD}(T)} \right) \tag{5.3}$$

We can rewrite this

$$\frac{G_{DD}(T)}{\mu_{DD}(T)} \log \left(\frac{2F_L(T)\alpha G_L(T)^2}{\mu_L^3(S)} \right) > \frac{G_{DD}(S)}{\mu_{DD}(S)} \log \left(\frac{2F_D(S)\alpha G_D(S)^2}{\mu_D^3(S)} \right) \tag{5.4}$$

If the shrub does better in the dark shade below the second canopy, the tree can must compensate by performing much (exponentially) better in the direct light above its canopy than the shrub does in its shade. We can summarize the consequences of the model as follows:

- The shrub can invade if (5.1) is positive

- The tree and shrub coexist if the tree canopy remains above that of the shrub, expression (5.3)

The first condition must be satisfied before we can consider the second: coexistence guarantees the shrub can invade. The converse is not true: if the shrub can invade it can either exhibit dominance or coexistence. However, unlike our earlier coexistence, we observe that this coexistence is independent of the tree's ability to invade the shrub.

5.3 Invading the resident shrub

Assuming the tree and shrub coexist, we have two possibilities:

- The tree can invade the shrub. Coexistence can be established regardless of which species is the founder.

- The tree cannot invade the shrub. Coexistence now depends on the founder. The shrub monoculture exhibits founder control, while the tree monoculture is invasible.

In the first case we have the familiar coexistence we encountered before: each species can invade the other's monoculture. This provides us with a simple, stable coexistence that can be created by introducing either species into the monoculture of the other. If the tree cannot invade the shrub, we experience something more novel: a founder-control mediated coexistence. Of course this condition for this is already familiar to us,

$$\tilde{D}_L^*(S,S) > D^*(T,S) \tag{5.5}$$

Where we explicitly remind ourselves that the $D^*(S,S)$, a shrub growing in monoculture, has access to direct sunlight, unlike the cases we have considered so far.

Stability of coexistence

Should the forest population colonize an area first, shrubs can move in and coexist. However, if some disturbance (fire, disease, logging) disrupts the forest canopy later, the tree population will not be able to return to the area. Species satisfying our simple coexistence condition (4.9) could survive the temporary removal of either species, as it could always be reintroduced later since each can invade the other. This coexistence is not so secure; it can only be established in the proper order. Starting with a forest in which shrub and tree coexist, we have no way of knowing whether or not the tree will be able to invade the shrub, since we do not have access to all the terms in (5.5). If we want the tree to be able to recover after a disturbance to its population, we need to know how the shrub's growth in the light.

Chapter 6

Succession

We now turn from coexistence to succession. A fundamental concept in ecological theory, forest succession is also taught to youth as a classic example of the dynamic nature of ecology. Despite its ubiquity, the details of the theory are less well understood [23]. Here we will see that succession is an immediate consequence of our model when (1) the interspecies interaction is dominance based and (2) we introduce a constraint on the parameter space of possible species. We have already seen that dominance is the simplest consequence of our model, and its conditions are easily satisfied by most species pairs [1]. We now introduce the second requirement, which will turn dominance into succession.

6.1   Physiological Trade-offs

Monoculture forests can always be invaded by trees with higher canopies. This corresponds primarily to trees that either grow faster or live longer in while in the dark. Thus far we have considered trees drawn from a five-dimensional space of coordinates $(\mu_D, \mu_L, G_D, G_L, F)$. Though α can in theory be sixth dimension, it tends to be constant between species and enters the model in the same way as fecundity F, hence we need not consider its role independently. Even with a few basic constraints such as $G_L > G_D$ and $\mu_D > \mu_L$, this remains a high

dimensional space. Real trees will not occupy this full space as a consequence of physiological design constraints: a tree cannot arbitrarily increase its growth rates and death rates. In fact, most species have been shown to fall on a much lower-dimensional manifold, even when more parameters are considered [22]. This results in relationships between the parameters that represent design trade-offs the tree faces, such as investing resources in growth or in defenses that will increase its life expectancy.

The relationship between growth rate in the light and survival in the dark will prove particularly interesting to us. As suggested by Figure 6.1, increased growth rate in direct sunlight (G_L) comes at the cost of a linear decrease in survival in the shade. This can be interpreted as a difference of strategies, where a tree bets its finite resources on either the optimistic promise of fast growth allowing it to close the canopy first and also generate more offspring faster, or plays it safe: pessimistically assuming it will be over topped and spending its resources defensively to increase its survival chances, knowing it can win out in the long run.

6.2   The Successional Manifold

Motivated by the observations in Figure 6.1, we assume that growth rate in direct sunlight, G_L can be predicted by a linear function of μ_D:

$$G_L(\mu_D) = m\mu_D + b \tag{6.1}$$

For simplicity, we will assume that the other parameters, G_D and μ_L remain essentially fixed by external factors, while species differ primarily on their position on this trade off curve (6.1). If we consider an open plot colonized by the seeds of a variety of tree species, those with the fastest direct-light growth rates G_L will close the canopy first. However, there offspring will manage less well than the shade-tolerant species, which will eventually over top the current canopy. The first population will now find itself permanently in the shade, and

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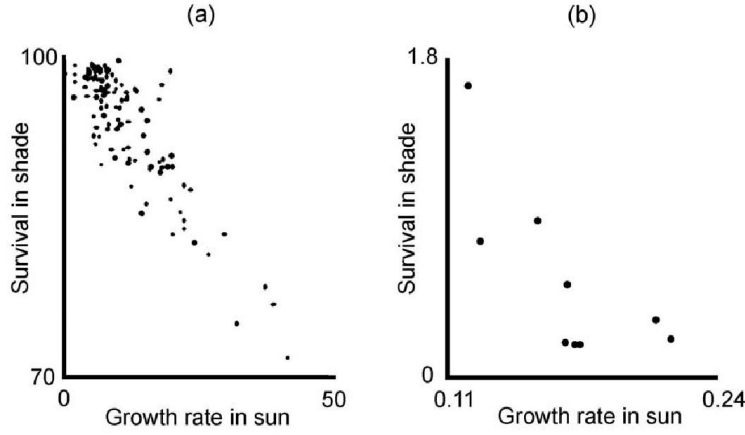
Figure 6.1: **Physiological trade-offs**

will die out in favor of the dominant species which it cannot invade. Meanwhile, species that grew even slower in the initial phase but with even better dark-based life-times will continue to out-compete the resident canopy, establishing ever higher canopies at later and later times. The forest moves from one originally filled with fast-growing, short lived species to a forest of trees that survive a long time in the understory, grow slowly in direct sunlight and have very high canopies.

The process described here, a consequence of our simple analytic model and the biological trade off manifold (6.1), Figure 6.1, would be readily identified by an ecologist as ecological succession. Succession is both easily understood and easily observed to be taught in the grade-school classroom, and remains a dominant a well-developed concept for the research ecologist. Though a fundamental part of forest dynamics, its details remain challenging [23]. Our analytic model offers a simple explanation of the phenomenon. Trees that grow quickly in the light and die quickly in the dark we term early-successionals. Trees with slower light-growth rates and lower dark death rates are then the late-successional species. The age of a forest can be easily approximated by its dominant species. A forest coexisting primarily of Virginia Pine is younger than one that is pri-

marily Eastern Hemlock. The beech saplings so visible in winter clinging onto their golden leaves represent the doom of the surrounding oak forest.

Successional Manifold

By assuming that all trees have approximately equal fecundities F, dark-growth rates G_D and light-death rates μ_L we reduce the possible species types to a single dimensional manifold. The position of any species on this manifold is determined by μ_D. We can characterize each position on this manifold as a stage in ecological succession, with early successionals at very high values of μ_D and late successionals at very low values. We refer to this as the successional manifold. The approximately one-dimensional manifold observed in characterizations of tree species with as many as 14 parameters fit to real forest species [3, 22] has also been referred to as a successional manifold. Though other parameters such as G_D do not remain constant in these models, the most common observation in successional patterns is that of increasing shade tolerance. [23] Consequently our manifold defined entirely along the shade-tolerance vector is likely a reasonable projection of the actual manifold. Hence when considering two different species, we will term the one with the higher μ_D the *early-successional* type, and the other the *late-successional* in reference to this manifold.

6.3   A climax community?

A common question in successional theory concerns the existence of a climax community. As we predict that subsequent invasions require higher canopies, (3.7), we can use our trade off manifold (6.1) in our expression for canopy diameter, (2.23) to see if it reaches a maximum:

$$D^* = \frac{\mu_D}{G_D} \ln \left(\frac{2F\alpha(m\mu_D + b)}{\mu_L^3} \right) \tag{6.2}$$

Plotting canopy diameter as a function of μ_D, Figure 6.2, we see that a critical value of $\mu_D = \tilde{\mu}_D$ gives the maximum canopy diameter. For $b = 0$ we can solve
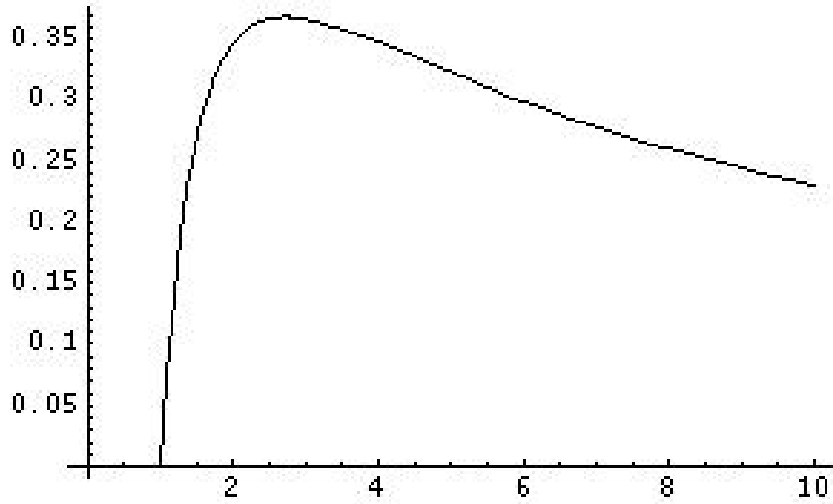
Figure 6.2: Diameter vs successional position μ_D, equation (6.2).

for this analytically,

$$\tilde{\mu}_D = \frac{\mu_L^3 e^1}{2F\alpha m} \tag{6.3}$$

The existence of this maximum suggests that succession leads to a climax value μ_D maximizing canopy height.

We generally require $\mu_D > \mu_L$, hence for $\tilde{\mu}_D$ to be attainable we would need

$$\mu_L > \sqrt{\frac{2F\alpha m}{e^1}} \tag{6.4}$$

For common values of fecundity rates F, scaling α, and m this would be quite unreasonable. Consequently we only have the limit on succession imposed by our fixed μ_L.

What about coexistence?

In a successional regime, diversity is only transient: species later on the successional axis (lower μ_D values) will always out-compete earlier-successional species given enough time. However, when time is measured in the lifetime of trees, a progression of only a few generations of trees can take hundreds to thousands

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of years (see Appendix A). Many forests remaining today are not nearly so old, having suffered some disturbance or another on a much more recent scale. In the next chapter we will see how including such disturbances not only makes our time-dynamics more realistic, but can also provide a mechanism for coexistence in an otherwise dominance-based interaction.

Chapter 7

Succession with Coexistence

In this chapter we introduce disturbances that destroy all of the trees living in a certain patch of the forest. This process could represent a variety of possible events, from forest fires or diseases to logging for timber. The patch is reseeded from the remaining forest, in proportion to abundance of each species in the canopy. Because the patch is once again open, the successional march of species begins again in that area. Early-successional trees that would otherwise be eliminated from the forest population can recover on these patches, allowing for coexistence in a successional, dominance-regime interaction. We demonstrate that this coexistence is indeed possible as long as two conditions are satisfied: (1) the disturbance frequency falls within a certain window (2) the two species have a limiting similarity: they must be separated by at least some minimum value on the successional axis.

Role of Transients

While ecological theory has traditionally operated under the assumption that the states of nature we observe correspond to stable equilibria of a simple model, much as we have done here, recent work emphasizes the importance of different timescales and transients in ecological understanding [6], including species coexistence problems [7,8]. Our current model has at least two important timescales:
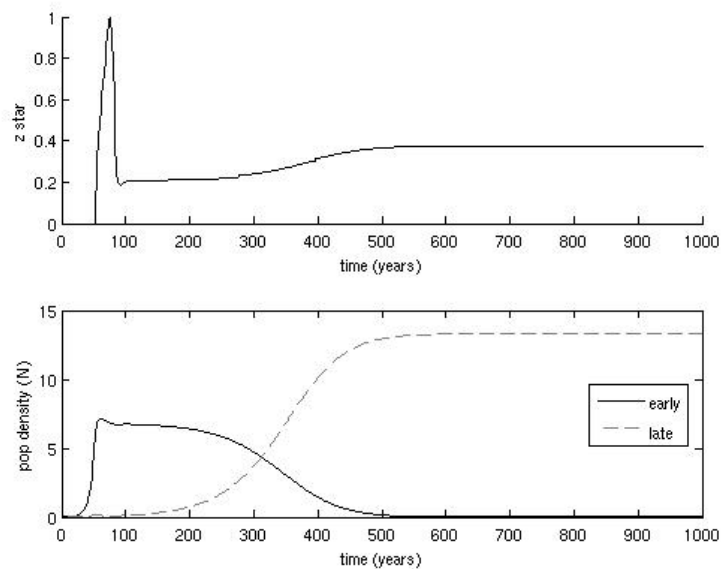
Figure 7.1: **Succession** Top: the canopy height passes through a transient phase, the equilibrium of the early successionals, then finally settles at the equilibrium of the late successionals. Bottom: Without disturbances, succession results in an early dominance of the early successional species which then vanish as the late successionals come to dominate (lower figure). In this example, $\mu_D(1) = 0.15$, $\mu_D(2) = 0.075$. All other parameter values are as stated in Table 7.1.

(a) the time required for the canopy to reach an equilibrium height, and (b) the time required for the late-successional to dominate. The dynamics that occur within both of these timescales will play an important part in our understanding of the interspecies interactions. Both can be seen in a traditional example of succession, such as the simulation in Figure 7.1. To this we will also add a third timescale: the time required for the total population densities of the forest to reach equilibrium in a given disturbance regime. While the first two timescales will be relevant to the dynamics of individual patches, this one pertains only to the forest as a whole. The importance of these transients means we will no longer be able to look only for steady state solutions, but will turn to numerical simulations to explore the time-dependence of our macroscopic equations.

7.1 Simulating Forest Cohorts

We will introduce a simple successional regime by assuming that all species cast identical shade and live on a manifold such as (6.1), as in Chapter 6. We can simulate the deterministic cohort model to investigate the full dynamics of the system. The model is parameterized by the values specified in Table 7.1. We assume all species have the same allometry, allowing us to compare diameters directly to determine which species tree is taller at any instant. The simulation keeps track of the density and height of each cohort for each species, advancing them according to our macroscopic equations. At each time step the canopy height must be redetermined, and then growth, death, fecundity, and dispersal can be computed. The simulation is implemented in MATLAB®; the base code can be found in Appendix B. As the computation of the canopy-height is the most subtle of these steps, we take a moment to explain how this is done.

Splitting cohorts at the canopy

The simulation is essentially identical to the analytic model: population densities, heights, areas, and offspring densities are all continuous variables. The model tracks age cohorts of trees rather than individual trees: each time-step

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Symbol	meaning	value
α	ratio of basal area to crown area	4
A	Total area	1
μ_L	Death rate in the light	0.05
G_D	Growth rate in the dark	0.008
F	Fecundity (in light only)	1
N_0	Initial population density	.01
m	Slope of G_L, μ_D tradeoff	1/5
b	y-intercept of tradeoff	0

Table 7.1: Values of constant parameters in simulation

a new cohort is born with a certain density and zero height. The cohort then grows and dies according to species-specific rates and whether it is above or below the canopy level. The canopy height is determined be equation 2.4, summing the area of each cohort, starting with the tallest, until that area matches the area of the plot. Of course the last cohort to be included in the canopy will generally take the running total area from just under the area of the plot to just over the total area. To enforce the boundary condition of finite area, this cohort is split. Just enough are taken into the canopy to close the area exactly, (and are increased in height by some small amount ϵ), leaving the rest below the canopy. One can imagine this as a statement of the fine-scale structure of the cohort: every tree the same age would not have exactly the same height, but differ slightly due to stochastic effects. We do not model this intra-cohort variation explicitly, but assume that some members of the cohort are in fact taller than others, and overlap the slightly shorter trees that do not enter the canopy.

Forest Patches

The disturbances we introduce will not effect the entire forest simultaneously, but will occur in continuous regions of the forest which we refer to as patches. For most purposes the patches are treated as independent forests, having their own population densities, distributions, and canopy height and confined to their own plot area. We assume that patches are large enough that we need not

worry about the boundaries between them. Patches will only interact through seed-dispersal: each patch contributes its seeds to the total forest pool each year, which is subsequently divided evenly between all patches to seed the next cohorts.

We will have a total P identically sized patches, each of which may be subjected to a disturbance in turn. For simplicity, we will assume this disturbance to be perfectly regular: a different patch is cleared every M years. One can imagine this to be the case in a forest grown for logging, though we can also generalize this to the case in which each patch has an independent probability $P(\tau)$ of being leveled, where τ represents the age of the patch (time since it was last leveled). After the first $M \cdot P$ years, the forest will consist of a patches with a uniform age distribution in our case, or one reflecting $P(\tau)$ in the general case. After an initial transient phase, the state of any patch will be uniquely determined by its age alone. Consequently, rather than ask what a particular patch looked like 50 years ago, we can simply find another patch in the forest that is 50 years younger than the patch in question. In this way, the spatial structure of the forest echoes the temporal structure of any one patch. The different temporal niches of early and late successional trees can now be realized as spatial niches as well.

7.2 Dynamics of Closing the Canopy

A step back: single patch monoculture

Before we consider the patch model in detail, We are going to take a moment to understand the time-dependence of the canopy height z^* before it reaches the familiar equilibrium level we have been dealing with thus far. Everything in this section holds for all of the forests we have been describing, down to the simplest case of monoculture on a single patch. We have only ignored it until now because we could. However, an understanding of the patch dynamics ahead will hinge on an understanding of this transient phase of the canopy formation.

So let us take a step back, and with the help of our simulation, consider what happens when a canopy closes in the Pacala forest.

Area growth in the light

We described the highest canopy trees continually overshadowing more and more lower-canopy cohorts. We can look at this process more precisely. For a given cohort living entirely in the light its area $A(t)$ grows as:

$$A(t) = N_0(1)\alpha[G_L\tau]^2 \exp(-\mu_L\tau) \tag{7.1}$$

which is plotted in figure 7.2 for several different cohorts. The curve is characterized by its initial increase due to the quadratic growth of the crown area, which eventually is overtaken by the exponential death term, causing the total area to decrease. We can easily solve for the location of this maximum, $\tilde{\tau}$,

$$\tilde{\tau} = \frac{2}{\mu_L} \tag{7.2}$$

As this depends only on τ_L, each cohort growing entirely in the light will reach its peak area at the same age, at $\tilde{\tau}$, regardless of its initial seedling density N_0. (In fact in the successional patch model it will be the same between species as well.) The early cohorts may pass this maximum before the canopy closes, such as the founding first cohort, plotted in solid black in Figure 7.2. Though they will remain in the canopy after it first closes, the total area of these early cohorts declines, opening new area that will be filled by the lower, younger cohorts.

The closure of the canopy is a consequence of the younger cohorts that have yet to reach their maximum area, such as the 35th cohort in Figure 7.2. The cohorts immediately following the founder cohort are negligibly small, as they are seeded entirely by the founder cohort when it is of negligible area itself. The later cohorts are larger and larger, which can be seen in comparing the 35th and 40th cohort in Figure 7.2. The increase in seedling numbers can be seen in Figure 7.8(a) and is discussed in more detail later. The contribution to the
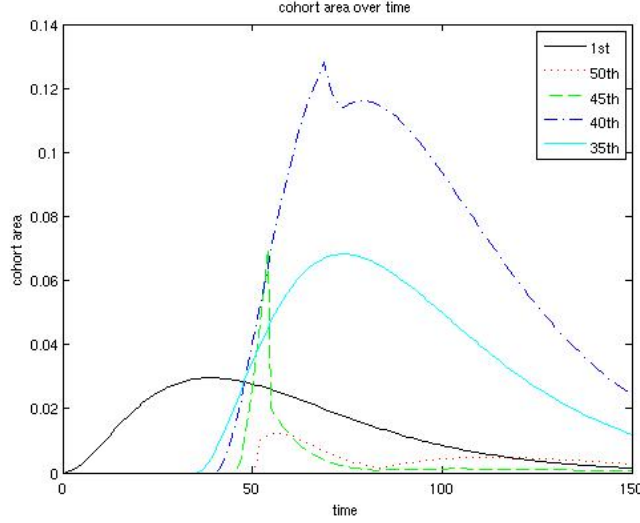
Figure 7.2: **Areas of individual cohorts over time.** The areas of each individual cohort living entirely in the direct sunlight follows equation (7.1).

total area of these cohorts younger than $\tilde{\tau}$ more than makes up for the decrease in area in all the cohorts older than $\tilde{\tau}$. When the canopy closes, the youngest couple of these will be left in the dark, condemned to grow at a slower rate μ_D.

Meanwhile, the cohort at the canopy height belongs to one of those younger than $\tilde{\tau}$, responsible for the still growing area. As the area of the cohorts younger than $\tilde{\tau}$ increases faster than space can open up from the cohorts older than $\tilde{\tau}$, those near the canopy height will soon find themselves overshadowed, and the height of the canopy continues to move up. This effect manifests itself in several ways. First, we can see it happen most directly in the 40th cohort in Figure 7.2, where it jumps down from its peak. The decrease in area is due to the cohort being split: some members were demoted to a cohort immediately below it, beneath the canopy. Soon after, it reaches age $\tilde{\tau} = 80$ (using μ_L from Table 7.1) and no longer increases in area.
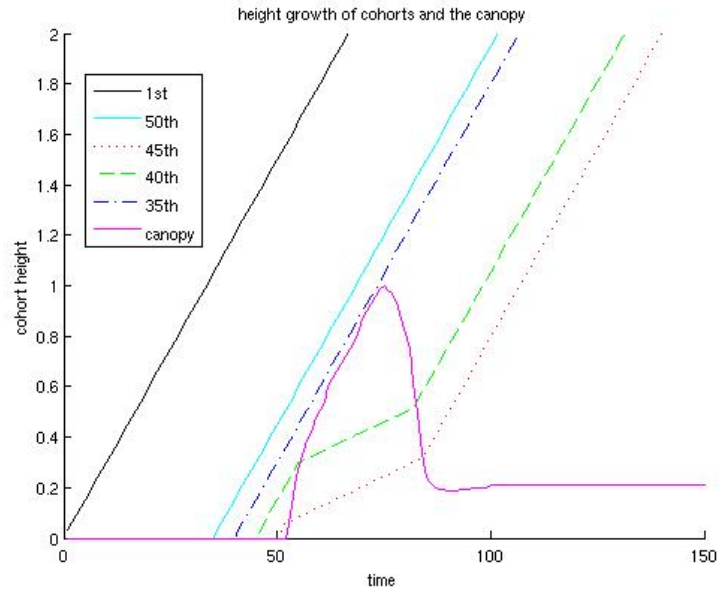
Figure 7.3: Canopy height and its effect on cohort height.

Initial canopy growth rate exceeds cohort growth rate

We have observed that the canopy height moves up through this process, as subsequent growth of cohorts that can still increase their total area continues to raise the canopy height, pushing more and more cohorts from the sun into the shade. The growth of the canopy height initially happens faster than the growth of an individual cohort, as it results from the sum of growths of several cohorts. Clearly this must be the case, otherwise it could never force cohorts growing in the light into the shade, which must happen to conserve sunlit area while the total tree-crown area increases.

This process is best visualized in Figure 7.3. The initial cohorts never see the shade below the canopy, such as cohort 1 and cohort 35. Cohort 40 just touches the canopy curve, losing some of its population below the canopy. Cohorts 45 and 50 run smack into the the canopy curve, entering a phase of darkness where they grow at a reduced rate before eventually breaking through. The encounter

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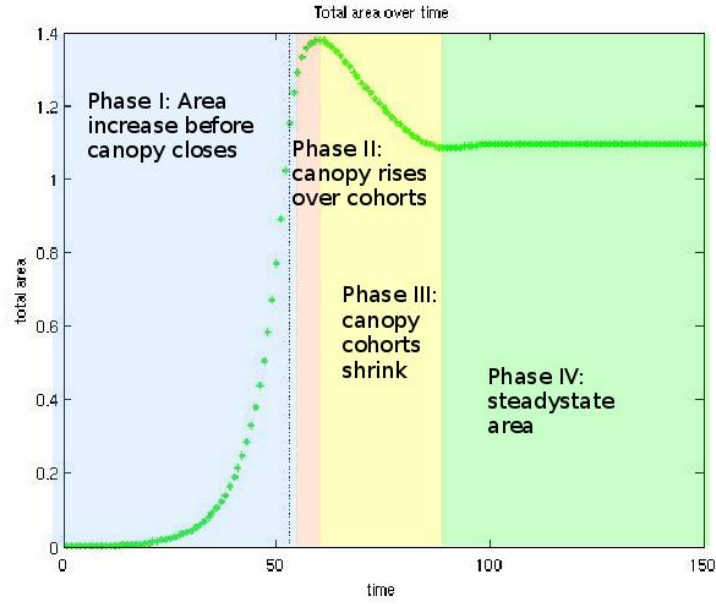
Figure 7.4: Phases in total crown area during canopy formation.

with the canopy is responsible for the dramatic change in the area of of these cohorts seen in Figure 7.2. The area of cohort 45 initially shrinks as the cohort is partitioned successively by the finite sunlit area restriction. By the time it reaches the light again, its area is already into its decreasing phase. Cohort 50 enters the darkness almost immediately, (the canopy closes at year 53), and displays an arc similar to that of the light-based area growth, only smaller due to the dark parameters. Once it breaks into the light it repeats this arc, once again increasing area initially before declining. The inflection between these two bumps in cohort 50 curve of Figure 7.2 corresponds exactly with its re-entrance into the light, seen in Figure 7.3.

Dynamics of the total crown area

Now that we have an understanding of the behavior of the individual cohorts, we can better interpret the total area of all tree crowns in the forest in Figure 7.4.

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The area initially grows rapidly, phase I. The inflection point in this growth corresponds to the moment the canopy first closes, phase II. From this point on, the total area can still increase, but the *rate* of that increase must now decrease, as fewer and fewer cohorts are growing at the rate G_L in each subsequent year. This process sweeps out the younger cohorts, which are the first to become overshadowed. Meanwhile, the older cohorts are all passing the age $\tilde{\tau}$ at which they can still increase in area. Eventually enough cohorts are shrinking in total area (due to the death of their members), to cause the total area of the entire forest plot to decrease, beginning phase III. This decrease continues until it can be balanced by new cohorts growing into these gaps, at which point the total area equilibrates, phase IV. Note that the equilibrium value is slightly greater than the plot area (unity), as this sum plotted in Figure 7.4 includes the area of the understory. This same transient overshoot in area is echoed by the overshoot in canopy height, as seen in Figure 7.3.

The transient overshoot of canopy height and the related variables can also be understood simply as the transition of populations starting their growth in the light as opposed to the dark. At the equilibrium canopy height $z*$, trees rise from the understory just fast enough to replace gaps opening in the canopy. When the canopy first closes, the trees below it have not started with the same initial conditions (growing in the dark) and are consequently larger than a cohort of that age would be at equilibrium. This excess forces the canopy to rise and overshoot before it can equilibrate. With an understanding of the early canopy dynamics in place, we turn back to the two-species problem.

7.3   Stopping Succession by Patch Disturbance

Early successionals close the canopy first

Our first test of the model occurs in a forest that consists of a single, undisturbed patch with two species. We initialize the patch with a small concentration of seeds of corresponding to an early successional type, $\mu_D(1) = 0.15$ (species

1) and an equal number of seeds corresponding to a later-successional type; $\mu_D(2) = 0.075$ (species 2). We track the population size of each species over time as well as the height of the canopy (which is a property of the plot, not a particular species), in Figure 7.1. Initially the early-successional population increases faster: thanks to its higher growth-rate in the light, which results in faster growing tree crowns and hence more offspring. At first the area of all the crowns is less than the area of the total plot, and the canopy height remains at zero. Suddenly the area of all the crowns is enough to close the canopy, and the canopy height jumps (discontinuously) up to some small value. At this point the youngest cohort still in the canopy may belong to the slower-growing late-successionals. However, as the cohorts above them continue to grow taller, they also increase their area, shutting out more and more of the cohorts below from direct sunlight. As the highest cohorts belong to the early-successional, soon there are no late-successionals in the canopy. Cut off from the direct sunlight, the late successional population cease reproducing, while dying off at a constant rate $\mu_D(2)$, and their population begins to shrink. Nevertheless, those remaining continue to grow, though at the slower rate $G_D(2)$, and do not die as fast as the new seedlings of the early-successional trees, born under the darkness of the canopy.

Late successionals break into the canopy

The canopy of the early-successionals ceases to rise not long after it closes. However, it fails to equilibrate: instead of finding own offspring rising to fill the gaps that open as the older sunlit trees slowly die, it finds the remaining late-successionals. What happens as these late successionals reach the sunlight? They have been growing at the same rate as the early-successional's own seedlings, $G_D(1) = G_D(2)$. However, they enjoyed an initial boost growing at G_L and dying at μ_L until the canopy closed (recall no late-successional cohorts have been born since the canopy first closed). Further, they have been dying at a slower rate than the seedlings of the early successionals. Consequently, while

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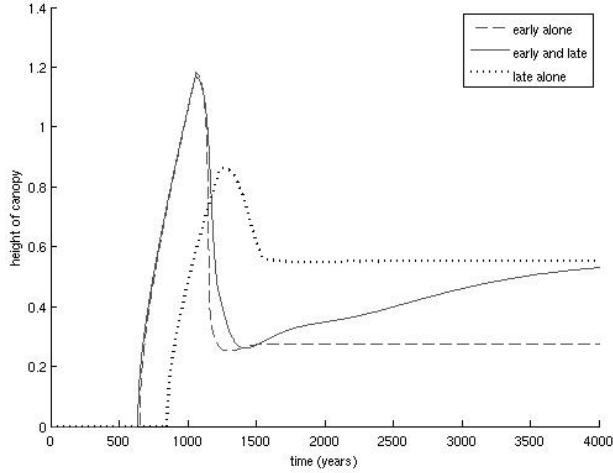
Figure 7.5: **Canopy height.** The time-evolution of the canopy height z^* for a two-species patch is compared with that of each species alone. The equilibrium canopy height matches with that predicted for each species by equation (2.23)

the early-successional seedlings arrive with just enough area to close the gaps opening above, these late-successionals arrive with the potential to increase the total area, raising the height of the canopy.

This time the canopy rises less dramatically then before, as seen in figure 7.5. The middle curve, shows the canopy increasing from the equilibrium height of the early successionals to that of the late successionals. This process is more gradual as the late-successional cohorts reaching the sunlight are older and hence farther along on the curve (7.1). Reaching the light allows them to resume seedling production, which has been absent throughout the time they were over-topped by the early-successionals, as seen in Figure 7.8(b). This second generation of seedlings will eventually continue to carry the canopy up. This gradual increase does not overshoot, settling into the steady state canopy of the late-successionals. Meanwhile, new early-successional cohorts can no longer reach the canopy. As the area of those early-successional cohorts above the canopy decreases with the exponential death, so does their offspring production, as seen in figure 7.8(a).
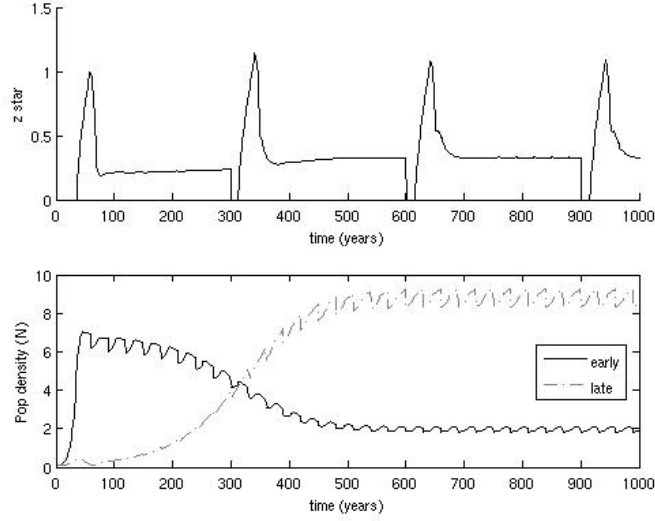
Figure 7.6: **Disturbances allow coexistence.** $P = 10$ patches, $M = 30$ years between disruptions. The top figure again shows the canopy height z^* for a particular patch, the bottom shows population densities for both types.

A disturbance restarts the competition cycle

If we wait long enough, the early successional population will vanish entirely. By introducing a disturbance, an entire patch is leveled, and begins its history again as an open area reseeded by the rest of the forest. The composition of the reseeding represents the age distribution of all the patches at the year the patch is leveled. Old patches contribute only late-successional seeds, younger patches contribute only early-successional seeds. The youngest patches as well as some intermediate patches may contribute seeds from both successional types. We initialize the forest with all patches empty and equal densities of early and late successional seeds on each patch. Every M years a new patch is leveled, cycling through once all patches have been leveled. Consequently each patch will grow for $M \cdot P$ years before being leveled again (after the first $M \cdot P$ years).

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(a)   (b)
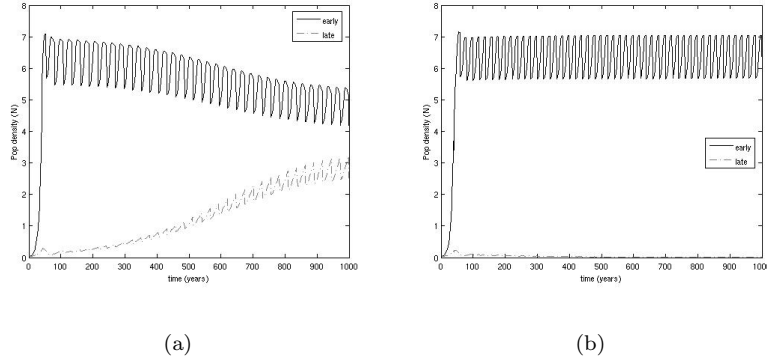
Figure 7.7: **Different disturbance regimes** (a) As the frequency of distur-
bances increases, the early successional trees perform better. This time a differ-
ent patch is leveled every 14 years, hence the maximum age of any patch is 140
years. (b) When the disturbances are too frequent, only early successionals can
survive. A different patch is leveled every eight years, making the maximum
age eighty years. This does not give enough time for a sufficient number of
late-successionals to reach the canopy and reproduce.

Consequences of the disturbance frequency

The introduction of these disruptions halts the process of succession, allowing
the two species to reach equilibrium densities, Figure 7.6. Because the forest
experiences the disruption every M years, the equilibrium is periodic rather
than constant. The populations of both species grow immediately after a dis-
ruption and drop by $1/P$ every M years when a plot is leveled. The frequency
of disturbance determines the equilibrium levels each population can reach. For
large values of $M \cdot P$, disturbances are just frequent enough to prevent the loss
of the early successional species, as seen in Figure 7.6. As the frequency of the
disturbances increases, the early successional population can maintain a higher
density, Figure 7.7(a). If disturbances are too rare, the early-successionals con-
tinually decrease, Figure 7.1. As densities are continuous, it is difficult to judge
if the population will equilibrate at extremely low densities at long times, though
this can be treated as effective extinction for real populations. Meanwhile, if the

(a)   (b)
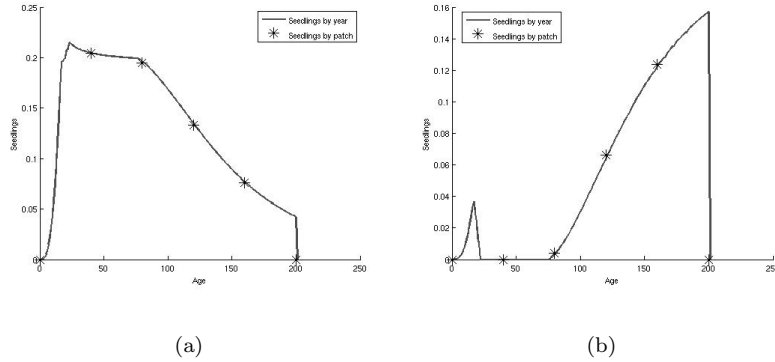
Figure 7.8: **Steady state reproduction**. (a) Early-successional. (b) Late-successional. Curve represents the steady state seedling output over time for a single patch. Consequently the dynamics of a single patch are periodic every 200 years. Asterisks plot the spatial distribution: seedlings produced by each of the five patches against the age of each patch. At equilibrium the spatial and temporal distributions match. Simulation included $P = 5$ patches, with one leveled every $M = 40$ years.

patch lifetime $M \cdot P$ is shorter than the time required for the late successionals to reach the canopy, they face extinction, Figure 7.7(b).

Coexistence, then, is possible even in the simple successional regime, provided patches of the forest can be disturbed. This effectively divides the forest into niches where an early successional species can perform well and patches where the late successional performs better. The niches are essentially temporal but have taken on a spatial reality by having patches of different ages. This coexistence is not contingent on the particular manner in which disturbances enter, it simply requires that patches exhibit a distribution of ages at all times. In some sense our simple model is not the simplest, as the age structure actually changes in between disturbances. Consequently the forest exhibits a periodic age structure, rather than a constant age structure it would have, say, if we leveled a patch every year ($M = 1$) and had enough patches so that the maximum age of any patch P was high enough to permit late-successionals to over top the early-successional canopy. Any of a variety of more complicated disturbance

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regimes could also be implemented to achieve coexistence.

Though no patch reaches equilibrium, it is clear from the simulations such as Figure 7.6 that the overall forest populations do settle into a periodic pattern. At this equilibrium, the distribution of any one patch over time is matched exactly by the distribution of all patches at any one instant. For instance, the seed production of each species on a single patch over its $M \cdot P$ periodic lifetime matches perfectly with the production of each patch at that age, Figure 7.8(a) and Figure 7.8(b) (a simple consequence of all patches being identical except for a phase shift). Consequently, we could reconstruct the history of seed production of a single patch by measuring the seed production of all patches in the forest at a single instant, rather than collecting time-sequence data.

Figure 7.8(a) and Figure 7.8(b) nicely summarize the overall behavior of the forest under the disturbance regime. The total time (or equivalently, number of patches) over which each species can produce seeds (the domain over which the seed-production functions have support) determines the size of the niche for each species. The size of these niches changes as the patches move through their periodic cycle, (the asterisks advancing cyclically along the curve), though the effect of this oscillation decreases with more patches for constant $M \cdot P$. If the disturbance regime is too short, the late successionals have no support after the initial open canopy period, where their seedling production is still less than that of the early-successionals. With no niche where they can outperform the early-successionals, their population is bound to decrease forever. Meanwhile, without disturbances the late-successionals have infinite support once they regain the canopy, and the early-successionals are doomed.

7.4 Niche Structure: Understanding Successional Coexistence

This concept of niche then suggests another way to understand the population dynamics. For coexistence to be possible, each species must have a niche in
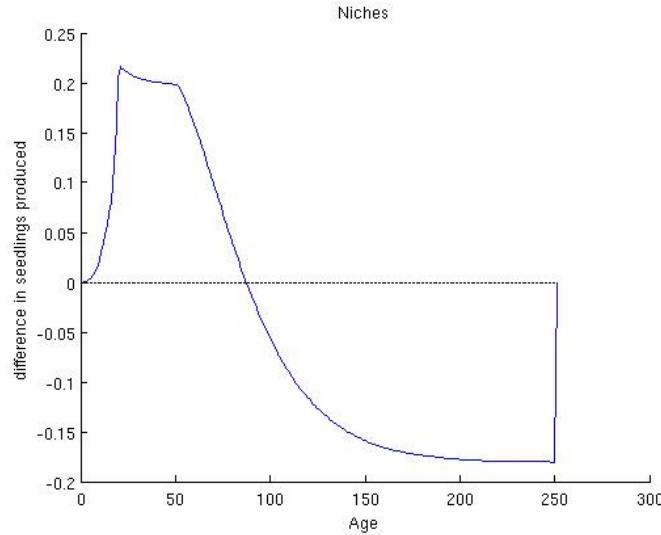
Figure 7.9: **Age structure niches.** Positive area represents earl-successional niche, negative represents late-successional niche.

the age structure. The figure we need, then, is actually the difference between Figure 7.8(a) and Figure 7.8(b), plotted in Figure 7.9. The positive region indicates the niche size for the early successionals, the negative region indicates the niche for the late successionals. The size of the niche reflects the size of the equilibrium population. When the disturbance regime is too frequent,the difference will always be positive and the late-successional population will continue to shrink forever. When the interval is too long, the seedling production of the late successionals will greatly exceed that of the early successionals. Consequently, the late successionals will produce more seeds even on the open patches despite growing slower, thanks to their higher initial seed density.

Changing the disturbance period is clearly not the only way to influence the curves determining the size of each niche in Figure 7.9. The position on the successional axis (value of μ_D) of each species will also influence these curves. Consider the identical disturbance regime in a forest initialized with the same early successional type, but with a late-successional that is not as quite as far
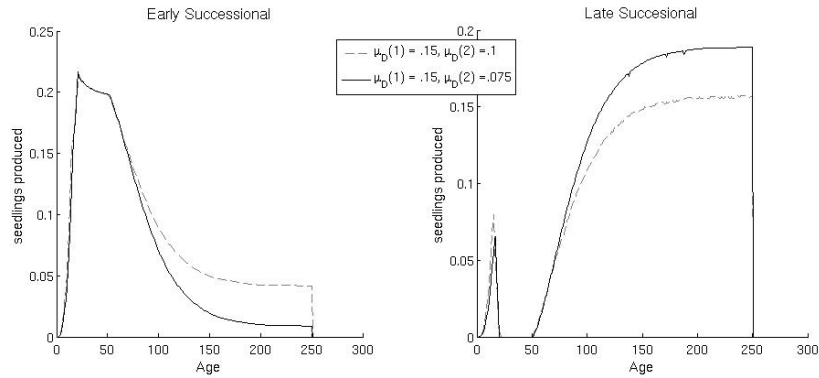
Figure 7.10: **Effects of species similarity**. Decreasing the successional distance between the two species decreases the seed output of the late successionals and increases that of the early successionals.

down the successional axis as before. The early-successional species will perform identically well at the beginning, but will do better on older patches in the second forest then in the first, Figure 7.10, even though its own species parameters are identical in both forests. Meanwhile, the late-successional will perform better in the second forest than in the first forest until the canopy closes, thanks to its higher light-growth rate. However, it performs less well in the second phase, due to its higher death-rate in the dark, Figure 7.10. Consequently, the size of the niche for the late-successional shrinks for species that are more similar. Clearly this would also be the case if we held the late successional fixed and picked an early-successional farther down the successional axis (lower μ_D).

7.5 Limiting Similarity

7.5.1 Ecological Consequences

The observations of Figure 7.10 suggest that a limiting similarity exists between two species. For a given disturbance regime, two species can only exist if each has a niche, which requires that the species differ by a critical amount. As the species become more similar, the size of the late-successional niche shrinks and then
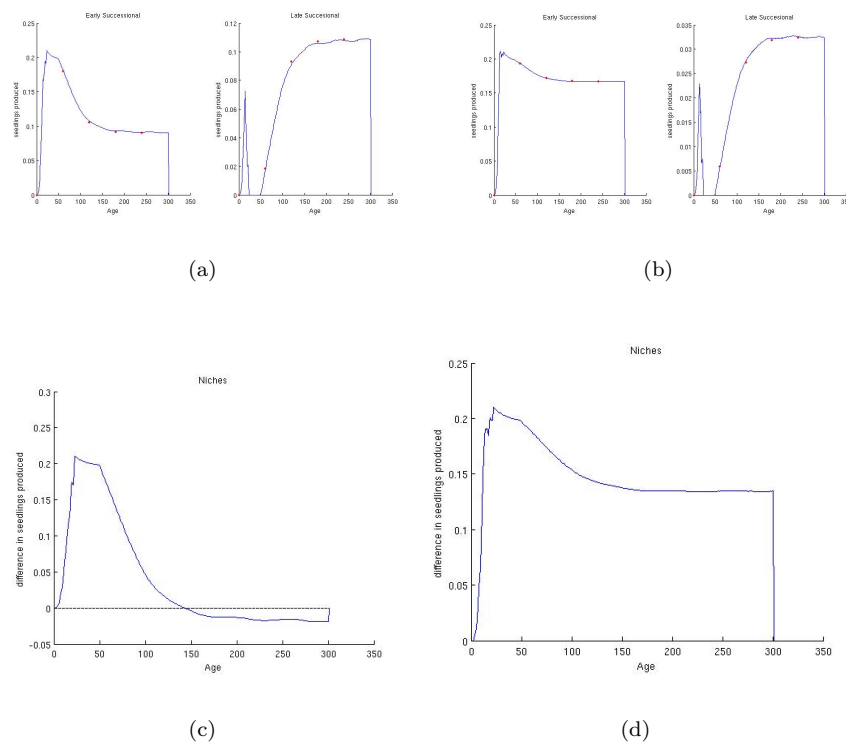
Figure 7.11: **The late successional niche vanishes.** Curves from the top pair of figures (a) or (b) are subtracted to determine the niche structure, (c) or (d), shown below. On the left side (a), (c) the late successional just hangs on, then vanishes on the right (b), (d) once the types are too similar.

vanishes, Figure 7.11. The consequences of this are clearly visible by tracking population densities, Figure 7.12. The late successional population shrinks and shrinks, while the early-successional population rises to the equilibrium density it would achieve if grown in the same patch-disturbance forest in isolation.

Through the niche-structure illustrated by Figure 7.9 and Figure 7.11, it is easy to see that in the case of limiting similarity, the early-successional species always wins out. However, this approach does more to illuminate the reason for a sharp transition between coexistence and dominance then to actually explain why the early successional must win out. We can better understand this by
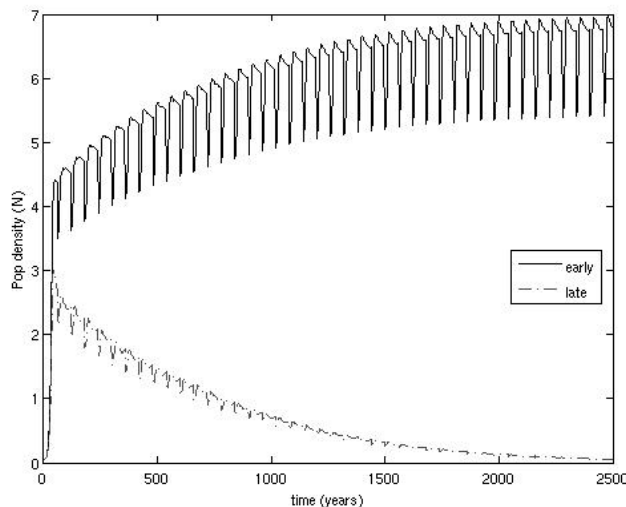
Figure 7.12: **Limiting Similarity.** In a given disturbance regime, coexistence requires a limiting similarity between the early and late successionals. Once species become too similar, the early successionals dominate. Here the late-successional (species 2) has a death rate in the dark $\mu_D(2) = .145$ while the early successional remains at $\mu_D(1) = .15$. The closer the similarity, the faster the extinction of whichever species is later-successional. This coexistence is summarized for different successional states in figure 7.14.

returning to our discussion of the transient formation of the closed canopy.

Consider an open patch with seeds of two very similar species. The one that is slightly earlier on the successional axis will close the canopy first, casting the second into shade. Though the species are very similar, the early-successional performs much better, as it has the advantage of direct sunlight. Meanwhile, the late-successional performs little better than the seedlings of the early successional. It will take a long time before the slightly higher density it can achieve by reduced death rate in the dark can make up for the setback it received in being closed out of the canopy. Under such conditions, the chief difference between species is only which one closes the canopy first. The early-successional strategy is simply to close the canopy first – it matters little by how much it wins. The late successional only wins out in the long run, adding up its higher den-
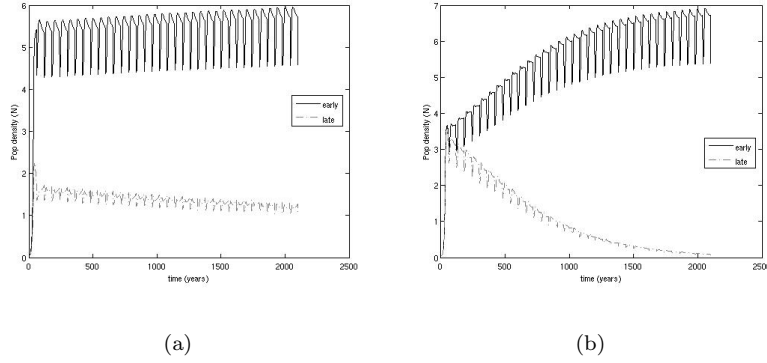
Figure 7.13: **More similar species face stronger competition**. When too similar, populations cannot coexist. The closer they are, the faster the extinction of the later-successional. (a): $\mu_D(1) = 0.15$, $\mu_D(2) = 0.1278$ (b): $\mu_D(1) = .1500$, $\mu_D(2) = .1499$

sities sustained by lower death rates which will eventually allow it to establish a higher canopy. Hence the late-successional niche shrinks and then vanishes, Figure 7.11.

Limiting similarity implies that any species can coexist with another that is either sufficiently earlier or sufficiently later on the successional axis. Exactly what corresponds to "sufficiently" depends exactly where on the successional axis we begin. To illustrate this, we construct a phase-diagram, Figure 7.14, where each axis represents the successional position μ_D of one of the species. As long as these species are sufficiently different, the forest exists in a region of coexistence. Two similar species result in a position very close to the line $y = x$, where coexistence becomes impossible. The size of the limiting similarity increases as we consider higher values of μ_D corresponding to earlier-successional species.

Maximum separation?

While coexistence is impossible for species that are too similar, species can be arbitrarily different and still coexist, provided the disturbance regime allows the
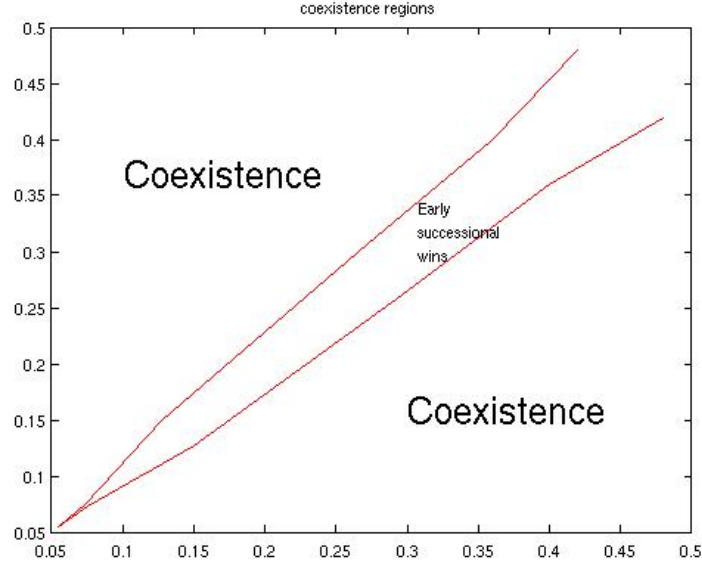
Figure 7.14: Coexistence Diagram

late successionals a niche. As we make the early successionals more and more early, for instance, the size of their niche shrinks and so does their equilibrium population value, as seen in the blue curves (run 2) of Figure 7.15(a). In this simulation the early successional (species 1) has the value $\mu_D(1) = 0.348$ and the late successional has the value $\mu_D = 0.055$. As these values are even farther apart then those in Figure 7.6, we see the equilibrium populations are also farther separated, with the late successionals doing much better than the early successionals.

However, as we make the early successional even earlier, $\mu_D(1) = .349$, keeping the late successional the same, we suddenly see a dramatic shift: the early-successional appears to dominate, Figure 7.15(a), red curves (run 1). A closer look shows that each population never completes its initial transient phase. Despite this surprising behavior, the result is simply a consequence of the initial conditions beginning with all open patches. This gives the early successionals a much greater advantage then they will ever have later. Starting with the same

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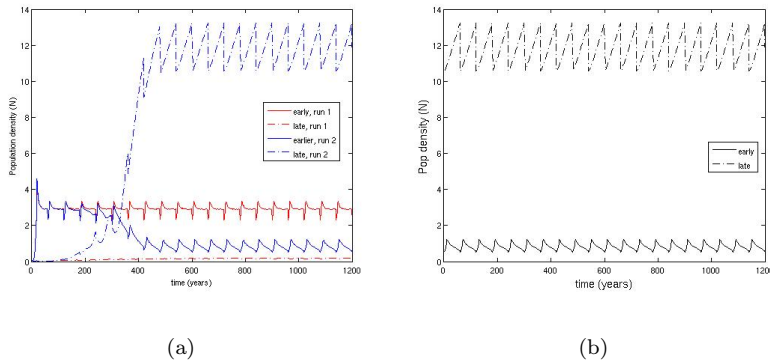
Figure 7.15: **Effects of initial conditions**. (a) Starting with all patches initially cleared results in a sudden dramatic switch in behavior of late and early successionals. (b) this behavior goes away when the forest is initialized with some closed patches.

value of $\mu_D = 0.349$ for the late successionals in a forest where some patches are closed results in approximately the same equilibrium as before, Figure 7.15(b). This example serves to illustrate not only how the initial conditions can dramatically influence the long-term dynamics, but also of some of the more subtle aspects that can arise in numerical analysis and seem somewhat mysterious or surprising until fully explored. With this in mind we turn to the more long-term consequences of limiting similarity.

7.5.2 Evolutionary Consequences

The concept of limiting similarity also enters when we turn from the ecological dynamics of forest populations to the evolutionary dynamics. Here the two populations competing represent a resident population and a rare mutant population, which will generally be quite similar to the resident species that created it. The question we ask is: can this rare mutant invade and take over the resident population? Unlike the cases of limiting similarity we have been considering, this time one of the species begins at much higher concentration than the other. If the rare mutant is later-successional, it has no hope of in-

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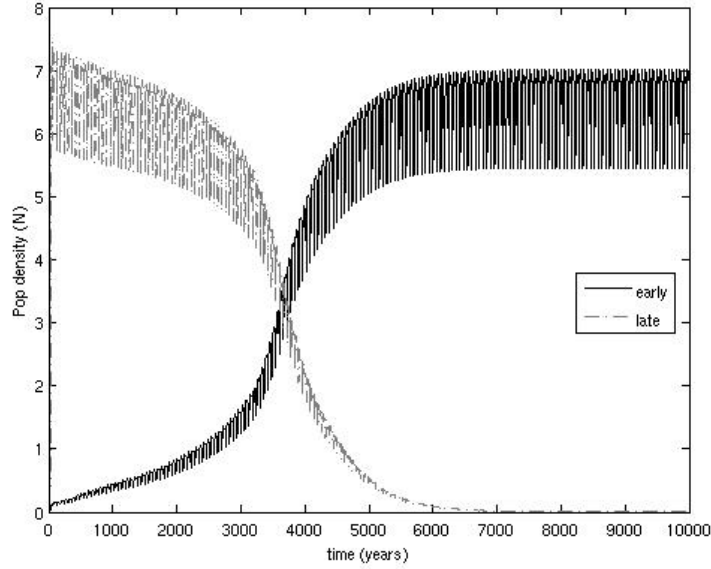
Figure 7.16: Rare early-successionals invade.

vading, since both numbers and limiting similarity work against it. If the rare mutant is slightly more early-successional than the resident, the dynamics take longer to play out, as seen in Figure 7.16.

The early successional population cannot close the canopy with its tiny starting population, and consequently the late successionals will be able to do so instead, hardly influenced at all by the presence of the early successionals. However, most of the early-successional cohorts born before the canopy closes will remain forever above the canopy, seeding a larger population than that in which they began. In this way the early successional eventually overcome the late successionals. In Figure 7.16, a few mutant seeds have a value $\mu_D(1) = .15$ in a clear patch where 99.9% of the seedlings are from the resident type, $\mu_D(2) = .14$. This falls outside the coexistence region (Figure 7.14), and eventually the early-successional type takes over. The evolutionary dynamics can be summarized in a plot of the resident trait value against the invader trait value for nearby, rare invaders, known as a pairwise invasibility plot in adaptive dynamics, Fig-

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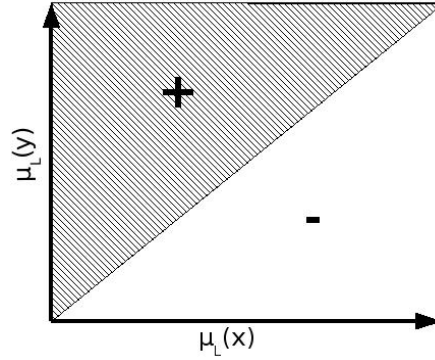
Figure 7.17: Pairwise invasibility plot

ure 7.17, see [5, 11]. The positive region above the line $y = x$ indicates that the invader must have a larger value μ_D to invade, regardless of the trait of the resident. Because the adaptive dynamics framework considers only nearby invaders, the ecological coexistence at a limiting similarity does not appear.

In a population where not all patches would live to the same maximum age, this process would result in differential rates of evolution that could eventually achieve the limiting similarity. This would result in species different enough to coexist, representing a mechanism of speciation not normally considered in the present allopatric speciation models or the framework of adaptive dynamics [5, 11].

Chapter 8

Conclusions

In this paper we have reviewed and applied the central concepts of what we refer to as the theory of Pacala forests. From a simple conception of the ideal tree that is motivated by detailed and successful individual based models, we have seen derived the macroscopic equations describing the overall behavior of the forest. This derivation has hinged on an approximation we call the Perfect Plasticity Assumption. We have then focused on how these equations can be used to understand interspecies interactions.

We formulated a simple invasion criterion from the macroscopic equations which serves as the basis for investigating interspecies competition. This leads us to three possible eigenmodes for the interaction: founder control, dominance, and coexistence. In the simple model the most likely mode among real tree populations is that of dominance. By adding in a constraint to the state space of possible trees, we have shown that dominance and this constraint together are sufficient to reproduce the successional dynamics that have formed the cornerstone of much of community-level forest theory.

We have shown that coexistence can result between an ideal tree species and a shrub that can reproduce in the dark, and determined necessary and sufficient criteria for it to do so. We have also shown that this coexistence interaction can exhibit founder control under certain circumstances, where the

presence or absence of coexistence is determined by which species first colonizes the plot. This represents an interesting complication to the simple coexistence and founder control possibilities previously treated.

Returning to the successional model, we have demonstrated that this too can exhibit coexistence of different species, provided the species differ sufficiently from each other in their trait-space. Because of this limiting similarity requirement, very similar species such as might be expected to result from mutational processes in evolution cannot coexist with their parental type. We have explored why the early successional species will always out-perform the late successional in cases of limiting similarity. Some other process, possibly not captured by the theory, will probably be responsible for a restoring force to generate late-successional types. The consequences of this observation merit further investigation.

Through our exploration of this theory we have only scratched the surface. Stephen Pacala's lab and collaborators are currently exploring many aspects that stem from this basic theory, ranging from a rigorous analysis of steady states and the exclusion of limit cycles in the formation of the canopy to consequences of the perfect plasticity assumption in more complicated models of forests as a way to remove spatial dependence [3, 22]. Many other aspects await further exploration, such as the evolutionary consequences of the interactions studied here.

This theory comes at an interesting time in theoretical ecology. Pioneering work in simple models by theoreticians such as Robert MacArthur and Robert May in the 1960s and 1970s gave way to skepticism and uncertainty about their connections to available data. [18]. While numerical simulation models started to bridge the gap, theory has emphasized the importance of spatial dependence [19] in these models, as well as other fundamentally challenging elements to treat mathematically such as stochasticity. The theory discussed represents a breakthrough allowing the return of a simple model while still retaining close ties to data and individual measurements that are better understood than community level measurements and models. It challenges the paradigm of spatial

dependence always being critical to an understanding of such complicated systems, but also shows that such dependence must nevertheless be dealt with carefully. The perfect plasticity assumption has been much more successful than previous mean-field approaches, representing the importance of the correct assumptions and simplifications in theory. In the end, it is these aspects that make this more than another simple model of trees; these aspects make it a theory.

Bibliography

[1] Tom Adams. Dynamics of temperate us forests: Monocultures and invasion dynamics. Unpublished manuscript, 2006.

[2] C. D. Canham, A. C. Finzi, S. W. Pacala, and D. H. Burbank. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*, 24:337–349, 1994.

[3] S. W. Pacala *et al*. Crown plasticity and large-scale forest dynamics: A new method of modeling vegetation dynamics. Unpublished manuscript, 2007.

[4] H. Von Foerster. Some remarks on changing populations. In Jr. F. Stohlman, editor, *The kinetics of cellular proliferation*, pages 382–407. Grune and Stratton, New York, 1959.

[5] S. Geritz, E. Kisdi, G. Meszena, and J Metz. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12:35–57, 1998.

[6] Alan Hastings. Transients: the key to long-term ecological understanding? *Trends in Ecology and Evolution*, 19(1):39–45, 2004.

[7] J. Huisman and F. J. Wessing. Biodiversity of plankton by species oscillations and chaos. *Nature*, 402:407–410, 1999.

[8] J. Huisman and F. J. Wessing. Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology*, 82:2682–2695, 2001.

[9] Charles Kittel and Herbert Kroemer. *Thermal Physics*. W. H. Freeman, New York, second edition, 1980.

[10] Simon Levin and R.T. Paine. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences, USA*, 71:2744–2747, 1974.

[11] J A J Metz, S A H Geritz, G Meszéna, F J A Jacobs, and J S van Heerwaarden. Adaptive dynamics: A geometrical study of the consequences of

nearly faithful reproduction. In S. J. van Strien and S. M. Verduyn Lunel, editors, *Stochastic and spatial structures of dynamical systems*, pages 183–231. KNAW Verhandelingen, Amsterdam, 1996.

[12] K. J. Mitchell. Simulation of growth of even-aged stands of white spruce. *Yale University Scholastic Forest Bulletin*, 75:1–48, 1969.

[13] K. J. Mitchell. Dynamics and simulated yield of douglas fir. *Forest Science Monographs*, 17:1–39, 1975.

[14] K. J. Mitchell. Distance dependent individual tree stand models. In K. M. Brown and F. R. Clarke, editors, *Forecasting forest stand dynamics: proceedings of the workshop, June 24,25*, pages 100–137. Lakehead University, Thunder Bay, Ontario, Canada, 1980.

[15] P.R. Moorcroft, G. C. Hurtt, and Stephen W. Pacala. A method for scaling vegetation dynamics: The ecosystem deomgraphy model. *Ecological Monographs*, 71:557–585, 2001.

[16] D. D. Munro. Forest growth models-a prognosis. In J. Fries, editor, *Growth Models for Tree and Stand Simulation*, pages 7–21. Royal Coll. For. Res., Stockholm, 1974.

[17] C. C. Muth and F. A. Bazzaz. Tree canopy displacement at forest gap edges. *Canadian Journal of Forest Research*, 32:247–254, 2002.

[18] S. W. Pacala, C. D. Canham, J. Saponara, R. K. Kobe, and E. Ribbens. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*, 66:1–43, 1996.

[19] Stephen W. Pacala and Douglas H. Deutschman. Details that matter: the spatial distribution of indvidual trees mantains forest ecosystem function. *Oikos*, 74:357–365, 1995.

[20] K. Polsson. British Columbia Ministry of Forests and Range. http://www.for.gov.bc.ca/hre/gymodels/TASS/features.htm.

[21] D. W. Purves, J. P. Caspersen, P. R. Moorcroft, G. C. Hurtt, and S. W. Pacala. Human-induced changes in US biogenic volatile organic compoind emissions: evidence from long-term forest inventory data. *Global change biology*, 10:1737–1755, 2004.

[22] D. W. Purves, J. W. Lichstein, and S. W. Pacala. Crown plasticity and competition for canopy space: a spatially implicit model parameterized for 250 north american tree species. Unpublished manuscript, 2007.

[23] Herman Shugart. *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models.* Springer-Verlag, New York, Berlin, Heidelberg, Tokyo, 1984.

Appendix A

Tree Data

The following data on growth and mortality taken from the USDA Forest Inventory database which contains measurements of several million individual trees. Estimates from Drew Purves, see [21] and [1].

English name	G_L	μ_L	$\mu_D(x,x)$	$G_D(x,x)$
Loblolly Pine	0.403	0.0123	0.098	0.072
Quaking Aspen	0.518	0.0142	0.085	0.050
Virginia Pine	0.538	0.0093	0.051	0.032
Water Oak	0.308	0.0112	0.057	0.134
Shortleaf Pine	0.365	0.0148	0.096	0.046
Southern Red Oak	0.338	0.0089	0.043	0.098
Sweetgum	0.315	0.0107	0.058	0.075
Yellow Popular	0.236	0.0192	0.134	0.118
Black Cherry	0.335	0.0079	0.058	0.062
Post Oak	0.391	0.0100	0.036	0.061
Red Maple	0.437	0.0054	0.027	0.041
Black Oak	0.576	0.0132	0.075	0.077
Paper Birch	0.283	0.0093	0.038	0.026
White Oak	0.383	0.0062	0.036	0.040
Red Oak	0.502	0.0076	0.054	0.043
White Ash	0.365	0.0104	0.058	0.080
Blackgum	0.490	0.0109	0.041	0.055
White Pine	0.572	0.0090	0.071	0.055
Chestnut Oak	0.373	0.0084	0.046	0.054
American Beech	0.433	0.0059	0.035	0.045
Sugar Maple	0.286	0.0048	0.025	0.029
Eastern Hemlock	0.420	0.0027	0.016	0.028

Appendix B

Simulation Code

Basic MATLAB®code used in simulations of Chapter 7 is provided on the following pages. To obtain this and related codes, email cboettig@princeton.edu.

```
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
%    _/                                                  _/              %
% _/_/_/_/  _/  _/_/    _/_/      _/_/     _/_/_/     _/_/_/ _/_/         %
%  _/      _/_/      _/_/_/_/  _/_/_/_/  _/ _/     _/ _/    _/     _/    %
% _/      _/         _/       _/         _/_  _/  _/     _/      _/     %
%  _/_/  _/          _/_/_/    _/_/_/  _/_/_/   _/  _/    _/    _/     %
%                                                                        %
%                                                                        %
%  Author: Carl Boettiger                                                %
%  Last modified: April 22, 2007                                         %
%                                                                        %
%  Description: Simulates the pacala forest according to the deterministic %
%  macroscopic equations for cohorts.                                    %
%                                                                        %
%  Written for MATLAB, 7.2                                               %
%                                                                        %
%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%

clear                    % clears workspace
Gens = 600;              % Number of years simulation runs
MaxAge = 60;             % Frequency at which patches are cut down
P = 5;                   % Number of patches
T = zeros(1, 3, P);      % Species 1 data:  cohort height, number; per patch
T2 = zeros(1, 3, P);     % Species 2 data (late successional)
G= @(u) u/5;             % Successional manifold
Gd = .008; Gd2 = .008;   % Dark-based growth rates for species
ul = .05; ul2 = .05;     % light-based mortality rates
Fl = 1;   Fl2 = 1;       % Fecundities
N_o = 1e-2; N_o2 = N_o;  % Starting population density
ud = .15; ud2= .075;     % dark-based mortality
Gl =G(ud); Gl2=G(ud2);   % Light-based growth (from successional manifold)
alpha = 4;               % diameter-crown scaling relation
Area = 1; A=Area/P;      % Area of total plot and of patches
dt=1; e = .0000001;      % Time constant and epsilon seperation for canopy closure

%Initial conditions
for i=1:P
    T(1,:,i) = [N_o, e, 1];
    T2(1,:,i) = [N_o2, e, 2];
end


%
J = zeros(Gens, 1);
N1 = zeros(Gens, 1); N2 = zeros(Gens, 1); %history of pop densities by species
zstar_of_t = zeros(Gens, P); % history of canopy height by patch
seedlings = zeros(1, P); seedlings2 = zeros(1, P); %seedlings produced per patch

death = 0; %counter for which patch to level next

%Begin simulation
for gen=1:Gens;
    if rem(gen/Gens*100, 1) == 0; fprintf('='); end %Print a progress bar
    for i = 1:P
        %Determine z_star
        heightorder = sortrows([T(:, :, i); T2(:,:,i)], 2);

        areas = alpha * heightorder(:,2).^2 .* heightorder(:, 1); %A*N
        j = 0; cum_area = 0; tallest = length(areas);
        if  sum(areas) > A;
            while cum_area < A
                cum_area = areas(tallest-j)+cum_area;
                j = j+1;
            end
        end
        J(gen) = j;
```

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```
        if j == 0; z_star = 0; end %Canopy not closed
        if j ~= 0; %Canopy closed
            %z_star is the height of the lowest trees in canopy (tallest - (j-1) )
            z_star =  heightorder(tallest-j+1, 2);
            %Split canopy
            Over = sum(areas(tallest-j+1:tallest) ); %area when borderline cohort is included
            if j > 1;
                CanopyArea = sum(areas(tallest-j+2:tallest));  %Area of cohorts fitting completely
            end;
            if j == 1, %No cohorts fit completely
                CanopyArea = 0;
            end;
            N_tallest = (A-CanopyArea)/(alpha*z_star^2); %N in split cohort needed to close canopy
            N_remaining = heightorder(tallest-j+1,1)-N_tallest;
            species_split = heightorder(tallest-j+1, 3);
            ss(i) = species_split;
            heightorder(tallest-j+1,:) =  [N_tallest, z_star+e, species_split]; %just enough move
into canopy to close, this is what remains behind
            heightorder = sortrows([heightorder; [N_remaining, z_star, species_split] ]);
            species1 = (heightorder(:,3) == 1); species2 = (heightorder(:,3) == 2);
            l = size(T(:,:,i), 1)+floor(1/species_split); %Expand if this species split and this is
the first patch
            T(1:l,:, i)  = heightorder(species1, :); %Tack on remaining at their original height
            T(:, 3, :) = 1;
            l2(i) = size(T2, 1) +floor(species_split/2);
            T2(1:l2(i),:, i)  = heightorder(species2, :); %Tack on remaining at their original
height
            T2(:, 3, :) = 2;

            z_star = z_star+e; %others are no longer in canopy

        end

        %Define Canopy
        zstar_of_t(gen, i) = z_star; %recording canopy height by patch
        canopy =  T(:, 2, i) >= z_star;
        understory = T(:, 2, i) < z_star;
        canopy2 =  T2(:, 2, i) >= z_star;
        understory2 = T2(:, 2, i) < z_star;


        %Growth
        T(understory, 2, i) = T(understory, 2, i) + dt*Gd; %Constant growth in understory
        T(canopy, 2, i) = T(canopy, 2, i) + dt*Gl; %constant Growth in canopy
        T2(understory2, 2, i) = T2(understory2, 2, i) + dt*Gd2; %Constant growth in understory
        T2(canopy2, 2, i) = T2(canopy2, 2, i) + dt*Gl2; %constant Growth in canopy

        %Death
        T(understory, 1, i) = T(understory, 1, i) - dt*ud*T(understory, 1, i); %Death in understory
        T(canopy, 1, i) = T(canopy, 1, i) - dt*ul*T(canopy, 1, i); %Death in canopy
        T2(understory2, 1, i) = T2(understory2, 1, i) - dt*ud2*T2(understory2, 1, i); %Death in
understory
        T2(canopy2, 1, i) = T2(canopy2, 1, i) - dt*ul2*T2(canopy2, 1, i); %Death in canopy

        % Max Age
        if rem(i+death, P) == 0 && gen == MaxAge*(death+1);
            death = death+1;
            T(:, 1:2, i) = 0;
            T2(:, 1:2, i) = 0;
        end


        % Fecundity
        %F * area * number = seedlings from plot entered into pool
        seedlings(i) = (dt*Fl*alpha*T(canopy, 2, i).^2 )' * T(canopy, 1, i);
```

```
        seedlings2(i) = (dt*Fl2*alpha*T2(canopy2, 2, i).^2 )' * T2(canopy2, 1, i);

    end   %LOOP BACK OVER PATCHES

    %Dispersal
    No = sum(seedlings)/P;  %Put seedlings in age 0, moving others up in age
    No2 = sum(seedlings2)/P;  %Put seedlings in age 0, moving others up in age

    %Add newly born cohort
    for i = 1:P;
        l = size(T(:,:,i), 1)+1;  %increase matrix only for the first patch, since all done
together
        T(1:l, :, i) = [ [No, e, 1]; T(1:l-1, :, i)];
        T(:, 3, :) = 1;
        l = size(T2(:,:,i), 1)+1;
        T2(1:l, :, i) = [ [No2, e, 2]; T2(1:l-1, :, i)];
        T2(:, 3, :) = 2;
        %Record population densities
        N1(gen) = N1(gen) + sum( T(:,1,i) );
        N2(gen) = N2(gen) + sum( T2(:,1,i) );
    end;

end;
figure(1);
subplot(2,1,1);
hold on; plot(zstar_of_t(:,1), 'k'); xlabel('time (years)'); ylabel('z star');
subplot(2,1,2);
plot(1:Gens, N1, 'k'); hold on; plot(1:Gens, N2, 'k-.'); legend('early', 'late', 'Location',
'Best'); xlabel('time (years)'); ylabel('Pop density (N)');
```

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