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Modeling ecological disturbances in the Southeastern United States

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MODELING ECOLOGICAL DISTURBANCES IN THE SOUTHEASTERN UNITED STATES

by

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"*To have the ultimate even if idealistic objective of fusing the shattered fragments [of ecosystem science] into the original unity is of great scientific and practical importance; practical because so many problems in nature are problems of ecosystem rather than of soil, animals, or plants, and scientific because it is our primary business to understand.*"

- Alex S. Watt, **Pattern and process in the plant community**

"The scope and complexity of some modern land surface models have reached the point that no individuals are able to comprehensively understand all facets of any one model"

- Rosie Fisher & Charles Koven, **Perspectives on the Future of Land Surface Models and the Challenges of Representing Complex Terrestrial Systems**

To my family.

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MODELING ECOLOGICAL DISTURBANCES IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Society requires better insights into how disturbances will alter the global carbon cycle. Ecosystem models help us understand the carbon cycle and make predictions about how the terrestrial land sink will change under future climate regimes. Disturbances drive ecosystem cycling, but modeling disturbances has unique challenges, particularly in incorporating heterogeneity and parameter uncertainty. In this dissertation, I explore two questions. 1) How can we capture disturbance ecology in models?, which I explore in my first and second chapters, and 2) How can we use those models to make projections for the Southeastern US?, which I explore in my third and fourth chapters.

Both my first and second chapters point to the practical trade-offs in model structure and realism. In my first chapter, I found that representing spatially implicit contagious disturbances in terms of shape and frequency accurately captured structural changes over time and separated the disturbance regimes of different regions. Representing spatially implicit disturbances in terms of shape and frequency sacrificed the specificity of a space-based approach but may be more computationally efficient. In my second chapter, I developed a framework for calibrating models based on an iterative

cycle between uncertainty analysis and literature synthesis, targeted field campaigns, and statistical constraint. I found that targeted field work and statistical constraint reduced parameter uncertainty until structural uncertainty began to dominate.

Models that capture disturbance dynamics can help us anticipate effects of global change factors like climate change and invasive species. In my third chapter, I found that elevated temperatures reduce cogongrass biomass, and that cogongrass facilitates pine dominance over oaks in a mixed pine-oak stand. This suggests that cogongrass mediates inter-species competition at an ecosystem scale. Prescribed burns are a management technique used to suppress cogongrass and has an add-on benefit of reducing tick populations. However, climate change may threaten how frequently prescribed fires can be safely deployed. In my fourth chapter, I found that tick populations are most sensitive to leaf litter and humidity, which allows for management strategies as an alternative to prescribed burns.

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LIST OF ABBREVIATIONS

AFB	Air Force Base
BARS	Bivens Arm Research Site
BAAD	Biomass And Allometry Database
C3	C_3 metabolic pathway
C4	C_4 metabolic pathway, Hatch-Slack photosynthetic pathway
CI	Confidence Interval
CM3	Coupled Physical Model
CO2, CO_2	Carbon Dioxide
CRPS	Continuous Ranked Probability Score
CV	Coefficient of Variation
DBH	Diameter at Breast Height
DoD	Department of Defense
DGVM	Dynamic Global Vegetation Model
DST	Decision Support Tool
DVM	Dynamic Vegetation Model
ED HYDRO	Ecosystem Demography Model Version 2.2 with Hydraulic Traits
ED2	Ecosystem Demography Model Version 2.2
ERA5	Fifth generation ECMWF (European Center for Medium-Range Weather Forecasts) atmospheric Reanalysis
FARSITE	Fire Area Simulator

FFI	FEAT/FIREMON Integrated
FRI	Fire Return Interval
Ft.	Fort
GIS	Geographic Information System
ha	hectare acres
IPCC	Intergovernmental Panel on Climate Change
IRB	Institutional Review Board (IRB)
LAI	Leaf Area Index
LI-COR 6400	Portable Photosynthesis System
LANDIS-II	Landscape Disturbance Simulator (II)
LANDFIRE	Landscape Fire and Resource Management Planning Tools Project
LANDSAT	Land Remote-Sensing Satellite
MODIS	Moderate Resolution Imaging Spectoradiometer
N	Sample size
NPP	Net Primary Productivity
PEcAn	Predictive Ecosystem Analyzer
PFT	Plant Functional Type
PINEMAP	Pine Integrated Network: Education, Mitigation and Adaptation Project
QGIS	Quantum Geographic Information System
RCP, RCP8.5	Radiative Carbon Pathway, Radiative Carbon Pathway Scenario 8.5

SD	Standard Deviation
SERDP	Strategic Environmental Research and Development Program
SLA	Specific Leaf Area
SPITFIRE	Spread and Intensity of Fire model
SSURGO	Soil Survey Geographic Database
STARI	Southern-Tick Associated Rash Illness
TBD	Tick Borne Disease(s)
US	United States
USA	United State of America
Vcmax, Vmax	Maximum rate of carboxylation, pathway dependent

INTRODUCTION

Definition of Southeastern United States

In this dissertation, I refer to the Southeastern United States as a region that roughly ecompasses the states of North Carolina, South Carolina, Georgia, Florida, Alabama and Mississippi. State-borders do not necessarily map onto ecological systems. Here, when we generalize to the "Southeast" we refer to the southeastern plains that contain areas of the piedmont, flat plains, and coastal plains (McMahon et al., 2001). We exclude the Appalachian mountains, subtropical forests like the Everglades, and tidal estuaries and marshes. The soils of Southeast can range from xeric sandhills to poorly drained flatwoods. These areas are known for open-canopy pine forests, and mixed pine-hardwood forests, with understory vegetation like bluestem grasses, wiregrass, and saw-palmetto (Jose et al., 2006; Allan et al., 2021).

A History of Anthropogenically Mediated Disturbances Across the Southeast

Humans have controlled the disturbance regime of the Southeast for hundreds of years, usually through fire. Fire has been a part of the southeastern landscape from before European settlement. In the 1500's longleaf pine was the dominant tree species, and its dominance was maintained by a combination of lightning ignition, and girdle-and-burn agriculture practiced by native populations (Carroll et al., 2002; Delcourt & Delcourt, 2004; Mitchell et al., 2014; Rother et al., 2020). The southeastern US hosted a native population of ~1.5-2 million that used fire to maintain an open savanna system for hunting and agriculture. By the 1700's European settlement and disease reduced native populations by 90-95% (Carroll et al., 2002). Use of fire-management declined, and forests became denser and less open (Carroll et al., 2002).

Concurrently, forests along the east coast were being settled, developed, and transitioned to agricultural use, aided by slave labor. By 1860 47% of Virginian forest was cleared for growing cotton and tobacco (Fox et al., 2007). From the 1600's through the colonial period, longleaf pine resin was used for the production of naval stores: turpentine, tar, rosin, and pitch (Fox et al., 2007; Frost, 1993; Vollmers, 2003). Much of the 92 million acres of longleaf pine was consumed by Southeast's growing timber industry, and replaced with faster-growing species of pine, like loblolly pine and slash pine.

Today, the Southeast supplies most of the timber used by the United States, and less than 4% of original longleaf pine archeage remains (Allen et al., 2005; Fox et al., 2007; Kirkman et al., 2017). This loss has led to conservation efforts from diverse groups to restore longleaf pine, including Department of Defense bases. Prescribed burns are a central tool for this restoration (Addington et al., 2015; Aschenbach et al., 2010; Holland et al., 2019; Martin, 2019; McIntyre et al., 2022). The southeast is subject to frequent low-intensity burns that are anthropogenically mediated. People and fire are so tightly coupled in the southeast that satellites tracking fires saw a dropoff of fire activity during the Covid-19 2020 shutdown (Voiland, A., 2020). However, the season when prescribed burns can be safely lit may be narrowing, as climate change raises temperatures and lengthens droughts (Flannigan et al., 2009; Mitchell et al., 2014; Platt et al., 2015).

Climate change, and society's response to it, will undoubtedly influence future disturbance regimes across the Southeast.

Cogongrass in the Southeastern United States

Invasive species can negatively affect ecosystem biodiversity and functioning (Vilà et al., 2011; Vitousek et al., 1996). Longleaf pine savannas have some of the highest species richness outside of the tropics (Hiatt & Flory, 2020; Jose et al., 2006). *Imperata cylindrica*, (cogongrass) is an invasive perennial C4 grass listed as a federal noxious weed (MacDonald, 2004; Noxious Weed Regulations, 2022). After two 1900's introductions into the United States, cogongrass has spread to 10 southeastern states, including remaining longleaf forests (EDDMapS, 2022; Estrada & Flory, 2015). In cogongrass' native ranges in Africa and Asia, cogongrass is used in traditional medicine, and has been studied for its potential anti-cancer treatment potential, and used for aggregating heavy metals in contaminated sites (Jung & Shin, 2021; Shaltout et al., 2016).

In the Southeastern US, when cogongrass invades it forms a dense monoculture with a thick layer of thatch that shades-out competing understory species (Alba et al., 2017; Fahey et al., 2018). Cogongrass is a tall grass that grows up to a meter and a half high, forms thick rhizomatous root networks, and can reproduce from seed or small sections of rhizome (Estrada et al., 2016). Cogognrass spreads quickly in disturbed areas and along transportation networks (Estrada et al., 2017; Yager et al., 2009). Cogongrass is managed with a combination of herbicides and prescribed fire (Emery et al., 2013;

Lucardi et al., 2020). Cogongrass has been shown to reduce understory species diversity in longleaf pine stands (Brewer, 2008).

Cogongrass' negative effect on southeastern US biodiversity is clear. Cogongrass' other potential effects on the landscape are less clear; few experiments have looked at how cogongrass affects ecosystem cycling, or ecosystem structure. In 2-4 year experiments, cogongrass has been shown to reduce longleaf seedling survival and primary productivity (Daneshgar et al., 2008; NeSmith et al., 2018). If cogongrass suppresses saplings, then over 10-100 year scales, cogongrass could change ecosystem structure. Cogongrass's effects on a landscape may be limited to changing biodiversity: but cogongrass establishment could have wider-ranging consequences in how the southeastern US forests function.

Another open question is if cogongrass' unique combination of traits make cogongrass a successful invader. Cogognrass is just one of many introduced grasses on the southeastern landscape, and not all have spread as extensively (Overholt & Franck, 2017). Knowing cogongrass' traits would guide comparisons to other grasses, and would allow us to better anticipate how cogongrass could affect the landscape.

Modeling Ecological Disturbances and the role of Dynamic Vegetation Models

Disturbances have enormous effects on forest structure and biogeochemical fluxes (Bormann & Likens, 1979). The need to predict disturbance effects has never been higher. Ecosystem disturbances could change how ecosystems store carbon, and could change what is presently a terrestrial land carbon sink into a source of carbon (IPCC, 2014). Earth system models are key tools to predict future effects on ecosystems. However, contrasting philosophies govern ecological models. In Chapters 1-3 of this dissertation, I focus on “process based” models, also called “mechanistic models” or “computational models” (Bonan, 2008). This class of models explicitly represents the components of a system it predicts. This contrasts to “empirical” models, also called “statistical”, “regression” or “machine-learning” models. Empirical models use statistical relationships between variables and observations to make predictions (Chapter 4). Empirical models can be faster to implement than process-based models and can identify novel processes, but can also make predictions that are not physically interpretable, or find associations that do not persist through time (Roundy, 2015). In ecosystem science, empirical and process-based models are both widely used for carbon cycle quantification and prediction (Dai & Fung, 1993; Xiao et al., 2019). Process-based models can be particularly useful for modeling disturbances, because they can simulate systems under novel conditions, and can test hypotheses inherent in model structures (Dietze, 2017; Medlyn et al., 2015).

In Chapters 1-3, I focus on a specific class of process model called a “dynamic vegetation model” (Fisher & Koven, 2020). Dynamic vegetation models grew out of a need to incorporate vegetation into models of the earth-system, and can represent plants in terms of their physiology. The level of detail can vary – plants can be abstracted to climate-grid-scale level or simulated individually, as in forest gap models and individual-based models (Fisher et al., 2018). The model I use, The Ecosystem Demography 2 model, is a cohort-based model, which allows for competition without representing individual plants (Moorcroft et al., 2001). Dynamic vegetation models are appropriate for disturbance modeling because they capture processes that mediate disturbance effects on an ecosystem; like succession, resource competition, regrowth, and climate effects (Fisher et al., 2018).

Many aspects of ecological disturbances have only been incorporated into earth system models in the last two decades. Dynamic vegetation and carbon cycles were incorporated in the 2000's, and the effects of land-use change, urbanization, and agriculture in the 2010's. Today, challenges to representing disturbances include representing heterogeneity, and understanding parametric dynamics in models (Fisher & Koven, 2020). Representing heterogeneity – or representing ecosystem processes and features that cannot be aggregated vertically (ie canopies, atmospheric profiles) or horizontally (ie urban development, topography, lakes), is a challenge for land surface models. Heterogeneity happening at small scales can have large effects. Models need to represent heterogeneity with enough detail to simulate how they mediate environmental conditions, and then apply that information to the scale of interest. Disturbances pose an additional challenge because they can create and respond to heterogeneity: forest structures can change how a wildfire spreads, and then the wildfire scare may create new forest structures. We need techniques to resolve heterogeneity on disturbance-scales to capture the effects of disturbances.

Model parameters - or the values describing a system incorporated into model simulations - can be difficult to set. Communities modeling novel systems, or systems that are underrepresented in the literature, may have to use uncertain parameters to describe the system, and produce uncertain predictions. This is an acute issue for disturbance modeling because disturbances introduce novelty into a system. Typically, including more data into estimates of model parameters reduces uncertainty, but it can be difficult or impossible to incorporate new data. We need tools that help us understand parameter uncertainty and flexible options to systematically reduce parameter uncertainty.

Structure of this Dissertation

This dissertation is organized around two questions: “How can we capture disturbance ecology in models?” and “How can we use those models to make projections for the Southeastern US?”. Under my first question, my first and second chapters struggle with two issues in disturbance modeling - heterogeneity and parameter uncertainty. In my first chapter, I explore if we can simulate disturbances and the heterogeneity of a landscape in a way simple enough to be incorporated into a dynamic vegetation model. In my second chapter, I introduce a workflow for systematically reducing parameter uncertainty. In my third chapter, I look at how cogongrass invasions affect pine-oak savannas, and how it may change under climate change. Finally, in my fourth chapter, I look at how prescribed burning, climate change, and vegetation interact to control tick populations.

CHAPTER ONE: SCALING CONTAGIOUS DISTURBANCE: A SPATIALLY-IMPLICIT DYNAMIC MODEL

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Abstract

Spatial processes often drive ecosystem processes, biogeochemical cycles, and land-atmosphere feedbacks at the landscape-scale. Climate-sensitive disturbances such as fire, land-use change, pests, and pathogens, often spread contagiously across the landscape. While the climate-change implications of these factors are often discussed, none of these processes are incorporated into earth system models as contagious disturbances because they occur at a spatial scale well below model resolution. Here we present a novel second-order spatially-implicit scheme for representing the size distribution of spatially contagious disturbances. We demonstrate a means for dynamically evolving spatial adjacency through time in response to disturbance. Our scheme shows that contagious disturbance types can be characterized as a function of their size and edge-to-interior ratio. This emergent disturbance characterization allows for description of disturbance across scales. This scheme lays the ground for a more realistic global-scale exploration of how spatially-complex disturbances interact with climate-change drivers, and forwards theoretical understanding of spatial and temporal evolution of disturbance.

1. Introduction

Disturbances pose a fundamental scaling problem because disturbances both create and respond to spatial heterogeneity in the environment (Turner, 2010). Seminal theoretical and experimental work in scaling explored how disturbances introduce heterogeneity in ecosystem at varying scales: patch-dynamics of Pickett and White, the “shifting-mosaic” of Bormann and Likens, and Turner’s landscape equilibrium all attempt to resolve the issue of how disturbances on a range of scales interact to create ecosystem-level patterns (Bormann & Likens, 1979; Turner, Romme, & Gardner, 1997; White & Pickett, 1985).

Among disturbance types, contagious disturbances such as fire are particularly important ecologically as they are not only large in total area, but can have large impacts on spatial pattern, process, and heterogeneity. Contagious disturbances mediate biogeochemical fluxes, are drivers of landscape ecology, and contribute uncertainty to understanding consequences of anthropogenic climate change. At the end of the 20th century on average 608 Mha burned per year globally, affecting nutrient cycles, community composition, and altering local energy budgets (Dannenmann et al., 2018; Marlon et al., 2012; Mouillot & Field, 2005; Parks et al., 2016). Anthropogenic land-use-change also often follows a contagious pattern, beyond its total area and carbon impact, it is a major driver of habitat fragmentation, with 75% of forests globally located < 1km from an edge (Haddad et al., 2015). Forest insects and pathogens also frequently spread as a spatially contagious process and impact a greater area in North America than fire and forestry combined (Hicke et al., 2012). Similarly, the spread of invasive species can alter nutrient cycling and change ecosystem composition by outcompeting local populations (Vitousek et al., 1996). Many of the disturbances listed here interact with one another, for example invasive plants and forest pests can alter the flammability of an ecosystem (D’Antonio & Vitousek, 1992), while land use creates breaks that alter fire regimes and other contagious disturbances (Carmo, Moreira, Casimiro, & Vaz, 2011). In addition, most contagious disturbances are sensitive to climate - suggesting that anthropogenic climate change could cause novel behavior or interactions (Harris, Remenyi, Williamson, Bindoff, & Bowman, 2016; Mitchell et al., 2014a). Contagious disturbances are a central component of understanding an ecosystem, and to understand how ecosystems will behave in the future we need an understanding of how to predict contagious disturbances.

Contagious disturbances pose a particular challenge to scaling as they not only create and respond to heterogeneity at a local scale, but they also respond to heterogeneity in neighboring locations, and in the process create larger scale spatial pattern. To date, most efforts at modeling contagious disturbance have focused on spatially-explicit simulations (Seidl et al., 2011). In such models, rules are implemented that govern when and where a disturbance is initiated and whether it spreads contagiously to adjacent locations. Such rules are easy to formulate, typically invoking properties of the disturbance (e.g. fire intensity), adjacent locations (e.g. fuel load), and some degree of stochasticity, and are well known for their ability to generate complex spatial pattern and temporal dynamics (Keane et al., 2004; Wolfram, 2017). While such simulation models have provided considerable insight into contagious disturbance, they have two critical limitations when it comes to scaling up disturbance. First, there are basic computational challenges to simulation at large scales. While contagious disturbance processes are common in landscape-scale models, they are absent from dynamic global vegetation models (DGVMs) because it is not currently possibly to run global models at the fine spatial resolution required to represent contagion, which has impacts on estimates of the carbon sink (Melton & Arora, 2014). Second, simulation models don't provide the same general theoretical insight found in analytical models.

The goal of this paper is to explore the development of a general, analytically-tractable, and spatially-implicit approach to modeling the scaling of contagious disturbance. This framework is general in the sense that it aims to capture a wide range of different disturbance types (including non-spreading disturbance as a special case) to provide a common framework for understanding their emergent scaling behaviors. It is spatially-implicit because we make the simplifying assumption that, when viewed from a large scale, the exact spatial locations of disturbances do not matter but rather their aggregate statistical properties. In moving up scales we are not focusing on the spread of individual disturbance events, but the broader distribution of disturbance sizes and shapes that characterizes a disturbance regime spatially.

In developing this approach, we separate the problem of spatial scaling into two components, heterogeneity and spatial arrangement. Problems characterized by spatial heterogeneity are conceptually easier to scale. If an ecological process is only responding to its local environment, then even if those responses are nonlinear, the emergent "whole" behavior at a larger scale is just the sum of all the local "parts". In this case spatial arrangement doesn't matter, just the frequency distribution of the different environmental conditions. This approach has been applied successfully to the upscaling of many key ecological processes, such as carbon and water fluxes, even when the heterogeneity of the process (e.g. distribution of vegetation stand ages) is evolving dynamically through time (Fisher et al., 2018; Moorcroft, Hurtt, & Pacala, 2001). In practice such approaches are typically modeled discretely, e.g. a finite number of age classes each with some fractional area on the landscape.

Ecological processes that depend on spatial arrangement are conceptually harder to scale, however we argue that not all spatial arrangement problems have to be spatially-explicit, as many only depend on *relative* spatial context. Herein we take the approach of focusing specifically on approximating the well-established landscape ecology concept of spatial adjacency, which is a key driver of many spatial processes. Similar to how we represent heterogeneity with a probability distribution, at a large scale we can likewise represent spatial adjacency with the probability that any two conditions will be adjacent to each other. And like with heterogeneity, this will typically be modeled discretely, in this case with a spatial adjacency matrix. If a vector of fractional abundances provides a first-order approximation of spatial variability, the combination of a vector of abundances and matrix of adjacencies thus provides a second-order model. Not all spatial processes can be approximated via adjacency, as sometimes higher-order shape and arrangement does matter, but we posit that this is a useful framework for considering contagious disturbance and spatial processes of adjacency or of dynamically evolving adjacency.

For processes where the heterogeneity in the landscape is fixed on ecological timescales (e.g. elevation, soils), fractional area and adjacency are likewise fixed and can be precomputed (e.g. in GIS). Spatial processes, such as movement across a landscape, can then be approximated based on adjacency (e.g. what's the probability of moving from class A to class C directly vs indirectly via B). The challenge with contagious disturbance arises because it not only responds to heterogeneity and adjacency, but it also alters both dynamically. Therefore, a successful approach to scaling contagious disturbance requires a means of updating both fractional areas and adjacencies in response to disturbances.

This paper examines three questions: First, how do we take advantage of adjacency to approximate spatial disturbance spread? Second, given that disturbance, how do we update the fractional areas and adjacencies (i.e. how do we make it dynamic)? Finally, given our ability to simulate disturbances in a spatially implicit manner, how does this theory compare to observations? Specifically, our spatially implicit disturbances model suggests that different disturbance regimes can be characterized by two metrics: (1) the size distribution of disturbances; and (2) the relationship between disturbance size and disturbance interior adjacency scaling. These two metrics were examined for different disturbance types and ecoregions for two contrasting locations, the states of Florida and Oregon, USA. We hypothesize: (1) that our metrics will distinguish between different disturbance types and different states; (2) our metrics will reflect the nested structure of the ecoregions, with ecoregions from the same state being more similar than comparisons across states. While many different configuration-based landscape metrics and indices exist and are used in management, evaluation of landscape change, and habitat analysis (Uuemaa, Antrop, & Marja, 2009), the strength of our metrics is that they are derived directly from a theoretical understanding of contagious disturbances, thus giving us an ability to predict how changes in either metric will translate into changes in future ecosystem processes, heterogeneity, and adjacency in both the short and long term.

2. Methods

2.1 Simulating Disturbance Spread

Before diving into how to approximate spatially-explicit models of contagious disturbance analytically, we first illustrate simple versions of these spatial models so as to clarify their key features. Arguably the simplest disturbance process is gap dynamics (e.g. mortality of individual canopy trees), which is often approximated as a stochastic process disturbing individual patches on a grid at random. If we simulate this process through time (Figure 1.1 top left), keeping track of the age of each patch (time since disturbance) and running the simulation until the stand age distribution reaches steady state, we see that this age distribution converges to a geometric (discrete exponential) distribution (Figure 1.1 mid left). Furthermore, since disturbance is random and doesn't depend on patch age or neighborhood, the spatial neighborhood of each patch is just a sample from this same geometric distribution. This can be shown by calculating an adjacency matrix, which tallies the probability that one age class is adjacent to another (Figure 1.1 bottom left).

Compare this gap dynamics model with a simple model of a contagious disturbance (e.g. fire, insects, land use), which is described first by a probability of disturbance initiation and second, conditional on initiation, a probability of spread to adjacent patches. In more complex versions of such models both these probabilities can vary with age and environmental conditions (Mann, Scott Rupp, Olson, & Duffy, 2012).

However, even in the simplest case, when both probabilities are fixed and disturbances are random, the model generates much more complex spatial patterns characterized by larger, contiguous disturbance patches (Figure 1.1 right). As before, the overall stand age distribution remains geometric (Figure 1.1 mid right), however the pattern of spatial adjacency is more complicated (Figure 1.1 bottom right). First, most newly disturbed patches (age class 0) are adjacent to other newly disturbed patches (60% in the example simulation). As we move along the diagonal of the adjacency matrix, patches in a given age class continue to remain adjacent to other patches of the same age through time (i.e. larger even-aged patches remain), but this adjacency decays geometrically as new disturbances chip away at even aged patches, leaving them adjacent to younger disturbances. Above the diagonal we see a pattern similar to gap dynamics, where each age class has some probability of being adjacent to newly disturbed patches (which in this simple class is equal for all age classes) and then this adjacency decays equally for each age class. Matrix elements that are below the diagonal, which represent the probability that a patch is adjacent to a patch older than it, age classes likewise decay geometrically, but each age class is along a different curve because of the different cumulative probabilities. In other words, because the elements along the diagonal differ for each age class, and because the cumulative probabilities must sum to 1, the remaining cumulative probability is different for each age class.

Armed with a basic understanding for the patterns spatially explicit simulations can produce, let’s next consider how to develop a spatially implicit model to approximate the spread of contagious disturbance. As in the simulation, let's start by assuming an age or stage structured approach with n discrete age classes. Next, let's assume that the disturbance has some initiation probability, p_0, that is a vector with the same length as the number of age classes, n. In other words, the initiation probability could vary by age class. In this general derivation, our timestep or "t" represents any discrete timestep (annually, monthly, etc). Because disturbance is simulated discretely in time, the probabilities map to that timestep and can be time varying (e.g. functions of environmental conditions) without loss of generality.

Given this initiation probability, the initial disturbance area (for disturbances with size = 1 patch) is given by $I_1 = p_0 \cdot a$, where a is a vector of the fractional areas of each age class and ∘ denotes element-wise (Hadamard) multiplication. Next, let's assume that we know the current adjacency matrix, A_t, that describes the probability that a patch of a given age/stage class is adjacent to patches of the same or other age/stage classes at time t. Individual elements within A_t are probabilities, and thus must be between 0 and 1, and all patches must be adjacent to some other patch so each row represents a discrete probability distribution whose elements must sum to 1. However, A_t does not need to be symmetric (e.g. Figure 1.1 bottom right). In practice the specification of these probabilities will depend on the spatial grain of the analysis (i.e. patch size) but this doesn't affect the mathematical derivation. Also, in practice the initial adjacency, A_0, would need to be derived from some sort of empirical GIS analysis or some steady-state assumption but this does not affect the derivation. Finally, except when deriving the dynamics of updating A_{t+1} given A_t we will drop the time subscript for simplicity, as we are not considering changes in A during a disturbance event.

To allow contagious disturbances to spread we also need to introduce a probability of spread, p_s, given initiation, which similar to I_1 is grain and timestep dependent and could be time varying. In the general case we will assume p_s is a $n \times n$ matrix describing the probability of spreading from one class into any other class, but in practice p_s could be a scalar or set to only vary by row (dependent on the class the disturbance is spreading from) or column (dependent on the class being spread into). It should also be noted that p_s does not need to be symmetric – the probability of spreading from one patch type into another (e.g. new regeneration into old-growth) need not be the same as the probability of spreading back. Given this framework we can next derive the probability of a disturbance spreading to a second patch as depending on initiation, probability of spread, and adjacency:

$$I_2 = (p_s \circ A)I_1$$

Furthermore, we can see that $I_3 = (p_s \circ A)I_2$ and so on leading to the more general recursion describing the probability of spreading to h+1 patches given that the disturbance has already spread to h patches.

$$I_{h+1} = (p_s \circ A)I_h = SI_h = S^h I_1$$

Where $S = p_s A$. Note that in this derivation the matrix A is fixed as it describes the adjacencies among the undisturbed age classes; the ongoing disturbance is not an explicit row/column in A and thus spread only occurs outward into undisturbed area and there's no need to account for the spread of a disturbance backward into patches that were just disturbed. We also make the simplifying assumption that we are operating on a sufficiently larger scale that no single disturbance event changes the adjacency among undisturbed patches enough to invalidate this approximation (and require updating A during a disturbance event). That said, adjacency does need to be updated on our coarser model timestep as what we generally see is small year-to-year changes that gradually accumulate to appreciable landscape-scale adjacency shifts over longer time (e.g. decades).

Accumulating the spread over different disturbance sizes leads to to an overall disturbance rate of

$$D = \sum_{h=1}^{\infty} I_h$$

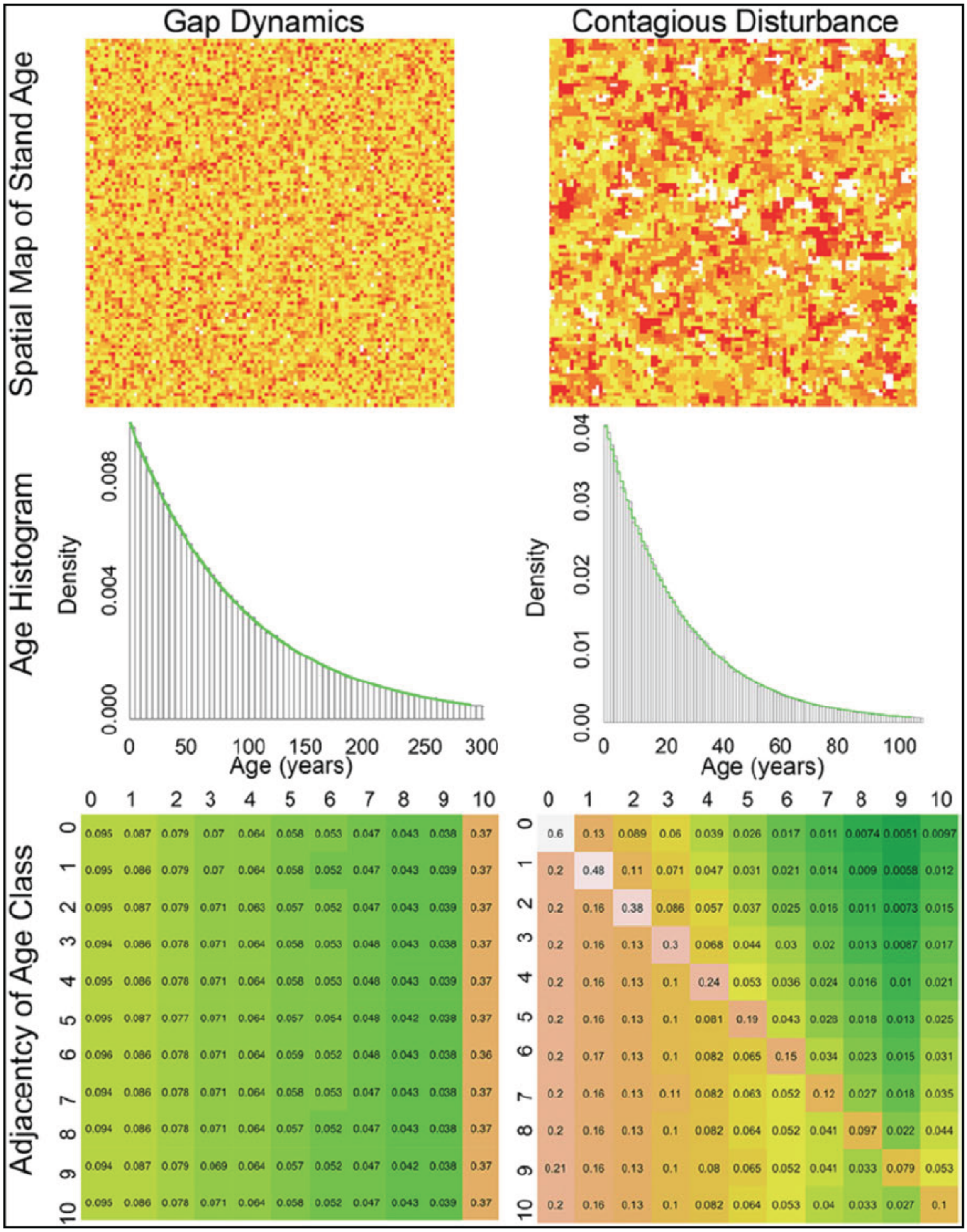
where D is a vector by class. Overall, while there is slight underestimation of disturbance extent at high spread probabilities (Figure 1.2), the analytical approximation performs well and incurs a tiny computational cost relative to spatially explicit models. Also note that this general forward model has an important special case, $p_s = 0$, which corresponds to non-contagious disturbances, such as our initial gap dynamics simulation.

In practice an infinite sum is not actually computable, but the result will asymptotically approach the analytical result and thus can be approximated with a finite sum. Furthermore, the relative proportions of the different age/stage classes within the ith

iteration in the sum (i.e. disturbance of size i), I_i, will rapidly approach a steady-state distribution. If $I_i/\sum I_i \approx \frac{I_{i+1}}{\sum I_{i+1}}$ then we approximate $I_{i+1} = I_i S$ with $I_{i+1} = I_i\lambda$ where λ is the dominant eigenvalue of A. The remainder of the summation $\sum_{h=i+1}^{\infty} \quad I_h$ can thus be approximated as $I_i \sum_{h=i+1}^{\infty} \quad \lambda^{h-i}$. This is just a geometric series, which has the analytical solution $I_i\lambda(1-\lambda)^{-1}$. Therefore our strategy is to solve the first i terms explicitly and analytically approximate the tail of the distribution

$$D = \sum_{h=1}^{i} \quad I_h + I_i\lambda(1-\lambda)^{-1}$$

As can be seen in Figure 1.3, this allows the full analytical model to be accurately approximated with only a small number of matrix multiplications (~5 in this scenario)



	0	1	2	3	4	5	6	7	8	9	10
0	0.095	0.087	0.079	0.07	0.064	0.058	0.053	0.047	0.043	0.038	0.37
1	0.095	0.086	0.079	0.07	0.064	0.058	0.052	0.047	0.043	0.039	0.37
2	0.095	0.087	0.079	0.071	0.063	0.057	0.052	0.047	0.043	0.039	0.37
3	0.094	0.086	0.078	0.071	0.064	0.058	0.053	0.048	0.043	0.038	0.37
4	0.095	0.086	0.078	0.071	0.064	0.058	0.053	0.048	0.043	0.039	0.37
5	0.095	0.087	0.077	0.071	0.064	0.057	0.054	0.048	0.042	0.038	0.37
6	0.096	0.086	0.078	0.071	0.064	0.059	0.052	0.048	0.043	0.038	0.36
7	0.094	0.086	0.078	0.071	0.064	0.058	0.053	0.047	0.043	0.038	0.37
8	0.094	0.086	0.078	0.071	0.064	0.057	0.052	0.047	0.043	0.038	0.37
9	0.094	0.087	0.079	0.069	0.064	0.057	0.052	0.047	0.042	0.038	0.37
10	0.095	0.086	0.078	0.071	0.064	0.058	0.052	0.047	0.043	0.039	0.37

	0	1	2	3	4	5	6	7	8	9	10
0	0.6	0.13	0.089	0.06	0.039	0.026	0.017	0.011	0.0074	0.0051	0.0097
1	0.2	0.48	0.11	0.071	0.047	0.031	0.021	0.014	0.009	0.0058	0.012
2	0.2	0.16	0.38	0.086	0.057	0.037	0.025	0.016	0.011	0.0073	0.015
3	0.2	0.16	0.13	0.3	0.068	0.044	0.03	0.02	0.013	0.0087	0.017
4	0.2	0.16	0.13	0.1	0.24	0.053	0.036	0.024	0.016	0.01	0.021
5	0.2	0.16	0.13	0.1	0.081	0.19	0.043	0.028	0.018	0.013	0.025
6	0.2	0.17	0.13	0.1	0.082	0.065	0.15	0.034	0.023	0.015	0.031
7	0.2	0.16	0.13	0.11	0.082	0.063	0.052	0.12	0.027	0.018	0.035
8	0.2	0.16	0.13	0.1	0.082	0.064	0.052	0.041	0.097	0.022	0.044
9	0.21	0.16	0.13	0.1	0.08	0.065	0.052	0.041	0.033	0.079	0.053
10	0.2	0.16	0.13	0.1	0.082	0.064	0.053	0.04	0.033	0.027	0.1

Figure 1.1: Comparison of Gap dynamics Contagious disturbance simulation. (Left column) Gap dynamic simulation. (Right column) Contagious disturbance simulation. (Top left) spatial map of stand age, with color on a log scale from youngest (red) to oldest (yellow), (Top right) spatial maps of stand age for contagious disturbance, with color on a

log scale from young (red) to old (yellow) and with new disturbances (age = 0) in white. (Middle left) simulated stand age distribution (black) when disturbance probability is 1% compared to geometric expectation (green), (Middle right) simulated stand age distribution (black) when disturbance probability is 1% and spread probability is 25% compared to geometric expectation (green), (Bottom) spatial adjacency matrix by age class aggregated into 10 year bins ([0-9]=0, [10-19]=1, etc.) with all patches 100 year or older in bin 10. (Bottom right) Matrix is colored from white (highest adjacency) through orange to green (lowest adjacency).

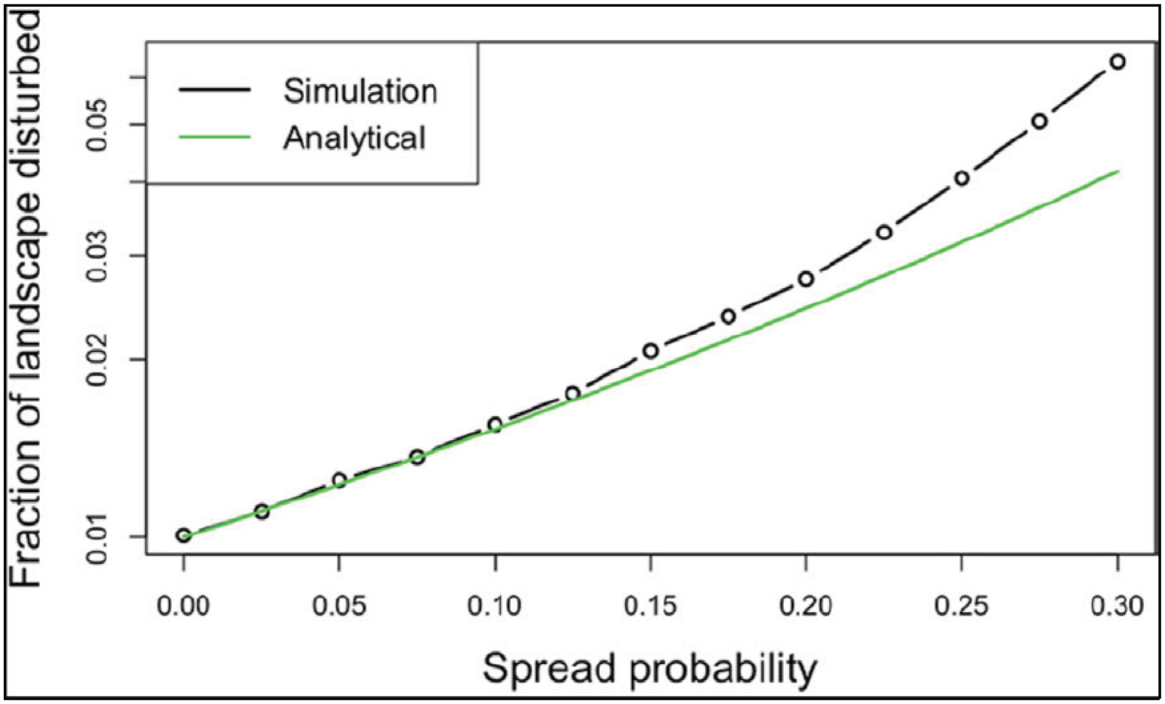


Figure 1.2: Validation of the analytical model's ability to predict disturbance area as a function of spread probability (disturbance initiation probability of 1%). Simulations run on a 4-sided grid so, for example, a 0.25 spread probability corresponds to four independent chances, each 25%, to spread. The analytical approximation appears to underestimate disturbance at high spread probabilities.

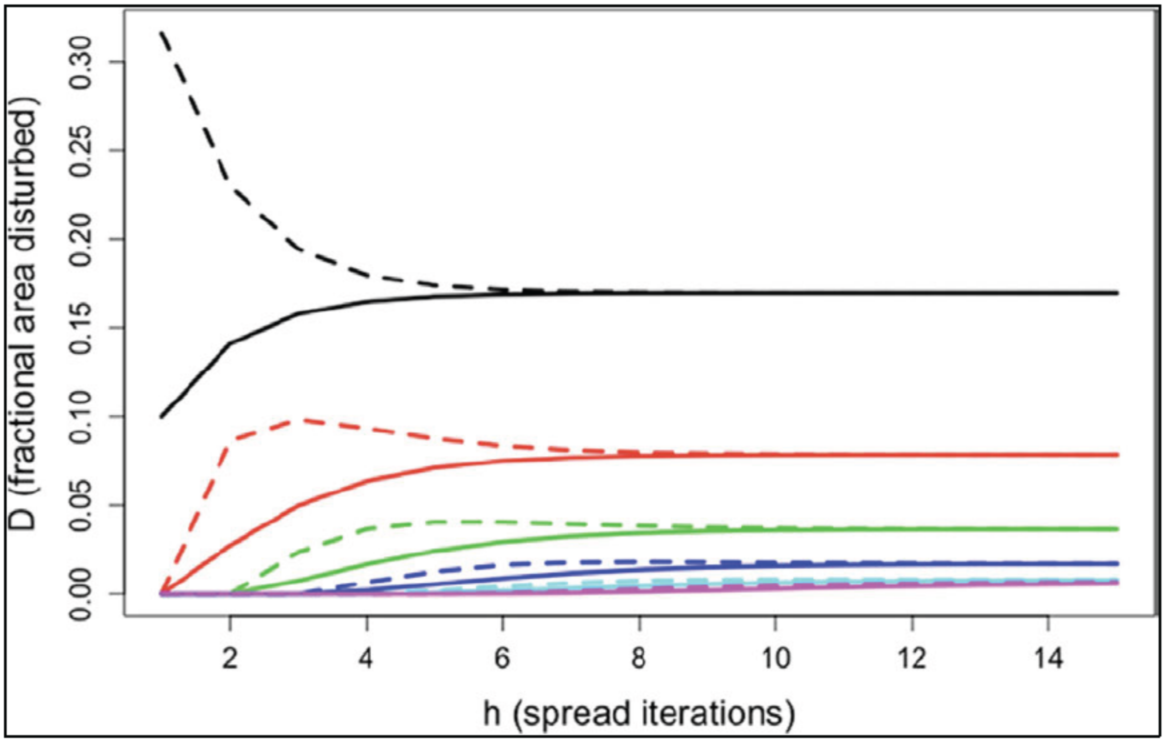


Figure 1.3: In this scenario, disturbance was initiated in one class (black) at 10%, and then spread to other classes (spread probability of 25%) based on differing probabilities of adjacency between classes (50% self adjacency, 50% adjacent to the next class). Solid and dashed lines are a comparison of how cumulative area disturbed increased with disturbance size for both the full model and the tail approximation (estimator).

2.2 Dynamic updating

2.2.1 Fractional Areas

Once the overall disturbance rate, D, has been calculated we need to update both the fractional areas describing the landscape and the adjacency matrix between those fractional areas. First, let's assume that $a_t = [a_0\ a_1\ \ldots\ a_{n-1}\ a_n\ ]$ is a vector describing the fractional areas of each of our age classes. Let's also assume that all disturbances reset patches to age class 0, which is the conventional assumption in cohort-based dynamic vegetation models (DVMs; Fisher et al., 2018; Moorcroft et al., 2001). Note that we are not assuming that disturbance removes all of the vegetation and that age class 0 is bare ground, but rather we are using age 0 to semantically indicate zero years since last disturbance. Following this assumption, the new fractional area in age class 0 at time t+1 is simply the sum of the disturbance rates in each age class times the current fractional area in each of those age classes, $a_{0,t+1} = \sum_{k=0}^{n} \quad a_{k,t} D_{k,t}$. Next, for all other age classes, each age class ages by one year and is reduced by the amount of disturbance that occured in that class

$$a_{k,t+1} = a_{k-1,t}(1 - D_{k-1,t})$$

Finally, the oldest age class is a special case, representing all stand equal or greater than the specified age, and thus is created by fusing the existing area in that class with the next youngest age class, minus the disturbance occurring in each

$$a_{n,t+1} = a_{n-1,t}(1 - D_{n-1,t}) + a_{n,t}(1 - D_{n,t})$$

2.2.2. Adjacency of newly disturbed patches

In addition to updating the fractional areas in different age classes we also need to be able to update their adjacencies. This updating is done after the disturbance events of a given time-step, not as part of the disturbance simulation itself. This distinction means that the adjacency at a timestep (A_t) is not tied to a disturbance but rather represents the cumulative effects of disturbance on the landscape over a timestep.

Let's start by focusing on the adjacency of the newly disturbed age class, a_0, with itself, which we'll denote as A_{00}. If we were assessing this adjacency in a spatially-explicit gridded dataset or simulation, we would estimate the probability of adjacency in terms of the frequency with which disturbed patches are adjacent to other disturbed patches versus non-disturbed patches. For example, for a disturbance of size 1, all four edges are facing non-disturbed patches, so the adjacency is 0/4 = 0 (Figure 4). With a disturbance of size 2, the two patches have a total of eight edges, two of which are on the interior of the disturbance (disturbed patch adjacent to disturbed patch) and six external edges that are along the perimeter of the disturbance, giving an adjacency of 2/8 = 0.25. At size 3 there are two possible disturbance configurations (in a line or an L), but both cases have a total of four interior edges and eight external edges, giving an adjacency of 4/12. At size 4 there are five possible configurations, and the different configurations do not all have the same perimeter – the square configuration has an adjacency of 8/16 while all other configurations have an adjacency of 6/16. If disturbance shapes are completely random then we could work through the combinatorics of how often each shape is likely to occur (squares occur 20% of the time) and calculate a weighted average (0.4). More generally, if we look at the whole map across disturbances of different sizes the overall mean adjacency of disturbed patches will be

$$A_{00} = \frac{\sum Int}{\sum Int + \sum Ext}$$

where Int are interior edges and Ext are external edges.

Thus far we've seen that the adjacency (interior/total edges) has tended to increase as the size of the disturbance increases. We could continue calculating this pattern to larger disturbances with more complex shapes and harder combinatorics (e.g. for a size 5 disturbance there are 372 possible spread scenarios that produces thirteen possible shapes). However, at this point it's worth noting that different types of disturbance may be more likely to produce certain disturbance shapes than others. For example, some disturbances may tend to produce shapes that tend to be round (wildfire) while others might tend to be linear or dendritic (urban development, riverine systems). These different shapes will tend to produce different characteristic interior/total ratios (i.e. different adjacencies). However, it is not the overall mean adjacency (interior/total) that characterizes a disturbance, nor any of the many other landscape metrics in use (e.g. Hesselbarth, Sciaini, and Nowosad 2018), but the functional relationship between disturbance size and adjacency, adj(size). For example, Figure 1.5 shows the adjacency/size curves for three important cases: random spread (purple), the minimum adjacency (blue) achieved through linear disturbances, and the maximum adjacency (red) achieved by circular disturbances that minimize the edge:area ratio.

To get the overall A_{00} for the spatially implicit model, we next replace

$$A_{00} = \frac{\sum Int}{\sum Int + \sum Ext}$$

which sums over individual disturbances, with

$$A_{00} = \frac{\sum_{size} \quad Int(size)p(size)}{\sum_{size} \quad Int(size)p(size) + \sum_{size} \quad Ext(size)p(size)}$$

which instead sums over each disturbance size. In this approximation, $Int(size)$ and $Ext(size)$ returns the expected number of interior and exterior edges while $p(size)$ is the probability of a disturbance of that size. In the denominator we can combine terms as $\sum_{size} \quad (Int(size) + Ext(size))p(size) = \sum_{size} \quad 4 \cdot size \cdot p(size)$ where the 4 arises from the assumption that patches are 4 sided. The size distribution itself can be calculated from the series of I_k, $p(h) = (I_h - I_{h+1}) \cdot h$, because I_h represents the probability of observing a disturbance of size greater or equal to size h+1. Differencing gives us the probability of a disturbance size h occurring, which is then multiplied by the disturbance size to give us the probability of encountering a disturbance of that size (e.g. the disturbances that stayed size 1 are the subset of disturbances that were initiated but didn't spread to another grid cell). Finally, just as we truncated the calculation of D in section 2.1, the tail of this distribution can be approximated by noting that the geometric series implies a geometric parameter distribution function with rate λ. In the numerator we can use our previously discussed relationship between adjacency and size class, $adj(size)$ to calculate $Int(size) = 4 \cdot size \cdot adj(size)$. Putting these together we see that the assumption about the number of sides to a patch cancels out leaving us with just the mean adjacency weighted by disturbance size and the disturbance size probability distribution

$$A_{00} = \frac{\sum_{size} \quad adj(size) \cdot size \cdot p(size)}{\sum_{size} \quad size \cdot p(size)}$$

This derivation makes sense because large disturbances should contribute more to the adjacency, but usually occur at lower probability. Our derivation states that the second-order spatial scaling of any disturbance regime can thus be understood in terms of its size distribution and $adj(size)$. In the analysis of empirical disturbances section, we will evaluate these two components empirically for different disturbance types and ecoregions in Florida and Oregon. In evaluating this approach against simple simulation models, we discovered an important inconsistency in the model, as independent disturbances do sometimes end up adjacent to each other by chance. Consider again our earlier example of simulating gap disturbance ($p_s = 0$). In this case there is no spread, and thus our adjacency-based model makes the prediction that all disturbances are size = 1, and thus $A_{00} = 0$, but in practice we find adjacent disturbances. To correct our model we thus need to add an additional term in the numerator that accounts for the adjacency between independent disturbances. The simplest such correction is to assume that other disturbances are encountered randomly at the overall disturbance rate, a_0.

$$A_{00} = \frac{\sum_{size} \quad Int(size)p(size) + \sum_{size} \quad a_0 Ext(size)p(size)}{\sum_{size} \quad Int(size)p(size) + \sum_{size} \quad Ext(size)p(size)}$$

$$A_{00} = \frac{\sum_{size} \quad [adj(size) + a_0(1 - adj(size))] \cdot size \cdot p(size)}{\sum_{size} \quad size \cdot p(size)}$$

The adjacency predictions corrected to account for this random self adjacency perform well (Figure 1.6).

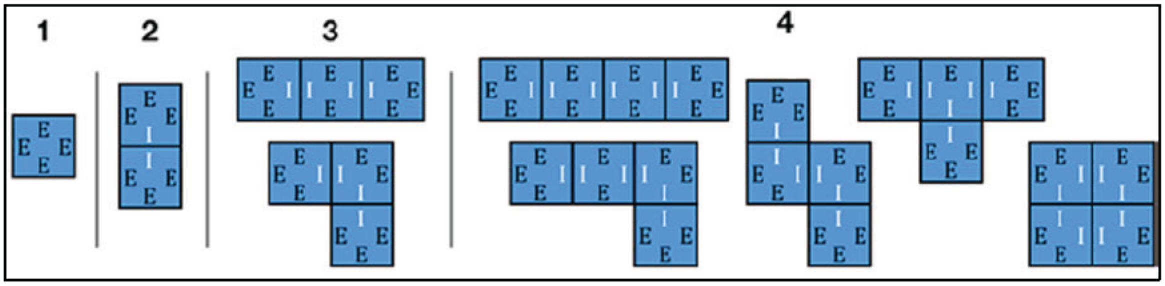


Figure 1.4: Adjacency for small disturbances. Edges are labeled as (E)xterior and (I)interior. For size 1, there is 0 probability of self-adjacency (disturbed patches adjacent to other disturbed patches). For size 2 and 3 it is 1/4 and 1/3 respectively, while for size 4 the adjacency is either 1/2 (square configuration) or 3/8 (all other configurations).

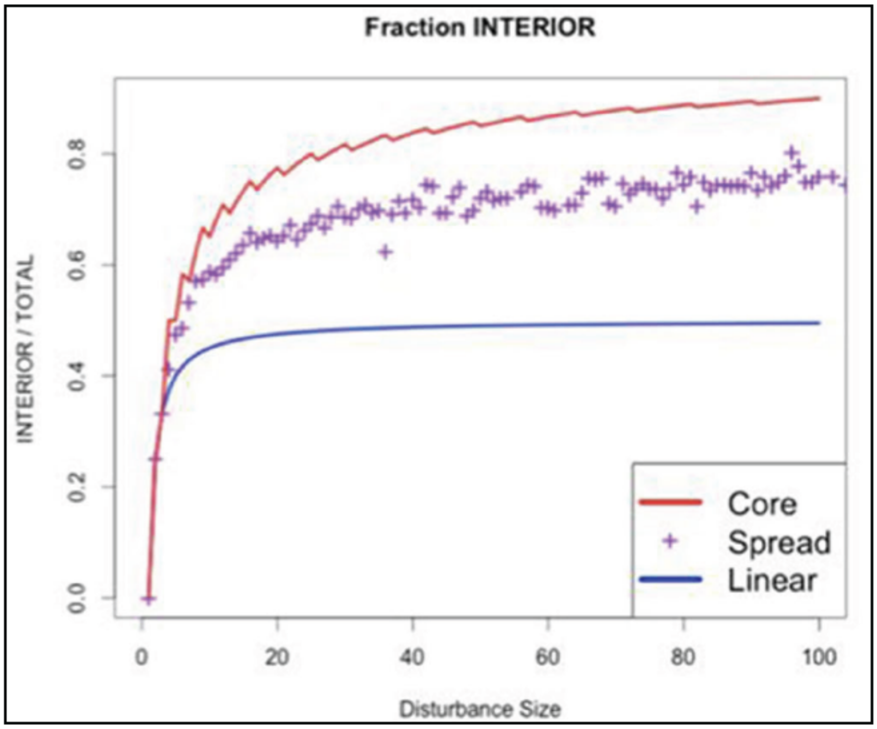


Figure 1.5: Self-adjacency as a function of disturbance size for different disturbance shapes. Core and Linear are the bounding cases of disturbance shapes that maximize and minimize self-adjacency (respectively). Spread is a single realization of the stochastic contagious spread model (Figure 1.2)

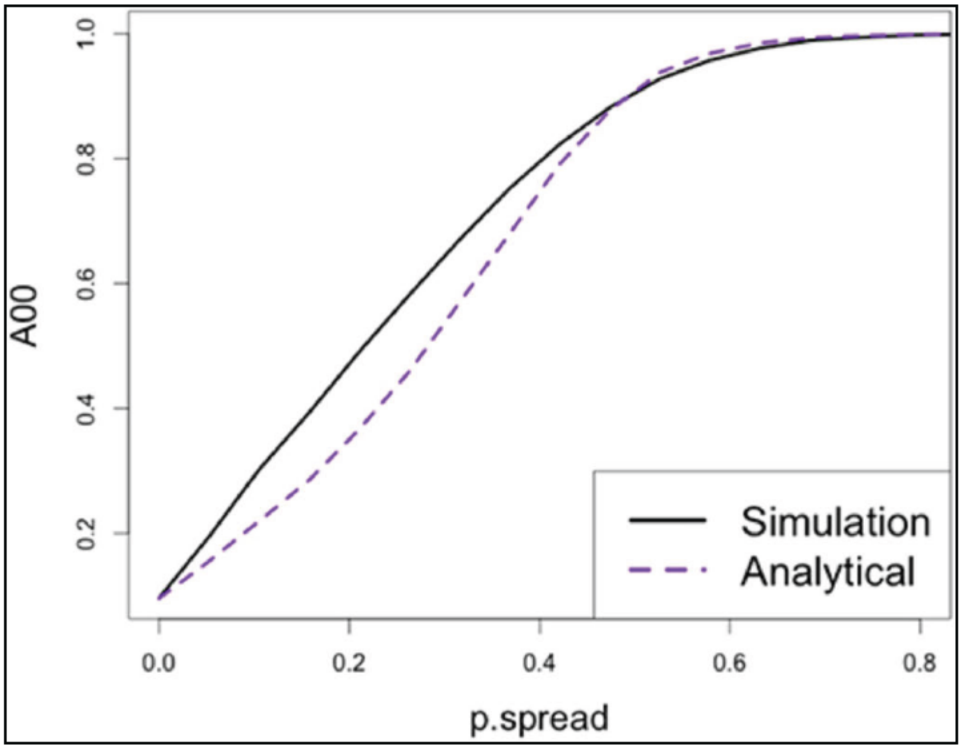


Figure 1.6: Validation of the ability of the analytical approximation to predict self-adjacency of newly-disturbed patches as a function of disturbance spread probability (disturbance initiation probability set to 10%).

2.2.3 Adjacency of non-disturbed patches

In addition to needing to update the adjacency of disturbed patches to each other, there are three other cases that need to be considered: the adjacency of newly disturbed patches to non-disturbed, the adjacency of non-disturbed to newly disturbed, and the adjacency of non-disturbed to each other. For these cases we're going to make the simplifying assumption that the adjacency in each age class changes in proportion to the disturbance rate in that age class, D_k. This assumption is likely reasonable when spread rates are similar among age classes, but very large differences in spread rates, or large asymmetries in spread direction, could be tested through a detailed accounting of the adjacency, A, and spread, ps, at every disturbance size, I, and age class, k. Doing so would come the expense of considerably more complicated accounting and notational complexity, and thus this is left to future work.

For the first case of disturbances adjacent to non-disturbances, we want to normalize D by its sum to generate the probability that the disturbance was in that age class. As with the age-class distribution, we also want to shift the age classes by 1, to account for aging, and sum the final two elements in this vector to account for age-class fusion. Next, because rows sum to zero this vector of probabilities needs to be reduced by $1 - A_{00}$, giving

$$A_{0k,t+1} = \frac{D_{k-1}}{\sum D}(1 - A_{00,t+1})$$

Next, consider the case of non-disturbed patches adjacent to other non-disturbed patches. Here the adjacency should be reduced by the amount of disturbance in that age class, which is the disturbance rate normalized by the fractional area.

$$A_{j,k,t+1} = A_{j-1,k-1,t}(1 - D_{j-1}/a_{j-1})$$

As before, age classes are shifted by 1 and the final two classes are merged, however in this case the merge is an average (weighted by fractional area), rather than a sum.

Finally, because rows sum to 1, the adjacency of non-disturbed to newly disturbed patches is one minus the sum of the other elements in the row

$$A_{j,0,t+1} = 1 - \sum_{k=1} \quad A_{j,k,t+1}$$

To test the performance of the analytical adjacency approximation, we compared the adjacency matrix predicted by this model to that generated by a fully spatial stochastic simulation, analogous to the one shown in the right column of Figure 1 but with a disturbance initiation probability of 1% and a spread probability of 10%. In both the analytical model and stochastic simulation we initiated the landscape from bare ground (age = 0) and ran the model for 1000 years to reach a steady-state.

2.3 Analysis of empirical disturbances

2.3.1 Data description

Our analysis looked at disturbances in Oregon and Florida from the LANDFIRE Disturbance product (Earth Resources Observation and Science Center, U.S. Geological Survey) for 2014, the most recent year available. Florida and Oregon were chosen as contrasting disturbance regimes because they are both areas with fire-based disturbance regimes and a large timber industry (Fox, Jokela, & Allen, 2007; Marlon et al., 2012; Mitchell et al., 2014b). The LANDFIRE disturbance product is a 30 x 30 m resolution gridded raster covering the entire US, with each disturbed cell assigned one of twenty different disturbance types. Disturbances were determined by a combination of LANDSAT satellite imagery, MODIS satellite imagery, vegetation change detection techniques, and a database of disturbance events detected by other federal agencies (Rollins, 2009; Vogelmann et al., 2011). Specifically, the 2014 LANDFIRE Disturbance dataset was constructed with best-pixel composite imagery, other composite imagery, or majority focal filling to account for missing data after the decommissioning of LANDSAT 5. In our analysis we treated the LANDFIRE Disturbance product as given, and did not consider associated levels of uncertainty within different disturbance types and pixels.

We downloaded US state data from the LANDFIRE repository, available at https://landfire.cr.usgs.gov/disturbance_2.php. The authors then subset Disturbance dataset for each US state based on and Environmental Protection Agency level II Ecoregion boundaries (Ecoregions; McMahon et al., 2001). Subsetting was done using with the R raster and rgdal packages (Bivand et al., 2018; Hijmans et al., 2018). We subset the US state-level rasters to focus on the two forested level II ecoregions within each state: Mississippi Alluvial and Southeast Coastal Plains (8.5) and the Southeastern USA Plains (8.3) in Florida; and the Western Cordilleras (6.2) and Marine West Coast Forest (7.1) in Oregon. In Oregon we excluded the Cold Deserts ecoregion (10.1) and in Florida we excluded the Everglades (15.4) (Figure 1.7). The resulting four rasters then had adjacency calculations done on all of the disturbance clumps within each raster (see below).

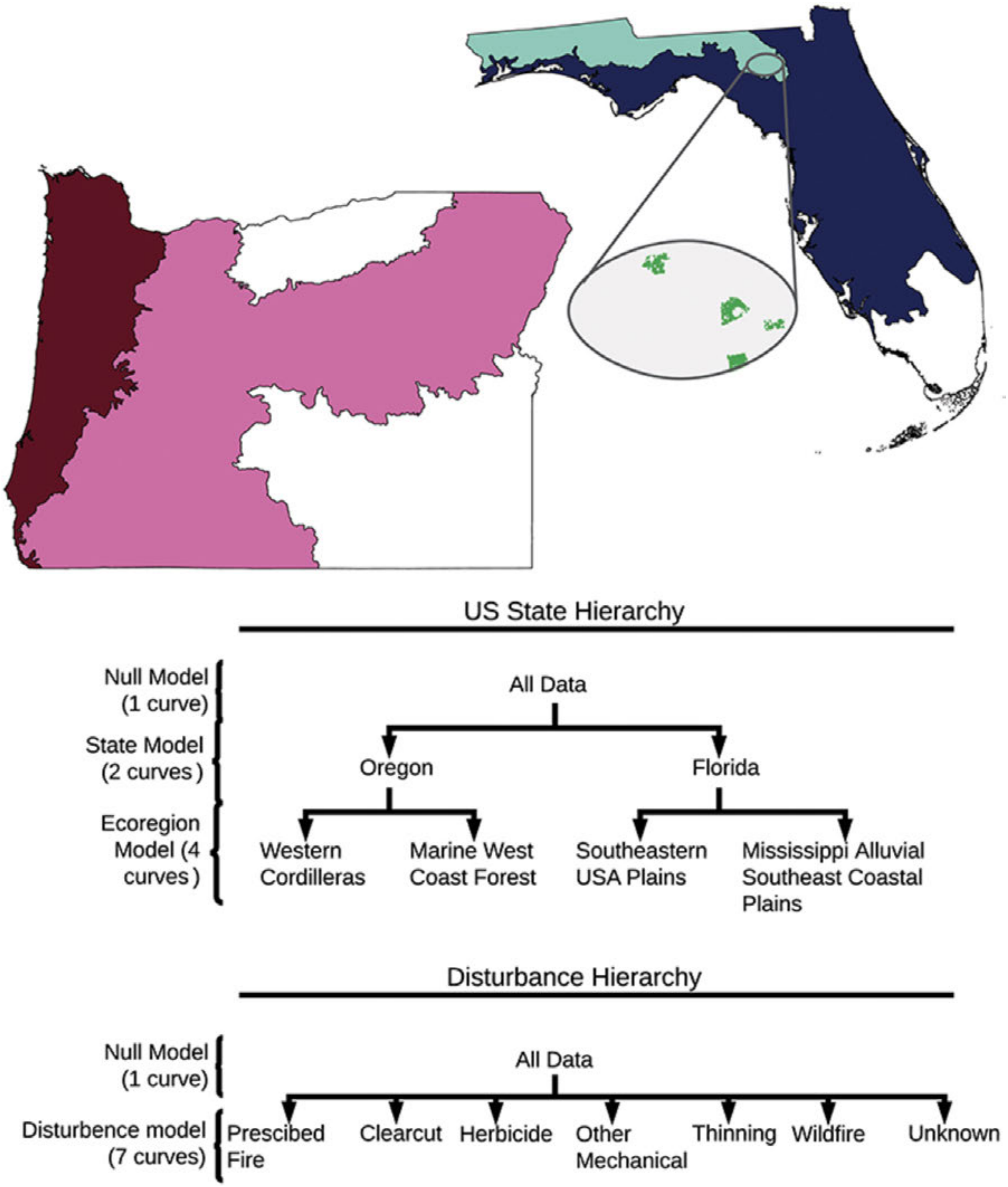


Figure 1.7: Visualization of data subsetting and model hierarchies. Colored regions show what portions of Oregon and Florida were used in analyses. Cutout shows a sample of LANDFIRE raster file with disturbances in green. Model hierarchies show the different models compared, and the data used to make each curve.

2.3.2 Calculation of Metrics

The analysis of empirical disturbances focused on the two metrics that emerged from our theoretical model: disturbance size distribution and the relationship between interior ratio and disturbance size. Analysis began by identifying individual disturbances that were surrounded on all sides by non-disturbance pixels. Adjacency was determined using the four cardinal “Rook’s Case” pixels (for two pixels to be adjacent they had to share a side). For each disturbance we then identified the disturbance class and calculated the disturbance area and interior ratio (number of interior edges / total number of edges, Figure 1.4). After processing the four rasters, we ended up with a table of each disturbance event in Florida and Oregon, with a record of its type, size, interior/ total ratio, eco region and US state. This table is the basis of all further empirical calculations and is publicly available along with the scripts used to generate it on Github at https://github.com/mccabete/SpatialAdjacency. This analysis has no way of distinguishing distinct but adjacent disturbance events that occurred at different times within a year, therefore these distinct but adjacent disturbance events were considered the same clump. This analysis also did not account for relative area of different disturbance types mixed within a single clump. Clumps of mixed disturbance types accounted for a small number of disturbance events (1%), but a large fraction of disturbance area (56 %) (Figure 1.9; Table S1.1). We treat Mixed disturbance as a separate class of disturbance in our comparison of size distributions. For calculating interior ratios curves these mixed disturbances were removed. Many of the disturbances most frequently co-occurring within mixed disturbances are represented in our curve fits (Figure S1.2).

2.3.3 Assessing Statistical Significance

We used two different statistical tests for the two different disturbance metrics. For the size distributions, we compared the size distributions of disturbance type, US states, and ecoregions using a two-sided Kolmogorov–Smirnov test. We corrected the P-values using a Bonferroni correction (Bland & Altman, 1995; Massey, 1951). We compared size distributions of all disturbance types present within Florida and Oregon that had 20 or more disturbance events. This excluded biological and disease disturbance classes (N = 4, N = 6; Table S1.1). We made 66 pairwise comparisons among 12 disturbance types, and 3 comparisons among state and two ecoregions. After correction, our alpha value was 0.000725 (Table S1.2).

For the interior to total ratio, we fit and statistically compared curves corresponding to null models and different hierarchy levels. The curves were fitted using a modified Michaelis- Menten curves of the form $y = \frac{ax^c}{b+x^c}$ using a maximum-likelihood approach assuming Gaussian error (Michaelis & Menten, 1913). The form was chosen based on visual agreement with the data and maximum likelihood after comparison with six other functional forms (Figure S1.1; Table S1.3). Different curves were compared using a likelihood ratio test. Comparing the curves meant comparing different hierarchical levels (Figure 1.7). We fit two hierarchies, one starting at the US state level, and one at the disturbance-type level (Figure 1.7). In the US state hierarchy, an all-data null model was compared to a model where Oregon and Florida were fit separately. The US state-model was then compared to a model where each ecoregion was fit separately. In the second hierarchy, an all-data null model was compared to a model where each disturbance type was fit separately. The disturbance-model was then compared to a disturbance-by- US state model (Figure 1.7 ; Table S1.4). We also separately compared a one-curve-Florida model to a two-curve-ecoregion model, and a one-curve-Oregon model to a two-ecoregion-curve model. We did this to see if the differences between ecoregions within Florida would be significant in isolation of the differences between Oregonian ecoregions (Table S1.4). Because all single-pixel, double-pixel, and triple-pixel configurations produce the same interior ratio (Figure 1.4), curves were fit only to disturbances over 3 pixels (0.27 ha) large. To meet requirements of likelihood ratio tests, the data was subset to include only the disturbance types that were common amongst all ecoregions. Disturbance types included: clearcut, herbicide, other mechanical, prescribed fire, thinning, wildfire, and unknown. The distinction between wildfire, and prescribed fire is that a wildfire is an unplanned fire, prescribed fires are intentionally set and managed fires (LANDFIRE Disturbance, 2016). To contextualize modeled curves, we included hexagonal density plots, representing the spread and overall shape of all the data used to generate curves (ggplot2, 3.0.0; Wickham et al., 2018). To aid in interpretation, the upper and lower bounds for the interior ratio were also visualized based on calculations of the theoretical minimum (linear disturbance) and maximum (round disturbance) interior ratios for a given disturbance size. All analyses were performed in R (3.5.0; R Core Team, 2018)) with adjacency calculations performed using the raster library (2.6-7; Hijmans, 2018).

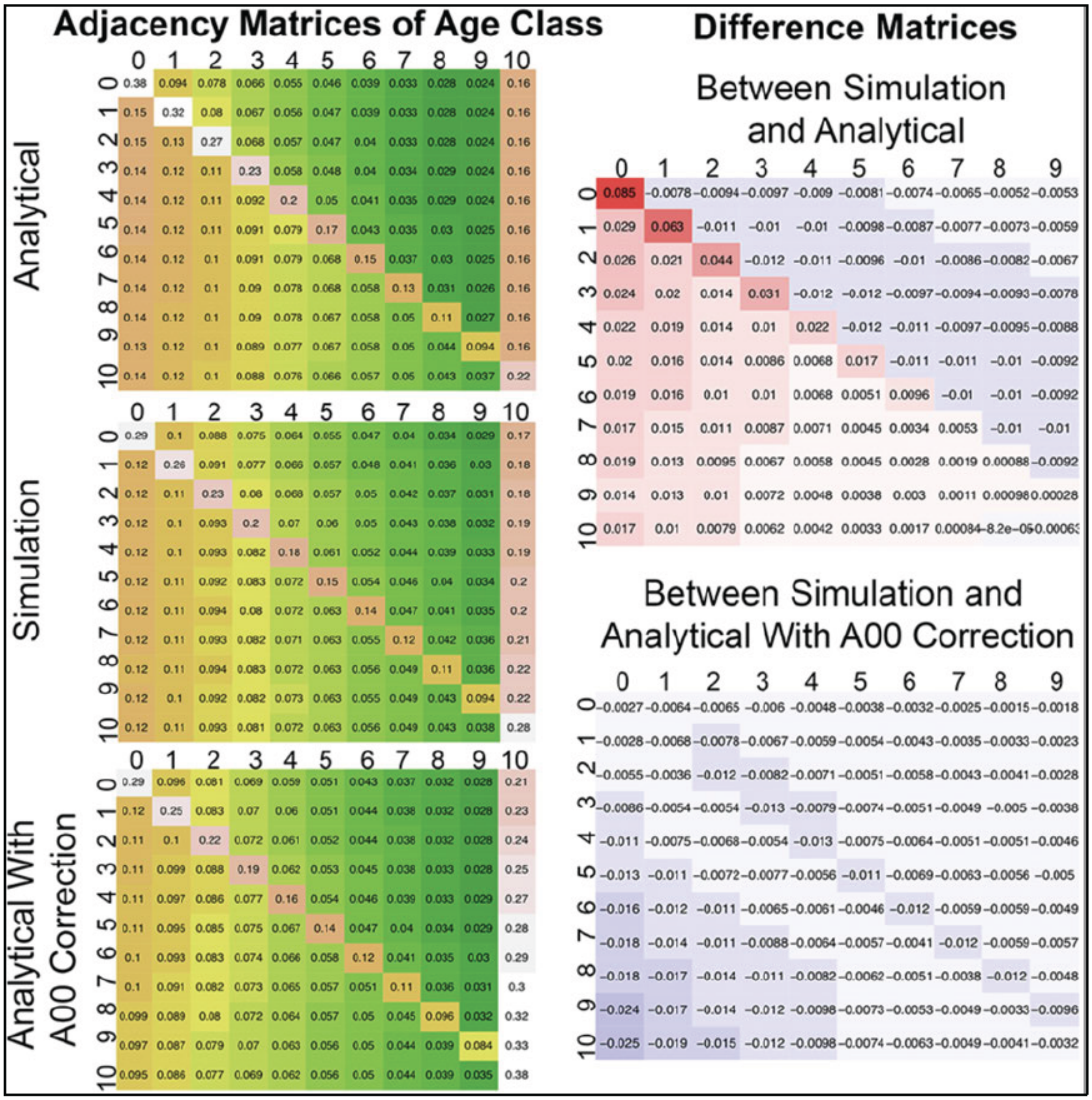
3 Results

3.1 Dynamic adjacency updating

The analytical model for calculating disturbance spread and dynamically updating landscape adjacency was assessed by comparing the analytical model to a spatially-explicit stochastic simulation. In both cases the landscape was initiated from bare ground (age = 0) and run 1000 years to reach a steady-state. Figure 1.8 shows that the steady-state adjacency predicted by both models had the same structural features, as summarized in section 2.1: patches within an age class tended to be more self-adjacent, but that self-adjacency decays geometrically with age; there is also a geometric decay along rows, but with greater adjacency above the diagonal. Numerically, the predicted adjacencies were also very similar, though with the analytical model slightly overpredicting $A_{0,0}$. Because so many of the other rates in the adjacency matrix decay from $A_{0,0}$, there are slight biases elsewhere. However, the error propagation from $A_{0,0}$ is consistent with having the underlying structure for updating the matrix correct, because it means that structural elements are preserved as the landscape ages.

This impact of errors in $A_{0,0}$ on the overall adjacency calculation was tested with a third model (Figure 1.8 bottom left), where the analytical model was run using the $A_{0,0}$ derived from the numerical simulation. Overall this model improved the overall pattern in the adjacency matrix, especially along the main diagonal. The remaining error (Figure 1.8 bottom right) is largely concentrated in two places. First, there is greater adjacency with the oldest 'absorbing' age class than observed in the simulation (left hand column).

Second, because of this the bottom left corner (adjacency of old age classes to young classes) is a bit lower than observed. Matrix rows have a sum-to-one constraint, so some of these errors are inevitable compensating errors. It is also worth noting that in nudging $A_{0,0}$ directly we are not nudging the underlying terms used to calculate $A_{0,0}$ (I, D, a), which are also used in update the rest of A, meaning this test is not strictly internally consistent. An open question is how much of the remaining error in the adjacency matrix updating is in the underlying analytical simulation of disturbance spread (I, D, a) versus approximations in the updating of A. This is something we hope to investigate further in the future.



Adjacency Matrices of Age Class

Analytical

	0	1	2	3	4	5	6	7	8	9	10
0	0.38	0.094	0.078	0.066	0.055	0.046	0.039	0.033	0.028	0.024	0.16
1	0.15	0.32	0.08	0.067	0.056	0.047	0.039	0.033	0.028	0.024	0.16
2	0.15	0.13	0.27	0.068	0.057	0.047	0.04	0.033	0.028	0.024	0.16
3	0.14	0.12	0.11	0.23	0.058	0.048	0.04	0.034	0.029	0.024	0.16
4	0.14	0.12	0.11	0.092	0.2	0.05	0.041	0.035	0.029	0.024	0.16
5	0.14	0.12	0.11	0.091	0.079	0.17	0.043	0.035	0.03	0.025	0.16
6	0.14	0.12	0.1	0.091	0.079	0.068	0.15	0.037	0.03	0.025	0.16
7	0.14	0.12	0.1	0.09	0.078	0.068	0.058	0.13	0.031	0.026	0.16
8	0.14	0.12	0.1	0.09	0.078	0.067	0.058	0.05	0.11	0.027	0.16
9	0.13	0.12	0.1	0.089	0.077	0.067	0.058	0.05	0.044	0.094	0.16
10	0.14	0.12	0.1	0.088	0.076	0.066	0.057	0.05	0.043	0.037	0.22

Simulation

	0	1	2	3	4	5	6	7	8	9	10
0	0.29	0.1	0.088	0.075	0.064	0.055	0.047	0.04	0.034	0.029	0.17
1	0.12	0.26	0.091	0.077	0.066	0.057	0.048	0.041	0.036	0.03	0.18
2	0.12	0.11	0.23	0.08	0.068	0.057	0.05	0.042	0.037	0.031	0.18
3	0.12	0.1	0.093	0.2	0.07	0.06	0.05	0.043	0.038	0.032	0.19
4	0.12	0.1	0.093	0.082	0.18	0.061	0.052	0.044	0.039	0.033	0.19
5	0.12	0.11	0.092	0.083	0.072	0.15	0.054	0.046	0.04	0.034	0.2
6	0.12	0.11	0.094	0.08	0.072	0.063	0.14	0.047	0.041	0.035	0.2
7	0.12	0.11	0.093	0.082	0.071	0.063	0.055	0.12	0.042	0.036	0.21
8	0.12	0.11	0.094	0.083	0.072	0.063	0.056	0.049	0.11	0.036	0.22
9	0.12	0.1	0.092	0.082	0.073	0.063	0.055	0.049	0.043	0.094	0.22
10	0.12	0.11	0.093	0.081	0.072	0.063	0.056	0.049	0.043	0.038	0.28

Analytical With A00 Correction

	0	1	2	3	4	5	6	7	8	9	10
0	0.29	0.096	0.081	0.069	0.059	0.051	0.043	0.037	0.032	0.028	0.21
1	0.12	0.25	0.083	0.07	0.06	0.051	0.044	0.038	0.032	0.028	0.23
2	0.11	0.1	0.22	0.072	0.061	0.052	0.044	0.038	0.032	0.028	0.24
3	0.11	0.099	0.088	0.19	0.062	0.053	0.045	0.038	0.033	0.028	0.25
4	0.11	0.097	0.086	0.077	0.16	0.054	0.046	0.039	0.033	0.029	0.27
5	0.11	0.095	0.085	0.075	0.067	0.14	0.047	0.04	0.034	0.029	0.28
6	0.1	0.093	0.083	0.074	0.066	0.058	0.12	0.041	0.035	0.03	0.29
7	0.1	0.091	0.082	0.073	0.065	0.057	0.051	0.11	0.036	0.031	0.3
8	0.099	0.089	0.08	0.072	0.064	0.057	0.05	0.045	0.096	0.032	0.32
9	0.097	0.087	0.079	0.07	0.063	0.056	0.05	0.044	0.039	0.084	0.33
10	0.095	0.086	0.077	0.069	0.062	0.056	0.05	0.044	0.039	0.035	0.38

Difference Matrices

Between Simulation and Analytical

	0	1	2	3	4	5	6	7	8	9
0	0.085	-0.0078	-0.0094	-0.0097	-0.009	-0.0081	-0.0074	-0.0065	-0.0052	-0.0053
1	0.029	0.063	-0.011	-0.01	-0.01	-0.0098	-0.0087	-0.0077	-0.0073	-0.0059
2	0.026	0.021	0.044	-0.012	-0.011	-0.0096	-0.01	-0.0086	-0.0082	-0.0067
3	0.024	0.02	0.014	0.031	-0.012	-0.012	-0.0097	-0.0094	-0.0093	-0.0078
4	0.022	0.019	0.014	0.01	0.022	-0.012	-0.011	-0.0097	-0.0095	-0.0088
5	0.02	0.016	0.014	0.0086	0.0068	0.017	-0.011	-0.011	-0.01	-0.0092
6	0.019	0.016	0.01	0.01	0.0068	0.0051	0.0096	-0.01	-0.01	-0.0092
7	0.017	0.015	0.011	0.0087	0.0071	0.0045	0.0034	0.0053	-0.01	-0.01
8	0.019	0.013	0.0095	0.0067	0.0058	0.0045	0.0028	0.0019	0.00088	-0.0092
9	0.014	0.013	0.01	0.0072	0.0048	0.0038	0.003	0.0011	0.00098	0.00028
10	0.017	0.01	0.0079	0.0062	0.0042	0.0033	0.0017	0.00084	-8.2e-05	0.0006

Between Simulation and Analytical With A00 Correction

	0	1	2	3	4	5	6	7	8	9
0	-0.0027	-0.0064	-0.0065	-0.006	-0.0048	-0.0038	-0.0032	-0.0025	-0.0015	-0.0018
1	-0.0028	-0.0068	-0.0078	-0.0067	-0.0059	-0.0054	-0.0043	-0.0035	-0.0033	-0.0023
2	-0.0055	-0.0036	-0.012	-0.0082	-0.0071	-0.0051	-0.0058	-0.0043	-0.0041	-0.0028
3	-0.0086	-0.0054	-0.0054	-0.013	-0.0079	-0.0074	-0.0051	-0.0049	-0.005	-0.0038
4	-0.011	-0.0075	-0.0068	-0.0054	-0.013	-0.0075	-0.0064	-0.0051	-0.0051	-0.0046
5	-0.013	-0.011	-0.0072	-0.0077	-0.0056	-0.011	-0.0069	-0.0063	-0.0056	-0.005
6	-0.016	-0.012	-0.011	-0.0065	-0.0061	-0.0046	-0.012	-0.0059	-0.0059	-0.0049
7	-0.018	-0.014	-0.011	-0.0088	-0.0064	-0.0057	-0.0041	-0.012	-0.0059	-0.0057
8	-0.018	-0.017	-0.014	-0.011	-0.0082	-0.0062	-0.0051	-0.0038	-0.012	-0.0048
9	-0.024	-0.017	-0.014	-0.012	-0.0098	-0.0073	-0.0053	-0.0049	-0.0033	-0.0096
10	-0.025	-0.019	-0.015	-0.012	-0.0098	-0.0074	-0.0063	-0.0049	-0.0041	-0.0032

Figure 1.8: Comparison between adjacency matrices for a stochastic spatial simulation (simulation from Figure 2, middle) analytical approximation (top), and analytical approximation where a correction was applied to A00. All adjacency matrices are after 1000 years (steady state). To the right are difference matrices between the simulation matrix and the two analytical matrices. The 10th column of the error matrices was removed because of a summing to 1 constraint.

3.2 Disturbance Size Distribution

Our Kolmogorov–Smirnov pairwise comparison of disturbance type size distributions found that the majority of disturbance types had significantly distinct distributions ($p << 0.001$) (Figure 1.9; Table S1.2). The three exceptions were clearcut, wildland fire, and harvest, which had non-significant differences with roughly half of the disturbance classes. Finally, mastication had no significant difference between wildfire or chemical (Table S1.2). The size distributions of Florida and Oregon were significantly different, as well as the two ecoregions nested within Oregon ($p < 0.001$; Table S1.4). The two ecoregions size distributions nested within Florida were not found to be significantly different. However, in other size distributions significant differences were found despite visual similarity in part due to large sample sizes. The size distributions have a large range in sample sizes. US state-level size distributions were based on very large sample sizes (Oregon $N = 27137$, Florida $N = 20329$). Disturbance sample sizes range from harvest with $N = 22$ to unknown $N = 34560$ (Table S1.1). Unknown disturbances accounted for the majority of disturbance events in the overall dataset, and a large proportion of the area (20%). All four ecoregions had a similarly shaped size distribution, with peaks at single-pixel (0.09 ha) disturbances and at 7 ha disturbances. The 7 ha peak aligns with disturbance peaks in the disturbance categories unknown, thinning, wildland fire, mixed, harvest and wildfire. Within Oregon, the Western Cordillera ecoregion has more small and mid-level size disturbances than the Marine West Coast Forest, the Western Cordillera also had both considerably more disturbance events than the Marine West Coast Forest, and a larger area of disturbance (75%).

Disturbance plots show more varied patterns, Wildfire and prescribed fire have a long tails, reflecting the influence of rare but large disturbances. In contrast, thinning and mastication have distinct peaks and sharper drop-offs, suggesting more standardized anthropogenic disturbances and smaller sizes. Mixed disturbance has the longest tail, and no peak at small disturbances. Herbicide and other mechanical have visually similar distributions, but were found to be significantly different (Herbicide N = 4655, Other Mechanical N = 3546). Within mixed disturbances, herbicide and other mechanical co-occurred most frequently (Figure S1.2).

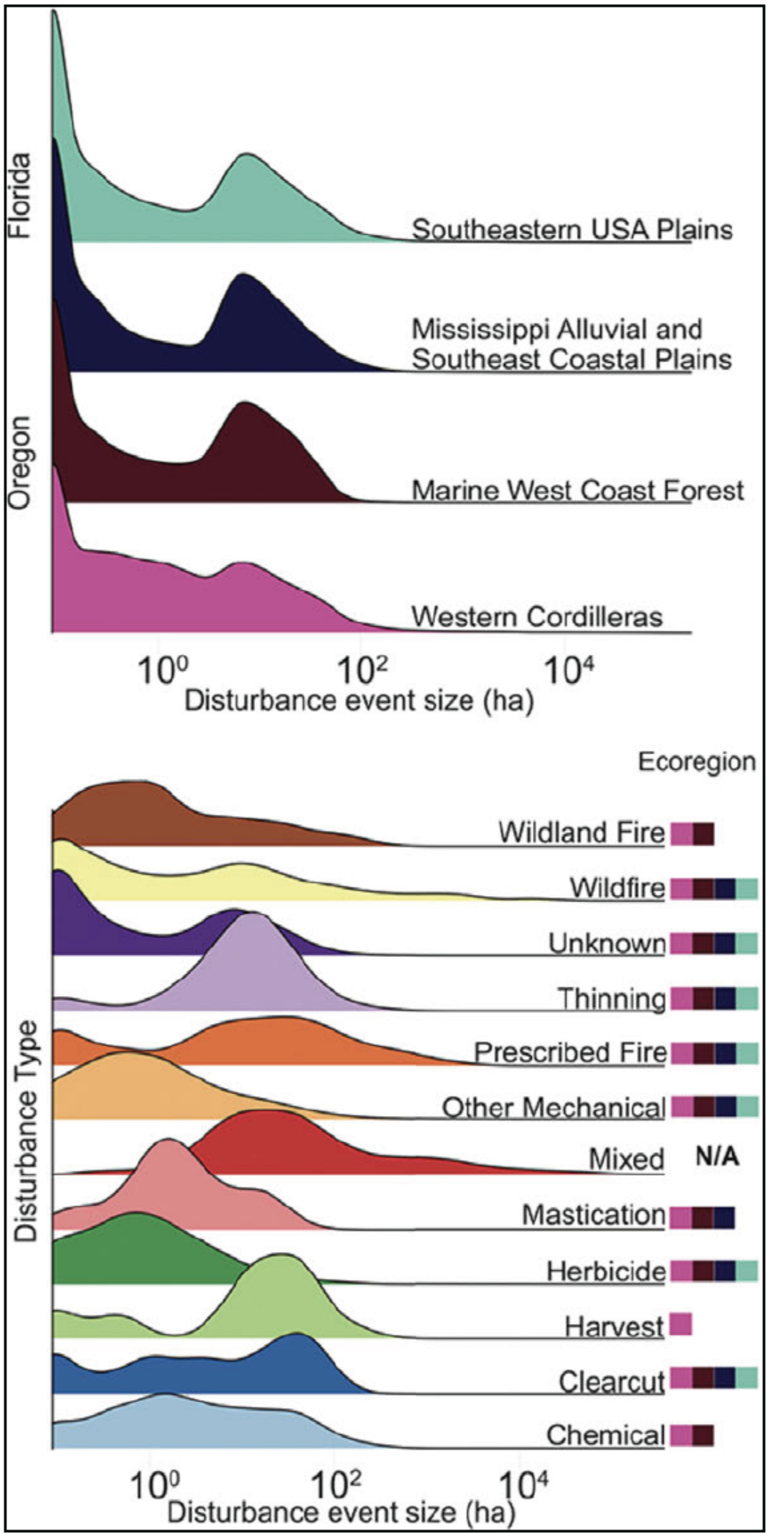


Figure 1.9: Size density plots showing the contrasts between ecoregion / state and disturbance type. Colored boxes next to disturbance size density curves show what

ecoregion contains the respective disturbance. Sample sizes associated with density plots can be found in Table S1.1.

3.3 Disturbance Interior Ratio Curves

We found a significant effect of US state ($p < 0.001$) and ecoregion nested within state ($p < 0.01$). Oregon had a wider range of interior ratios, with a higher occurrence of linear disturbances than Florida (Figure 1.10). Florida and Oregon have similar numbers of overall disturbance occurrence, but Oregon disturbances have a larger proportion of the total area of disturbances (%79). Within Oregon, small disturbances were more compact in Marine West Coast forests than in the Western Cordillera small disturbances, but this relationship crosses, such that Marine West Coast disturbances were less round at large disturbance sizes. The curves fit for the two ecoregions in Florida are nearly identical (Figure 1.10). Despite visual similarity, the two ecoregion curves were found to be significantly different even when compared to just a Florida curve model. Best fit parameters for all curves are in Table S1.5.

In our second hierarchy, there was a significant effect of disturbance type ($p < 0.0001$), but not US state nested within disturbance ($p > 0.1$). Herbicide is the most distinctively linear, followed by other mechanical, and then unknown. Fire disturbance types (prescribed and wildfire) were closer to the maximum interior ratio curve, suggesting that fires tended to be compact and burned pixels were predominantly adjacent to other burned pixels (Figure 1.11). Disturbance-level curves show that prescribed fires are less compact at smaller sizes and larger sizes than natural fires, but at the most frequent size are similarly shaped. Thinning resembles other compact disturbances, but begins to become more linear at large sizes relative to wildfire. Clearcut follows a similarly compact pattern to wildfire.

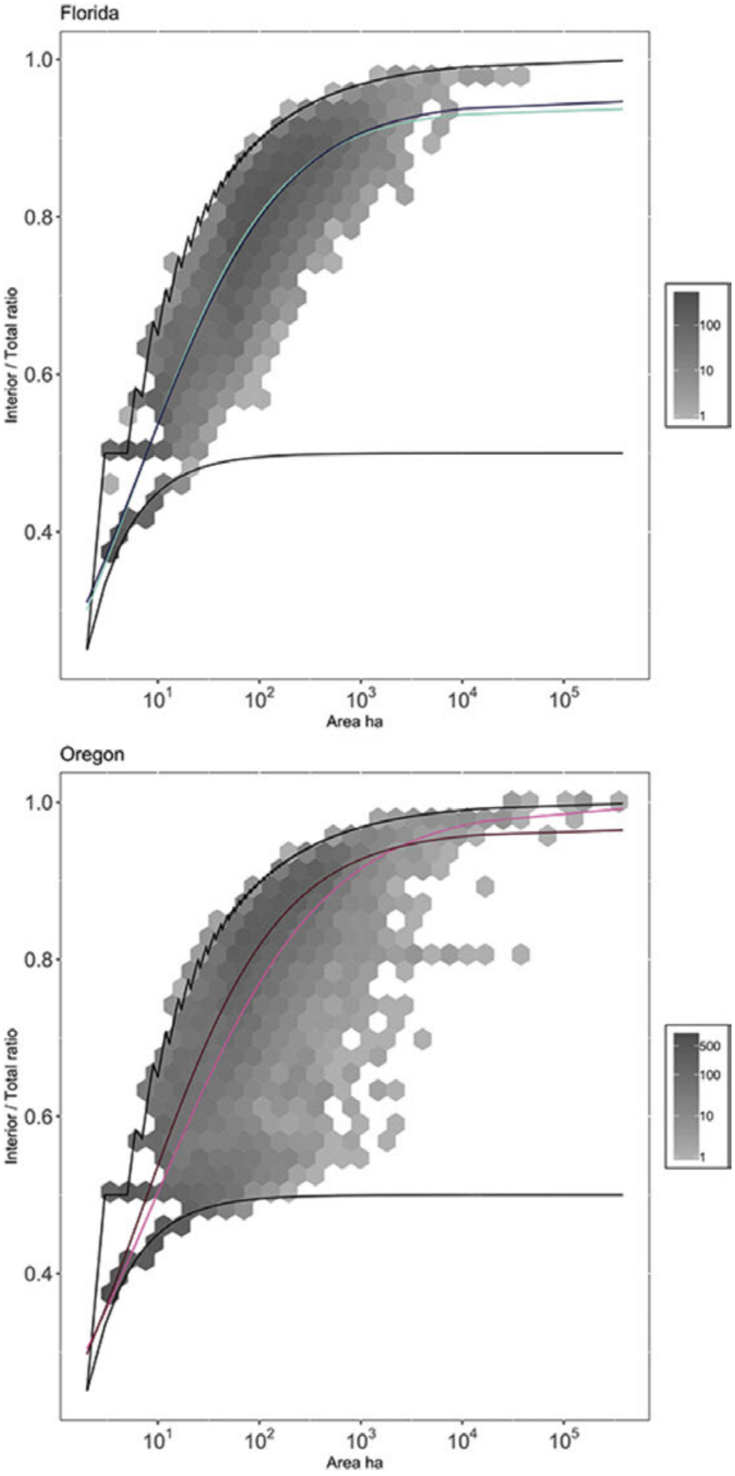


Figure 1.10: Mean trends of Ecoregion within State. Curves match Ecoregion model curves referenced in Figure 1.7. Gray hexes correspond to binned-counts of number of

disturbance events. Black lines correspond to core and linear bounding cases. Parameter values associated with curves can be found in Table S1.5.

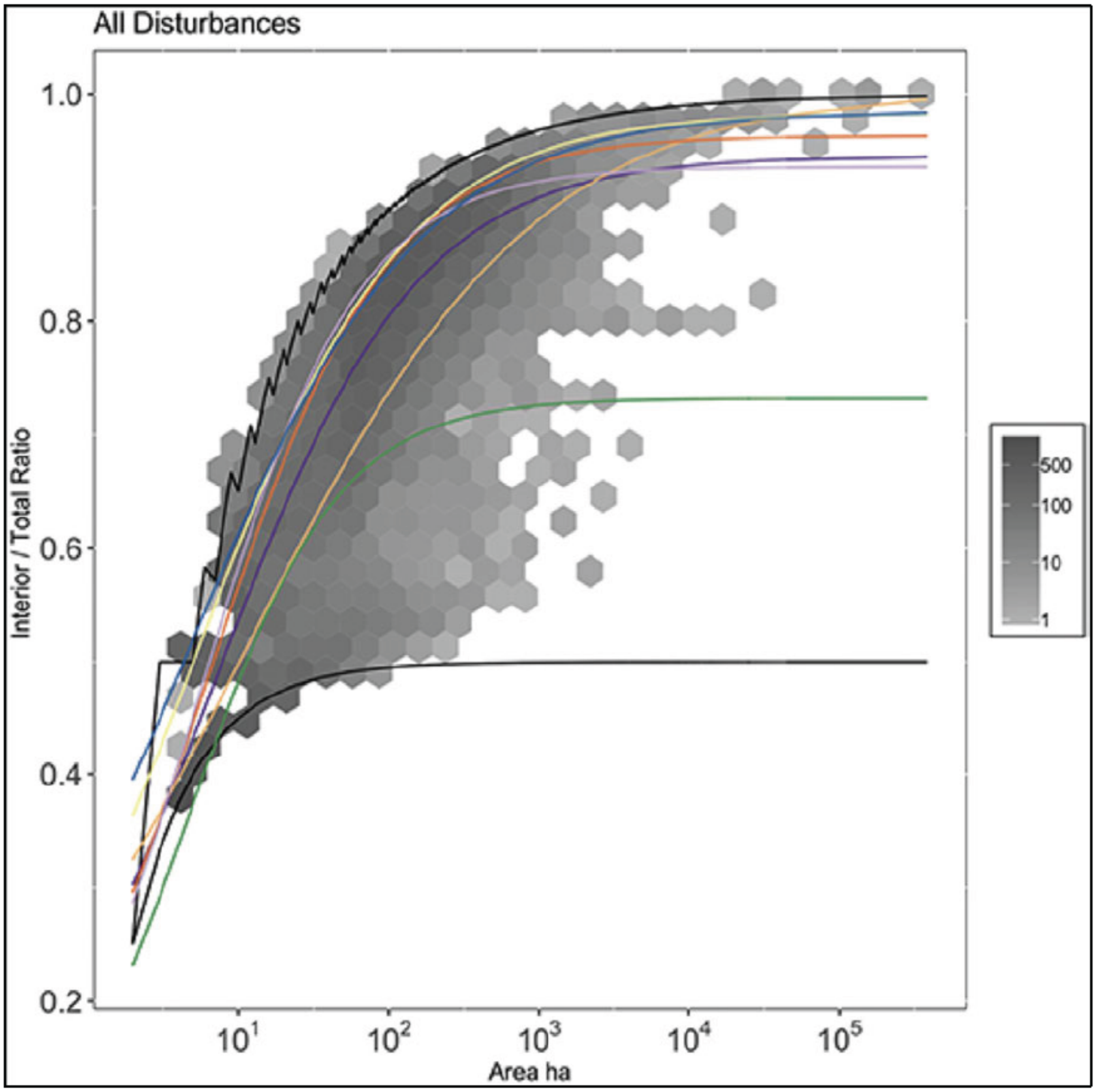


Figure 1.11: Mean trends of disturbance type. Curves match Disturbance model curves referenced in Figure 1.7. Gray hexes correspond to binned-counts of number of disturbance events. Black lines correspond to linear bounding cases. Parameter values associated with curves can be found in Table S1.5.

4. Discussion

4.1 Theoretical Framework

Our framework for scaling spatially-implicit contagious disturbances is reasonably accurate, computationally efficient, and theoretically provocative. Our framework was able to estimate the fraction of the landscape that was disturbed as a function of disturbance initiation, adjacency, and spread probabilities (Figure 1.2). We were able to show that disturbance initiated in one age class would spread into stands of different ages based on their relative adjacencies (Figure 1.3). We demonstrated not only the ability to predict the self-adjacency of newly-disturbed areas (Figure 1.5), but also the adjacency of newly-disturbed areas to non-disturbed areas and the ability to update the adjacency of non-disturbed areas to each other in light of new disturbance. While the corrected self-adjacency predictions perform well (Figure 1.8), improving this correction is a useful area for future research, for example by accounting for the size of disturbed patches in calculating the probability that they will merge. In addition, it is important to note that when simulating disturbance using empirical adj functions that this correction term does not need to be included unless distinct, but adjacent, disturbances occurring during the same time step, were separated in the original data (usually this is not possible). We were able to successfully update adjacency over 1000 years within a reasonable level of accumulated error and capture the major emergent features of contagious disturbance adjacency (Figure 1.8), such as the geometric decay of self-adjacency as even-aged stands mature and the geometric decay of adjacency within an age class (greater probability of being adjacent to newer disturbances) with greater adjacency above the diagonal (young) than old. That said, if older age classes are aggregated (bottom row) then considerable self-adjacency among old-growth stands can develop.

There are a number of important applications where this modeling framework can be immediately applied and expanded upon. At the top of this list is improving the incorporation of sub-grid scale disturbance processes within regional and global scale models, such as Dynamic Global Vegetation Models (DGVMs), Dynamic Vegetation Models (DVMs, Fisher et al. 2018), and coupled Earth System Models. These models operate at a scale where spatially-explicit approaches are not computationally feasible– a typical landscape model operating at LANDSAT (30x30m) resolution would require simulating hundreds of billions of grid cells to capture the Earth's land surface. As a result, disturbances that we know to be spatially contagious are either absent from these models altogether (e.g. insects and pathogens; Dietze & Matthes, 2014; Hicke et al., 2012) or represented using much simpler zeroth-order (spatially homogeneous) or first-order (fractional area) approximations (e.g. fire, land use). By using these simpler approximations, existing models miss important ecological phenomena, such as the spread of disturbance initiated in one age class or vegetation type into other vegetation within that grid cell. Depending on whether these models assume fractional areas are completely independent or randomly-distributed, these approaches will systematically either over- or underestimate (respectively) the degree of spatial adjacency occurring on the landscape. This will potentially bias estimates of dispersal limitation, lateral shading, microclimate, and lateral hydrologic and biogeochemical fluxes (Melton & Arora, 2014).

Even where spatially-explicit models are computable (e.g. landscape-scale models of vegetation communities and biogeochemistry), there is often considerable uncertainty in the initial conditions. Spatially explicit models require state variables to be estimated at a fine spatial resolution (Shifley, Thompson, Dijak, & Fan, 2008), which is very data intensive and frequently underconstrained. Furthermore, the errors in spatial maps of initial conditions are not independent, so the uncertainties do not simply average out with the number of grid cells. In contrast, with spatially-implicit models we can often generate estimates of the probability distributions of age classes and their adjacency with much greater confidence (law of large numbers) than we can map explicitly. For example, I may be able to estimate the fraction of a landscape that's a certain age class (e.g. 10-20 year old) much more precisely than I can estimate the age of a specific 30x30m pixel. Because of this, the total predictive uncertainty in a spatially explicit model could be larger than a spatially-implicit approximation, for example if the initial condition uncertainties of the spatial model outweigh the approximation errors of the implicit model (Dietze, 2017). Without detailed inventory data, initializing a spatially explicit model presents a trade-off between feasibility and accuracy.

Beyond the global and vegetation modeling communities, our derivation can act as a null model for spatial processes like arrangement, location dependence, and absolute distance dependence. Arrangement can have an effect on certain contagious disturbances: for example, corridors can differentially affect seed dispersal dependent on angle relative to prevailing wind direction (Damschen et al., 2014). Habitat fragmentation can correlate with overall abundance of habitat, raising questions about the separability of configuration from size in occupancy modeling (Fahrig, 2002; Prugh, Hodges, Sinclair, & Brashares, 2008; With & King, 2018). Absolute distance dependence is common in invasion ecology, where rare dispersal events over long distances can have a large effect on the subsequent colonization rates (Nathan, Cronin, Strand, & Cain, 2003). While some processes have spatial dependence that cannot be captured in our framework, the assumptions of our approach allow it to act as a nontrivial null-model to separate those effects (Rosindell, Hubbell, & Etienne, 2011). Explicitly accounting for size with adjacency is useful for disentangling the effects of size and arrangement, which often co-occur and can lead to misattribution (Prugh et al., 2008).

4.2 Empirical analysis

In this analysis we characterized Oregon's and Florida's disturbance regimes based on their size distributions and the relationship between disturbance size and interior ratio. We hypothesized that these metrics would differentiate between contrasting US state-wide disturbance regimes and disturbance types, and would reflect the nested structure of ecoregions. Broadly, we found this to be true. Our interior ratio curves were able to significantly differentiate between US state, ecoregion, and disturbance types (Table S1.4). In particular, different disturbances had characteristic interior ratios curves. Fire disturbances had compact configurations while several anthropogenically controlled classes (herbicide and other mechanical) spread dendritically. Relative to other mechanical and herbicide thinning spread in a compact way, but notably spread more dendritically at large disturbance sizes. This could indicate that thinning management strategies are fragmenting landscapes compared to natural disturbances. That said, the hierarchical structure of our analysis did not capture all possible permutations of lumping and splitting disturbance types, so similar curves (ie Clearcut and Wildfire; Figure 1.11) might have been lumped if evaluated independent of other disturbance classes. Overall, these results suggest that our metric captures the major features of the regions' disturbance regimes, and highlights the effects of anthropogenically mediated disturbances.

Size distributions of disturbances were generally distinct, but not sufficient to differentiate all disturbance types. That said, ecoregion-level size distributions had similar shapes (Figure 1.9). The consistent shape of the size distributions could be an artifact of the LANDFIRE disturbance attribution (Unknowns were the largest class of disturbance events) and could reflect the dominance of fire and thinning in both Florida and Oregon. Visually and statistically, the ecoregion size distributions support the nesting structure of the ecoregions: Florida ecoregions are more similar to each other than they are to the Oregon ecoregions (Figure 1.9; Table S1.2). Disturbances reflect that high spreading probability creates larger disturbances: prescribed fire, wildland fire, and wildfire are the most long-tailed distributions (Figure 1.9).

Overall, a strength of this empirical analysis is that it describes disturbances in terms of size and of configuration separately, which contrasts with many spatial metrics which convolve the two (e.g. mean interior/total). That different sources of disturbance have different spatial patterns in disturbances alone is not an unexpected result. Intuitively, different disturbance mechanisms have different spatial signatures. A roadway-construction is smaller and narrower than a typical commercial thinning. These findings take that intuition a step farther and explore the patterns that emerge at larger scales. When an ecosystem's disturbance regime is changing, that change will manifest as changes to disturbance size, or disturbance configuration (the interior ratio curve), or both. In the future, if we characterize more disturbance regimes in terms of these metrics, and better understand what factors drive their variability in time and across large spatial scales, it should be possible to use these relationships to forecast the spatial scaling of changing disturbance.

As an example, consider a shift in disturbance regime that doesn't change the disturbance size, but shifts the shape from dendritic to compact. Dendritic disturbances create corridors through the landscape, which effects the demography of the ecosystem by changing migration, favoring certain dispersal mechanisms, and increasing the propagule pressure of certain areas. Size and shape of patch plays a role in the success of invaders (Fahrig, 2002; McConnaughay & Bazzaz, 1987). Dendritic disturbances alter the abiotic properties of a system through the creation of edges. Edge-effects have been found in forest systems to increase carbon uptake, increase available light, and increase nutrient deposition (Reinmann & Hutyra, 2017). At the other extreme, more compact disturbances could cause more evenly aged composition and introduce more within-patch homogeneity by having a larger fraction of the disturbed pixels "sheltered" from surrounding areas.

Many contagious disturbances are projected to change in magnitude, severity, and location with climate change (Bradley, Wilcove, & Oppenheimer, 2010; Flannigan, Stocks, & Wotton, 2000; Mitchell et al., 2014a; Parks et al., 2016). Ultimately, these metrics will help us make concrete predictions of how to scale up these disturbances' regime changes. To be able to do this the variability within these metrics needs to be explored: How do they change year-to-year and place-to-place? How is this variability related to changes in weather, climate, and characteristics of the biotic and abiotic environment? This analysis demonstrates that interior ratio curves have the potential to communicate unique information about contagious processes and we encourage evaluating its utility in future work.

4.3 Opportunities and Challenges in Future Implementation

Implementing this spatially-implicit framework in real-world models requires a number of inputs be to derived through empirical analysis. First, the initial condition for adjacency, $A_{t=0}$, needs to be estimated for every large-scale grid cell. Given maps of current vegetation, this is computationally intensive but a relatively straightforward operation either within GIS or scripting languages with geospatial libraries (e.g. R). Next, users need to then decide whether to forward simulate disturbances and interior ratios based on initiation probability and spread probability (Section 2.1), or to rely on empirically observed size distributions and interior ratios (Sections 3.2 and 3.3). For short-term simulations, relying on empirically-derived statistics, such as those derived here for Florida and Oregon, is probably the easiest way to implement a wide range of different disturbance types. The empirical analyses conducted here could be further broken down using empirical covariates, such as weather, to capture changes interannual variability in disturbance size and shape (Hu et al., 2010). For longer-term simulation, forward simulations have the advantage of being able to extrapolate to new conditions. In the simplest simulations explored so far, the initiation and spread probabilities were typically held constant through time, for different age classes, and as a function of disturbance size, but as discussed earlier all of these can be made to vary based on either mechanistic models (e.g. fire ignition and spread; Kitzberger, Aráoz, Gowda, Mermoz, & Morales, 2012) or empirical observations. In these cases, there is a well-established body of literature deriving such relationships for spatially-explicit landscape models that should be directly translatable to inform spatially-implicit approaches (Mann et al., 2012; Seidl et al., 2011).

Once the concept of dynamic adjacency is in place within large-scale models, this opens the door for improving the representation of many other ecological processes within large-scale models. First and foremost is probably the addition of edge effects, such as lateral light penetration versus shading, as 75% of forests globally located < 1km from an edge (Haddad et al., 2015). Depending on the default assumption, which varies from model to model, current approaches are either massively underestimating how bright large disturbances are, or treating small disturbances as receiving full sun. Edge effects are known to have large impacts on microclimate (temperature, humidity, wind, etc.), which will have impacts on all aspects of modeled ecosystem function (productivity, biogeochemistry, hydrology, carbon storage, etc.). In addition to edges, adjacency can also be used to improve representations of dispersal limitation within large scale models, which typically assume seed is equally available at all points within a large grid cell, using the same approach of iterative multiplication of an adjacency matrix that we used here to simulate contagious spread. This could also be particularly useful for representing invasive species in large-scale models. Finally, adjacency could also be used to improve the representation of other lateral fluxes, such as hydrologic or nutrient flows.

We have argued that our size distribution and interior/total ratio metrics describe disturbance regimes in a way that forwards our fundamental understanding of disturbances. However, for a metric to be useful it has to be practical to measure. How difficult are these metrics to estimate empirically? Potential challenges arise depending on the scale of interest. At scales where spatial data is common (remote-sensing products, GIS analyses) calibration is straightforward. More work needs to be done to see how these metrics vary with environmental variables and time to clarify exactly how much data is required to fully characterize a disturbance regime. However, our results suggest that these metrics capture nuanced information about a disturbance regime. Measuring these metrics across landscapes presents the dual opportunity to model disturbance and probe theoretical implications of these metrics.

5. Conclusion

In this paper we lay out a theoretical derivation for spatially implicit scaling of disturbances, and explore the descriptive capacity of metrics that emerge from our derivation. We found that we were able to capture how different spread probabilities alter a landscape, and could update adjacency dynamically with new disturbances and stand age. We note the implications of this technique apply widely to multiple problems in scaling through the improvement of ecosystem models, development of null models and characterization of disturbance regimes.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

MCD contributed conception of the study and mathematical derivation; TDM and implemented simulation tools and MCD ran simulations; TDM performed the empirical analysis; TDM and MCD both wrote sections of the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

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Data Availability Statement

The publicly available LANDFIRE Disturbance dataset used in this study can be found in at the LANDFIRE host website https://www.landfire.gov/disturbance_2.php. All code used to generate intermediate measures and analysis is publicly available at https://github.com/mccabete/SpatialAdjacency.

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CHAPTER TWO: A WORKFLOW FOR ITERATIVELY CONSTRAINING PARAMETER UNCERTAINTY IN PROCESS-BASED MODELS

Abstract

In process-based models, parameter uncertainty can dominate overall uncertainty, especially in novel circumstances. We introduce an iterative workflow for reducing parametric uncertainty that we demonstrate by calibrating a vegetation demographic model, the Ecosystem Demography model v2.2 (ED2), for the invasive grass cogongrass. Our workflow suggests using uncertainty analyses to iteratively progress through three different forms of constraint: 1) synthesis of literature data, 2) targeted field work, and 3) statistical constraint. For cogongrass, few literature values existed, so we used the results of an uncertainty analysis to design a target field season, followed by a round of statistical constraint to fit parameters not directly estimateable from field data. From our field collection, we found that cogongrass had a lower quantum efficiency than average C4 grasses, and a higher stomatal slope. This suggests cogongrass is adapted to low-water and high-heat situations, but may be light limited. We found that our targeted field data reduced parameter uncertainty and output uncertainty, allowing model-specific parameters to dominate output uncertainty. Finally, statistical constraint further reduced parameter uncertainty, but did not reduce output uncertainty, as model structural error began to dominate.

Introduction

Predictions of future ecosystem trends allow society to anticipate environmental challenges, design policy, and adapt to climate change. Models that simulate processes under future conditions are central tools that can generate these predictions. For example, process-based Earth system models of the land, ocean, climate, and energy sector are what generate the predictions used in the Intergovernmental Panel on Climate Change's Sixth Assessment Report (Chen et al., 2021; Masson-Delmotte et al., 2021). Process-based models have clear strengths: they embody our current knowledge and hypotheses about how systems work, and they can predict a system's response to novel circumstances (Dietze, 2017b). However, such models often contain large numbers of parameters that can be difficult to measure, which can result in high parameter uncertainty. In the terrestrial carbon cycle modeling community, parameter uncertainty has been a dominant source of overall uncertainty (Quetin et al., 2020; Shiklomanov et al., 2020). Even in cases where other sources of uncertainty dominate (i.e. climate Lovenduski & Bonan, 2017, model structure Raiho et al., 2020), parameter uncertainty is usually still a large source of uncertainty, and represents a source of uncertainty that can be reduced by incorporating more information. Here we present a workflow for constraining parameter uncertainty, using a model of an invasive grass as a case study.

There are three broad techniques for constraining parameter uncertainty: incorporating parameter estimates reported in the scientific literature, measuring parameters directly, and constraining parameters indirectly using statistical inversion techniques (Figure 2.1). Each method has trade-offs. Literature values can be incorporated into parameter distributions via the construction of informative Bayesian priors, formal meta-analyses, and hierarchical literature synthesis (LeBauer et al., 2013). Databases of trait values like the TRY and BAAD databases have made literature synthesis easier by collating diverse datasets across a research community (Falster et al., 2015; Kattge et al., 2011). But pre-existing scientific literature may not inform parameters for emerging systems, like novel diseases or invasive species, because the system itself has yet to be described. In addition, the existing body of scientific literature has biases. In terrestrial ecology, above ground measurements are more common than belowground measurements (Dietze et al., 2014), despite roots' control over carbon, water, and nutrient cycles (Fan et al., 2017; Jackson et al., 1997). More insidiously, higher income areas are better sampled (Raja et al., 2022), researchers from the global South, women, and minorities are less likely to be cited or participate in research (Collyer, 2018; National Center for Science and Engineering Statistics, 2021; Ross et al., 2022). Relying on pre-existing measures synthesizes existing knowledge, but carries forward gaps, biases, and does not capture new systems.

Measuring data offers the opportunity to correct gaps, biases, and tackle the unknown. With good reason, conducting measurements is a foundational part of the scientific method. Measurements allow us to test hypotheses built into models (Dietze, 2017a; Medlyn et al., 2015). New measurements can observe "surprising" results that spark new lines of inquiry (Lindenmayer et al., 2010). However, measurements come with financial, personnel, and time costs. Getting data to constrain some parameters can be logistically difficult, or impossible. If parameter values change over environmental gradients, limited measurements can introduce bias (Fisher et al., 2018; Reich et al., 2014). Not all parameters in process-based models have real-world analogues that can be measured.

Statistical methods can constrain model-specific parameters, and can be faster to implement than data collection. However, different statistical techniques have their own trade-offs in computational needs, the error introduced by the method, and how well the method matches the model structure (Fer et al., 2018; Pandit et al., 2019; Raiho et al., 2021). However, using only statistical constraints can calibrate parameters to solutions that do not reflect real-world understanding, and could limit applying models to new contexts (Luo et al., 2011; Medlyn et al., 2015).

Navigating the tradeoffs in each constraint technique can require expertise as diverse as weighing the feasibility of making difference type of field measurements, that gen get specific (i.e. arctic root measurements Euskirchen et al., 2022) to the computational gains made with model parallelization (Raiho et al., 2021). The varied disciplines that each constraint technique operates in can obscure when one technique becomes more appropriate, or when multiple techniques can work in concert.

We developed a workflow to weigh how and when to use each technique (Figure 2.1). As a case study, we constrain the parameters around the invasive grass *Imperata Cylindrica*, or cogongrass. We start with broad priors for a generic grass and then use a combination of targeted field work and statistical calibration to constrain uncertainty in our parameters. We quantify how much parametric uncertainty and output uncertainty each technique reduced, and the decision making process surrounding each choice.

In this study we use Cogongrass as our model system because it is a societally relevant invasive species, and we were interested in using an ecosystem model to understand how cogongrass affects the native forests it invades (Chapter 3). Cogongrass is a C4 perennial grass classified as a federal noxious weed with a widespread range reaching from Texas to Virginia. This range is growing; it is predicted to spread to Oklahoma and Tennessee (Noxious Weed Regulations, 2022; Holzmueller & Jose, 2011). Cogongrass' effect on the US landscape and many of its invasion mechanisms have not yet been tested (Estrada & Flory, 2015). Because cogongrass is an invasive species with few traits measured in the literature, our initial representation of cogongrass in an ecosystem model had high parameter uncertainty, and high output uncertainty. We use our workflow to systematically reduce cogongrass parametric uncertainty with two aims: 1) capturing cogongrass's distinct attributes that could make it an effective invader, and 2) reducing uncertainty in our model outputs.

Cogongrass may have traits that set it apart from native grasses, and make cogongrass an effective invader (Pyšek et al., 2012). Grasses with tall stature and drought resistant photosynthesis have been found to be more likely to invade (Canavan et al., 2019; Chuine et al., 2012). However, the traits of invasive grasses and native grasses can be similar (van Klinken et al., 2013). "Invasiveness" may be a product of introduction rate (Estrada & Flory, 2015; van Klinken et al., 2015) or the area being invaded (Pyšek et al., 2012).

When cogongrass invades, it forms a dense clonal monoculture that outcompetes other understory plants, including native C4 grasses (Daneshgar et al., 2008). Because of this, we hypothesize that cogongrass parameters (Table 2.1) will be more consistent with a highly productive plant photosynthesizing more efficiently than other C4 grasses. We expect Cogongrass to have higher values for measures of photosynthesis efficiency (quantum efficiency), higher values for measures of intrinsic water-use efficiency (stomatal slope), and lower values of root respiration compared to a generic C4 grass (Leakey et al., 2006; Leuning, 1995). By constraining parameter uncertainty, we can weigh how and if cogongrass traits are distinct from C4 grasses overall.

Using our workflow we aimed to reduce uncertainty in model predictions of cogongrass's leaf area index, net primary productivity, and evapotranspiration. By using our workflow, we hoped to reduce parameter uncertainty and in turn reduce output uncertainty. We hypothesize that each new form of constraint will reduce output uncertainty.

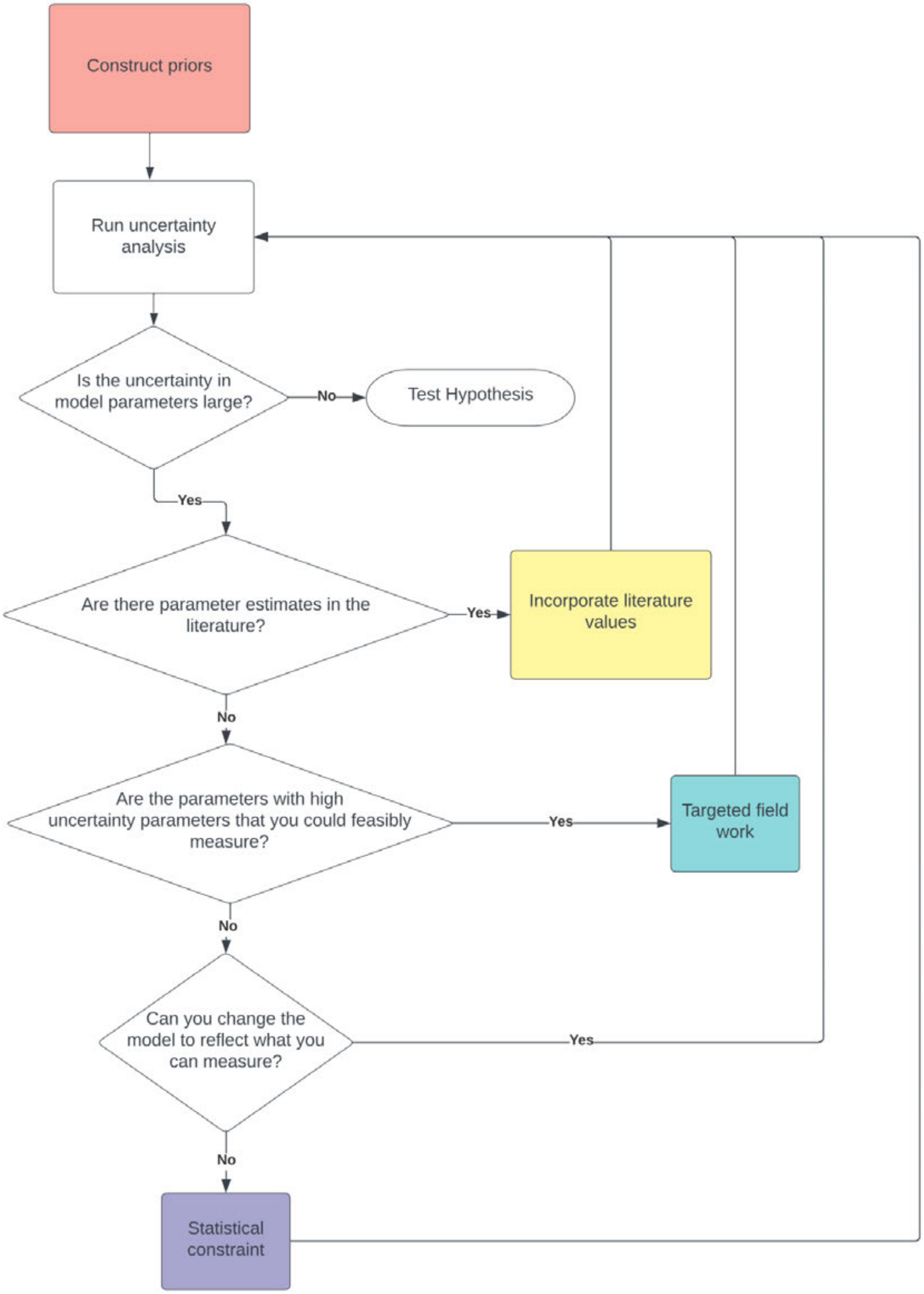

Figure 2.1: A Flowchart of Our Suggested Workflow. 1) Construct priors, 2) Run an uncertainty analysis that quantifies parameter uncertainty and identifies highly uncertain

parameters, 3) if parameter uncertainty is large, check scientific literature for parameter measures, and repeat uncertainty analysis, 3) if parameter uncertainty if still large, collect data on highly uncertainty parameters 4) if parameter uncertainty is still large, consider restructuring the model or using statistical constraint.

Methods

Workflow Overview

Our workflow has roughly four stages of iterative constraint. First, construct priors using external data (ie LeBauer et al., 2013) or techniques like expert elicitation (Dietze, 2017a; Marvin et al., 2009). Second, quantify and attribute which parameters are contributing the most uncertainty and focus data efforts (e.g. literature synthesis) on these parameters. In our case, because we were working with a single invasive species there was limited trait data in the literature, but in other literature-synthesis projects have had success (Dietze et al., 2014; Dokoohaki et al., 2022; Euskirchen et al., 2022; LeBauer et al., 2013; Meunier, van der Heijden, et al., 2021; Raczka et al., 2018; Viskari et al., 2019; Wang et al., 2013). Third, evaluate which uncertain parameters can be constrained with measurements. If after targeted field work parameters uncertainties are still large, evaluate if parameters are good candidates for statistical calibration (Dietze, 2017a; Fer et al., 2018; Pinnington et al., 2020; Raiho et al., 2021). Finally, if after statistical calibration, certain model parameters are still a large source of uncertainty, further reduction in uncertainty may require model restructuring.

To implement this workflow in our study, we began with broad priors that provided a functioning model-representation of cogongrass that could be run at our test site but which had a high level of parameter uncertainty. To reduce this uncertainty we ran an uncertainty analysis that quantified how uncertainty in different cogongrass traits contributes to uncertainty in model outputs including evapotranspiration, net primary production, and leaf area index. We focus on these ecosystem variables because they correspond to the ways cogongrass likely influences the system: water fluxes, carbon fluxes, and vegetation structure.

Based on the uncertainty associated with parameters, we determined what parameters needed to be targeted for field sampling (Figure 2.1, See Results: Priors and Targeted Field Work). After targeted data collection (See Targeted Field Work), we incorporated our field data into the meta analysis to constrain the posterior parameter distributions used for model runs described in the Statistical Constraint Section (Figure 2.1). We then conducted a second uncertainty analysis to translate parameter constraint into uncertainty reduction (Figures 2.3-2.5).

Finally, after using statistical inversion techniques to constrain the unmeasurable parameters (Figure 2.1, Section Priors + Targeted Field Work + Statistical Constraint), we performed a third round of uncertainty analyses. By comparing the uncertainty reductions that occur between different rounds of uncertainty analysis we can quantify the contributions of literature synthesis, targeted field data collection, and inverse calibration to the overall model improvement.

The Ecosystem Demography Model

The Ecosystem Demography 2 model (ED2) is a spatially-implicit cohort-based vegetation demographic model (VDM) (Longo et al., 2019a & b; Medvigy et al., 2009;

Moorcroft et al., 2001). Tpo capture biogeochemical cycles, ED2 tracks plant-level ecophysiological processes (photosynthesis, respiration, allocation, turnover) and demographic rates (growth, mortality, reproduction, disturbance). To simulate ecological processes like succession and competition, ED2 aggregates individuals into cohorts of similar size and the same plant functional type (PFT), keeping track of changes in cohort size and density. ED2 is well suited for this project because it is able to capture water, light, and carbon competition, and has a history of applications in the southeastern US (Dietze et al., 2014; Miller et al., 2016;De Kauwe et al., 2014; Medlyn et al., 2015; Walker et al., 2014;).

Grasses are represented as having three carbon pools: leaves, fine-roots, and non-structural carbon. Acquired carbon is allocated to each pool according to allometries, and then carbon is consumed via respiration to maintain living biomass. If the carbon balance is negative enough to consume the non-structural carbon pool, the plants will not grow and mortality will increase, killing plants as they age and crowd. If the carbon balance is positive, plants will grow new biomass and allocate carbon to reproduction. Leaf area index (LAI) is calculated by multiplying specific leaf areas with leaf biomass, and then LAI is used to modify the amount of possible photosynthesis.

ED2's representation of cogongrass is controlled by parameters described in Table 2.1. In ED2's representation of C4 grasses, photosynthesis is determined by stomatal slope, Vmax, and quantum efficiency. These parameters are used to fit the Farquar model of photosynthesis with modifications for C4 plants (Collatz et al., 1992; Farquhar et al., 1980) where photosynthesis is not limited by a CO_2 compensation point

(Longo, Knox, Levine, et al., 2019). Photosynthesis is also modified by the amount of available water. Water conductance controls water availability as modified by root biomass.

Detailed explanations of ED2 components and each parameter's definitions can be found in the supplement of Longo, Knox, Levine, et al., (2019).

Table 2.1: Cogongrass Parameter Definitions and Data used to constrain Parameters

Parameter	**Definition**	**Unit**		**Data Source**	**Prior**	**Physical Analog**
Fine Root Allocation	ratio of fine root to leaf biomass	ratio		2019 Biomass measurements	grasses	Yes
Stomatal Slope	The slope of relationship between stomatal conductance and photosynthesis	ratio	1 2	2019 Photosynthesis measurements	C4 grasses	Yes
Vmax	Maximum rate of carboxylation	umol CO_2 m-2 s-1	3	2019 Photosynthesis measurements	graminoids	Yes
Quantum Efficiency	Percentage of light converted to carbon	Mol CO_2 fixed per mol irradiance	3	2019 Photosynthesis measurements	C4 grasses	Yes
Specific Leaf Area (SLA)	Leaf area per unit dry biomass	m2 kg-1	1	Dataset from concurrent project. (Hiatt & Flory, 2020)	grasses	Yes
Root Respiration	Temperature dependent rate of CO_2 released by roots	umol CO_2 kg-1 s-1	1	Root Respiration measurements	C4 grasses	Yes

Root Turnover Rate	Temperature dependent rate of fine root loss	ratio year -1	1	-	grasses	Yes
Reproduction Fraction	Fraction of storage carbon converted to seed reproduction	ratio	1	-	plants	Yes
Mortality Coefficient	Carbon Balance Ratio for which morality rapidly increases	ratio year -1	1	-	plants	No
Growth Respiration	Proportion of daily carbon gain lost to growth respiration	ratio	1	-	grasses	No
Water Conductance	Rate of water supplied to plant	m2 kg-1 s-1	1	-	plants	No

[1] Longo, Knox, Levine, et al., 2019
[2] Leuning 1995
[3] Farquhar et al. 1980

Site Description

Our measurements for cogongrass come from both natural cogongrass invasions and a 6-year ongoing garden experiment at the University of Florida Bivens Arm Research Site (BARS) in Gainesville, Florida (29°37′42.4″N, 82°21′14.4″W). The long-term garden experiment has ten 4m x 4m replicates of four treatments: native vegetation and ambient precipitation, cogongrass and ambient precipitation, native vegetation and drought, cogongrass and drought (Alba et al., 2017). BARS also has a naturally occurring cogongrass invasion. We measured Vmax, stomatal slope, quantum efficiency, aboveground and belowground biomass on the ambient treatments of the garden experiment. Because the planting timing and initial biomass of cogongrass at the experiment was known, we used that information to initialize our ED2 model simulations (See Statistical Constraint Section). Root respiration was measured on samples taken from the natural invasion.

The Predictive Ecosystem Analyzer: PEcAn

PEcAn provides a common toolbox for working with and analyzing ecosystem models as well as accessible web-based tools for model execution (LeBauer et al., 2013, Fer et al. 2021). PEcAn contains a workflow for parameterizing new vegetation types by compiling field and literature data that provide constraints for individual model parameters. These data are synthesized within PEcAn in an automated Hierarchical Bayes literature synthesis that estimates each model parameter as a probability distribution (LeBauer et al., 2013). Parameter values used for PFT's can be found at http://psql-pecan.bu.edu/bety. PEcAn also hosts specific software tools used in the analyses below. Tools used are documented in Table 2.2.

Table 2. 2: PEcAn Modules Used in this Paper

	Paper Subsection	Citation
Hierarchical Bayes literature synthesis	The Predictive Ecosystem Analyzer	(LeBauer et al., 2013)
Sensitivity and Uncertainty Analysis	Uncertainty Analyses	(LeBauer et al., 2013)

Parameter Data Assimilation	Inverse Calibration of Cogongrass Water Conductance and Growth Respiration	(Fer et al., 2018)
Photosynthesis Parameter Estimation	Constraint of Cogongrass Photosynthesis -- Parameter Estimation	(Feng & Dietze, 2013)

Analyses were done using PEcAn v1.7.1 available at https://github.com/PecanProject/pecan.

Uncertainty Analyses

PEcAn uncertainty analyses begin by estimating model parameter sensitivities using a one-step-at-a-time sensitivity analysis. PEcAn evaluates each parameter at the posterior median, and at +1 SD and -1SD, while all other parameter values are held at their median.Then, PEcAn fits a natural cubic spline to the relationship between the model output and parameter values. How sensitive model output is to change in parameters is approximated as the derivative of the spline.

Model output uncertainty was estimated by running 50-ensemble member runs sampling from posterior distribution sets associated with different stages of our workflow (Figure 2.1). For uncertainty at Priors, Targeted Field Data, and Statistical Constraint stages, ED2 was run from 2013-2019 at BARS. 2013 was the time of initial planting. We initialized ED2 with cogongrasses starting biomass and density identical to the experimental planting biomass and density described by (Alba et al., 2017). ED2 used the ERA5 Reanalysis product as meteorological drivers (Hersbach et al., 2018.).

The uncertainty attributed to each parameter is estimated by comparing the sum of the variance in each parameter to the total variance in model output as estimated by the 50 ensemble members. The variance in each parameter comes from the estimate from the hierarchical literature synthesis (See Predictive Ecosystem Analyzer section), and is translated from the parameter domain into the model output domain by the sensitivity spline.

For visualization purposes, this spline approximation is also used to approximate the elasticity of model output, and partial variance decomposition seen in Figures 2.3-2.5. “Coefficient of Variation” refers to normalized parameter variance, which is a unit-corrected, and output-mean corrected measure of variance. By contrast “Variance” in figures 2.3-2.5 refers to the raw variance in model output attributed to a specific parameter. “Elasticity” is the spline-approximation sensitivity corrected for the mean value of the parameter. Further details described in (LeBauer et al., 2013)

Priors

Cogongrass is an invasive species, and few measurements of the traits ED2 requires exist in the literature. Because of this, we began our development of our single-species cogongrass PFT by starting with the priors from a similar ED2 PFT developed for a grass of the same family with the same photosynthetic strategy (switchgrass; *Panicum virgatum*). The priors for switchgrass were taken from literature estimates (Figure 2.1) of trait-values based on board categories: like “plants”, “grasses”, “C4 grasses”, and "graminoids" that are equally applicable to cogongrass (LeBauer et al., 2013; Table S2.1).

Targeted Field Work

Constraint of Cogongrass Root Respiration

Root respiration is a difficult parameter to constrain because it is often measured in conjunction with soil respiration, and the partitioning between fine roots, rhizosphere, and soil aggregates is ill-defined and difficult to separate physically (Kelting et al. 1998, Kuzyakov 2006). We measured root respiration with a closed-path technique that used a sealed soil respiration chamber (Figure S2.1). Respiration measures were taken by running the soil respiration program on washed roots placed in a small jar that was then put into the sealed soil chamber 6400-09 (Figure S2.1 A). As part of the automatic soil program, a target CO_2 is set based on ambient CO_2, and then the CO_2 level in the chamber is drawn down to below the target and allowed to increase past the target for a number of cycles (Figure S2.1 C). The program estimates the respiration rate by recording how quickly CO_2 levels grow to the target amount (Healy et al., 1996). 1-3 wet biomass grams of fine roots and rhizomes were rinsed of soil, patted dry, and weighed. Then roots were measured within the soil-respiration chamber (Figure S2.1 B). To amplify the signal, roots from multiple plants were aggregated. In cases where our mass of fine-root biomass was still not enough to distinguish a signal, we measured rhizomes and fine roots both independently and together. For all samples we then dried the roots and rhizomes in a drying oven set to 60 degrees C for 48 hours, and normalized the respiration rate by dried biomass. After quality control, we had 10 estimates of rhizome respiration and 9 estimates of fine root respiration.

Constraint of Cogongrass Biomass and Allometries

Fine root biomass allocation (expressed in ED2 in terms of the fine root to leaf biomass ratio) is another important parameter to constrain cogongrass uncertainty (Figures 2.3-2.5). We made measurements of fine root and leaf biomass at BARS.

For each of the 10 4m X 4m plot, a 30 cm^2 quadrat was placed in a subplot location for biomass harvesting. Quadrats were moved within a subplot to avoid seedlings and pre-existing measurements. All the live tillers were counted, and then harvested with garden shears. The harvested aboveground biomass was put into a drying oven set at 60 degrees C for 7 days. A soil core was taken from the center of the plot. Soil cores were taken using a hammer-style soil corer, with a depth of 15.5 cm and a diameter of 5.5 cm. The cores were then stored in a freezer until processing.

The belowground biomass was processed by first thawing the soil core, then sieving through a 2mm sieve and a 420 micron sieve. When possible, the soil was sieved dry; however, most soil cores required water-draining. Rhizomes and fine roots were kept separate. Roots were rinsed of soil before drying. Roots clearly dead or non-cogongrass were excluded. Roots with unknown origin were included. Because fine roots can become quite small, the stopping point for root picking was to remove roots until the only roots found were unbranched roots 4mm in length or smaller. After that, roots were removed for an additional ten minutes. Each soil core took approximately two hours to process. After roots and rhizomes were removed from the soil they were put into a drying oven at 60 degrees C degrees for 48 hours and then weighed. Aboveground biomass was calculated as the sum of the leaf and tillar biomass. Belowground biomass was the sum of fine root biomass and rhizomes. We collected 9 fine-root to leaf ratio measurements, 10 aboveground biomass measurements, and 9 Belowground biomass measurements.

Constraint of Cogongrass Photosynthesis -- Data Collection

In order to measure the parameters Stomatal slope, Vmax, and quantum efficiency, we used a LI-COR 6400 to measure light response curves where the level of light is started at maximum and slowly ramped down to zero, over 8-21 measurements, while other environmental variables are held constant. Light curves used a standard leaf-chamber portable infrared gas analyzer with a 1098 light source. CO_2 was held at either 400 ppm or 450 ppm depending on ambient levels. The LI-COR 6400 was calibrated before all measurements by zeroing the flow rate, CO_2 and humidity levels.

Standard photosynthetic response curves progress too quickly to be able to measure stomata at equilibrium, which is required to estimate stomatal slope, therefore light curves were taken following the techniques described by Leakey et. all (2006), and in the supplement of Wolz et al. (2017). Our methods differ from Leakey and Wolz's in three small ways. First, measurements were performed on a combination of in vivo and excised leaves. Excised leaves were harvested pre-dawn and cut underwater. Leaves were harvested from the BARS long-term garden experiment using edge leaves that had grown out from under the precipitation exclosures. Leaves suspected of embolism were discarded. We attempted five excised leaf light curves, and were only able to produce two reliable curves. We measured field curves separately to compare to the excised curves and found that excised leaves occasionally had comparable levels of photosynthesis – but sometimes had low or no detectable photosynthesis. We attributed this to embolisms forming during the excising process. Leaf-harvesting proved difficult enough that we switched to in-vivo leaves early in our measurements. Second, Leakey was able to hold all other environmental variables constant. Because the majority of our curves were taken in vivo, temperature varied as the day progressed and several curves were subject to humidity swings. Finally, the area for cogongrass leaves was smaller than that of the chamber. To estimate leaf area the width of the leaf was measured, and multiplied by the length of one side of the leaf gasket chamber ($\sqrt{6}$cm^2).

In order to let the stomatal slope stabilize, we set a minimum wait period between two light steps to ten minutes, and a maximum wait period of a half hour. In addition, CO_2, humidity and flow rate had to be stable for a full minute before measurements were taken. All light curves but one began at a starting value of 2000 photon flux density before measurement began at 1500 photon flux density. We set the final light curve to start at 2300 based on observations that typical days in Florida can achieve up to 2300 photon flux densities. The LI-COR 6400 was matched before each measurement. Field curves were taken during a range of times, from dawn until roughly 2:00 pm.

To provide additional constraint, two humidity curves were taken. For the first curve, incoming radiation was fixed at 1500 photon flux density. The second was 700 photon flux density. We started at roughly 80% humidity, and kept it steady for about 15 mins. Every 15 minutes, we would manually reduce the humidity by about 20-25%. Humidity reached a minimum of about 10%.

Constraint of Cogongrass Photosynthesis -- Parameter Estimation

Light and humidity curves were used to estimate values for stomatal slope, Vmax, and quantum efficiency. Stomatal slope represents how quickly plants adjust their stomata to environmental changes like light, humidity, and temperature (Table 2.1). Stomatal slope was estimated by fitting a linear model to a plot of stomatal conductance versus photosynthesis corrected for humidity and temperature, using the light curves from 6 different plants (Figure S2.2). Specifically, stomatal slope was estimated using the Leuning (1995) model:

$$stomatal\ conductance = conductance_{closed\ stomata} + stomatal\ slope * \frac{photosynthesis}{respiration * (1 + \frac{vapor\ pressure\ deficit}{leaf\ level\ water\ deficit})}$$

where leaf-level water deficit was set to a C4 default, 0.016. Photosynthesis, respiration, vapor pressure deficit, and stomatal conductance were all measured. Vmax and quantum efficiency are both parameters that describe how photosynthesis could be limited by the plant's photosynthetic machinery itself (Table 2.1). We estimated Vmax and quantum efficiency using a hierarchical Bayesian implementation of the Farquhar, von Caemmerer, and Berry (1980) photosynthesis model as described in Feng and Dietze

(2013), and implemented in the PEcAn photosynthesis module (https://github.com/PecanProject/pecan/tree/develop/modules/photosynthesis).

Statistical Constraint

Inverse Calibration of Cogongrass Water Conductance and Growth Respiration

After the inclusion of field data, the largest sources of uncertainty in LAI, NPP, and Evapotranspiration were water conductance, fine root allocation, and growth respiration (Figures 2.3-2.5). Water conductance and growth respiration pose a challenge because they have no physical analog to measure.

Any additional constraint of water conductance and growth respiration required statistical techniques. We used a particle filter to use the field observations of aboveground and belowground biomass to narrow the possible values of water conductance and growth respiration (Dietze, 2017a).

This analysis consisted of four steps.

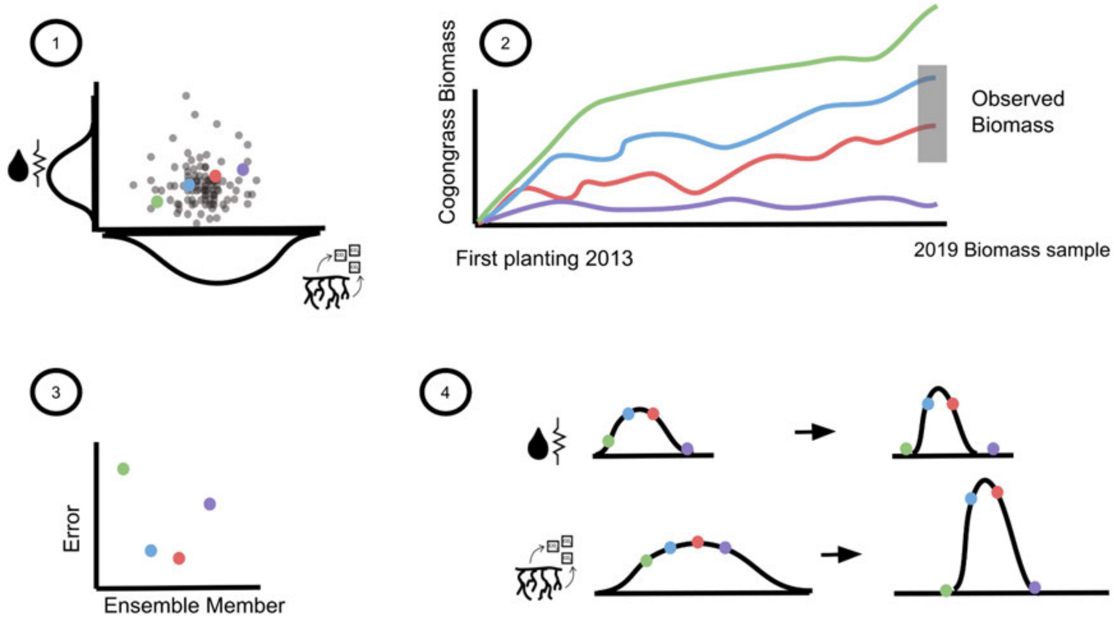

Figure 2.2: Conceptual Diagram of Inverse Calibration using a particle filter. 1) Representative values from the joint distribution of water conductance and growth respiration are chosen. 2) The parameter values are used to generate an ensemble of model runs from the first planting until observations are collected. 3) Parameter values are weighted based on an ensemble's agreement with data. 4) Weights are used to constrain initial water conductance and growth respiration parameter distributions.

First, we sampled from the joint distribution of water conductance and growth respiration using a Latin hyper cube method described in Fer et al., (2018). Second, we ran ED2 200 times using different values for water conductance and growth respiration (Figure S2.3). ED2 was run from Cogongrass first planting in 2013 until 2019 to match when aboveground and belowground biomass was collected in 2019. ED2 used the same initialization and meteorological forcing described in the Uncertainty Analysis section. Third, we weighted each ensemble based on prior weight and its ability to recreate observations. To calculate this, we compared each model run to our observations and calculated the sum of squares error. We used 9 belowground biomass observations, and 10 Aboveground biomass observations for constraint.

$$Aboveground\ ss_i = \sum^{n} (Aboveground\ Biomass_n - \theta_i)^2$$

$$Belowground\ ss_i = \sum^{n} (Belowground\ Biomass_n - \theta_i)^2$$

$Aboveground\ ss_i$ is the sum of squares error for each ensemble member compared to aboveground biomass observations. θ_i is a single ensemble member's estimate of biomass, and $Biomass_n$ is an observation of biomass.

We then used our error estimates to calculate the standard deviation for each ensemble member, Were σ_{ab_min} , and $\sigma_{bb_min}$are the smallest standard deviation between an ensemble's estimate of biomass and observed biomass for aboveground and belowground.

$$\sigma_{ab\_min} = \sqrt{min(Aboveground\ ss/10)}$$

$$\sigma_{bb\_min} = \sqrt{min(Belowground\ ss/9)}$$

Then, we calculated the log likelihood of our observations given the model output.

$$L(Aboveground\ Biomass\ |\theta_i) = \sum^{n} N\left(Aboveground\ Biomass_n, \theta_i, \sigma_{ab\_min}\right)$$

$$L(Belowground\ Biomass\ |\theta_i) = \sum^{n} N\left(Belowground\ Biomass_n, \theta_i, \sigma_{bb\_min}\right)$$

Then, we added the logged priors of growth respiration and water conductance.

$$P(\theta_i) = P_{wc}(\theta_i) + P_{gr}(\theta_i)$$

Where $P_{wc}(\theta_i)$ and $P_{gr}(\theta_i)$ are the logged priors on water conductance and growth respiration respectively. The full prior definitions are found in Table S2.2.

We weighted each ensemble member by the likelihoods and priors, and calculated an effective sample size from that weight, to verify that we had the power to estimate the mean and variance of our posterior distributions after weighting.

$$L(Obs \mid \theta_i) = L(Aboveground\ Biomass \mid \theta_i) + L(Belowground\ Biomass \mid \theta_i)$$

$$Weight_i = \frac{e^{L(Obs \mid \theta_i) + P(\theta_i)}}{\sum^{i} e^{L(Obs \mid \theta_i) + P(\theta_i)}}$$

$$Effective\ Sample\ Size = 1 \div \sum^{i} Weight_i^{2}$$

Fourth, to constrain our parameter distributions of water conductance and growth respiration, we calculated a weighted mean and variance of our ensembles. We then used moment matching to translate the weighted mean and variance of our ensemble into matching beta (growth respiration) and lognormal (water conductance) posterior distributions (Table S2.3).

Model Assessment

To check the effectiveness of our particle filter, we compared our model's ability to recreate biomass observations constrained via just targeted field work, or both targeted field work and statistical constraint. We compared two sets of 50 ensemble member runs, that were generated as described in the Uncertainty Analysis section. The two ensembles of modeled biomass evaluated on their ability to capture the median observed biomass using a Continuous Ranked Probability Score (CRPS) (Jordan et al., 2019). We used the median observation because observations were right-skewed (Figure 2.8). When interpreting CRPS scores, smaller numbers represent a better score.

Results

Priors

The parameters with the largest partial variances were fine root allocation, specific leaf area, and stomatal slope. Specific leaf area and fine root allocation were important across all three outputs (Figures 3-5 Priors Only). Some outputs had high partial variance attributed to growth respiration (NPP, LAI), quantum efficiency (NPP), vmax (Evap), and water conductance (LAI). Growth respiration has the largest partial variance for NPP.

Targeted Field Work

Based on our analysis we designed a targeted field season to measure highly uncertain parameters (Figure 2.1). We included field data from 6 photosynthesis curves, 19 root respiration estimates, 9 fine-root to leaf ratio measurements, and 96 SLA measurements.

With the constraint from our field data, we reduced parametric uncertainty for the majority of parameters (Figure 2.6; Figures 2.3-2.5 CV%). We had large parametric uncertainty reductions in specific leaf area, root respiration, and Vmax. Fine root allocation, quantum efficiency and stomatal slope all had smaller levels of constraint (Figure 2.6; Figures 2.3-2.5 CV%). Vmax and quantum efficiency's means shifted lower; Vmax (from 248 to 18), and quantum efficiency (from 0.057 to 0.047). Stomatal slope's mean shifted higher (from 3.4 to 4.53) (Figure 2.6; Table S2.4).

Field data reduced output uncertainty as well. The SD in LAI decreased by a factor of 2.52, and the mean shifted to a smaller LAI, from 1.62 to 0.98 with field data (Figure 2.7). NPP had an ~ 30 % reduction in SD, and had a lower mean NPP value (from 2.57×10^{-8} to 1.78×10^{-8} with field data) (Figure 2.7). Evapotranspiration SD reduced by ~ 43 % and moved to a lower rate of water loss (form 4.16×10^{-6} to 3.69×10^{-6} with field data) (Figure 2.7).

Partial variance attributed to model-specific parameters grew after incorporating field data. Across LAI, Evapotranspiration, and NPP, the most important parameters became water conductance, growth respiration, and fine root allocation (Figures 2.3-2.5 Variance). Elasticity for several parameters changed, but only translated into an increase in partial variance for water conductance and growth respiration. This suggested 1) that model-specific parameters started to become the dominant source of uncertainty after incorporating field data, and 2) that the updates in field-constrained parameters caused the model to shift to a part of parameter space that was more sensitive to trade-offs in the water and carbon balance.

Statistical Constraint

Because cogongrass may have effects on water and carbon cycling in the southeast (Fahey et al., 2018), we elected to pursue statistical methods to constrain water conductance and growth respiration (Figure 2.1). After applying a particle filter, we found that our overall ensemble had an effective sample of 40.23.

Water conductance was constrained by 2.5 fold on a log scale (~270-fold on the linear scale) and mean water conductance lowered (from 0.7003 to 0.0008) (Figure 2.6; Table S2.4). Growth respiration saw a 1.6 fold reduction in uncertainty, and narrowed the distribution at both ends, with a larger mean (from 0.29 to 0.35) (Figure 2.6; Table S2.4). When compared to the biomass data, model outputs were closer to observations after statistical calibration. When we compared the CRPS scores of model output with statistical constraint and field data constraint, the CRPS scores were lower than the CSRP scores of model output when constrained with field data alone. CRPS for aboveground biomass fell from 0.0187 to 0.0164. The CRPS for belowground biomass fell from 0.0205 to 0.0191(Figure 2.8). Finally, CRPS score for the ratio of above to belowground biomass fell from 1.443 to 0.9148 after statistical calibration (Table S2.5; Figure S2.5).

Despite the reduction in parameter uncertainty associated with calibrating the model with the particle filter (Figure 2.6), the partial variance associated with water conductance for NPP, LAI and evapotranspiration actually increased due to a further increase in elasticity (Figures 2.3-2.5 Variance).

The uncertainty around NPP standard deviation increased by 4% from the field-work only condition, and had a lower mean (from 1.78 x 10^{-8} to 1.33 x 10^{-8}) (Figure 2.7).

Evapotranspiration's SD increased by 36 %, and the mean decreased (from 3.69 x 10 $^{-6}$ to 3.18 x 10^{-6}) (Figure 2.7). For LAI, the combined field data and PF SD decreased by 16%, and shifted even lower than with field data alone (from 0.98 to 0.71) (Figure 2.7).

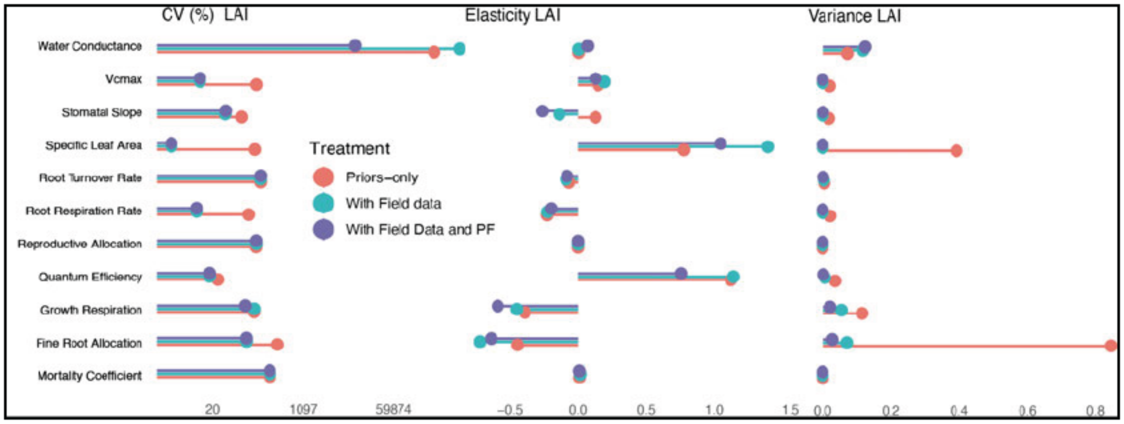

Figure 2.3: Variance of modeled Leaf Area Index (LAI) (m^2/m^2) attributed to parameters, parameter elasticity, and parameter coefficient of variation (normalized parameter variance). Parameter definitions Table 2.1.

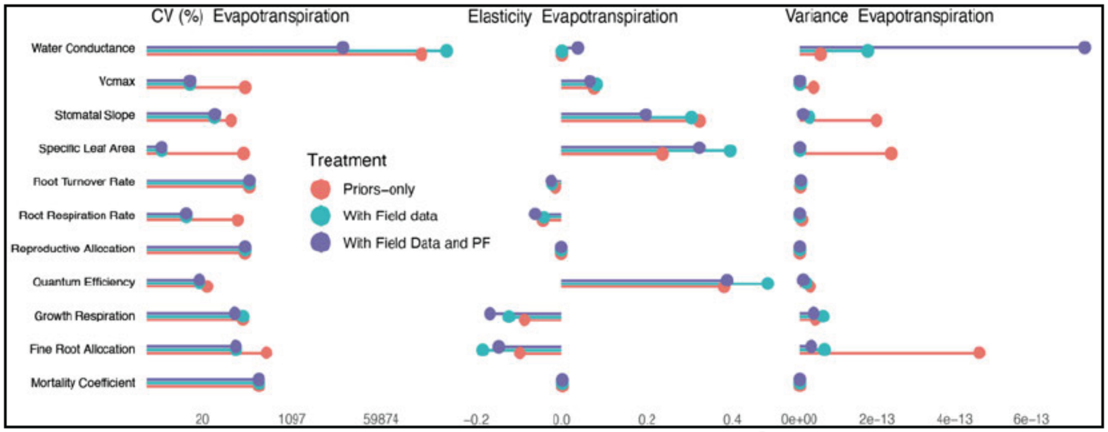

Figure 2.4: Variance of modeled Evapotranspiration (kg/m^2/s) attributed to parameters, parameter elasticity, and parameter coefficient of variation (normalized parameter variance). Parameter definitions Table 2.1.

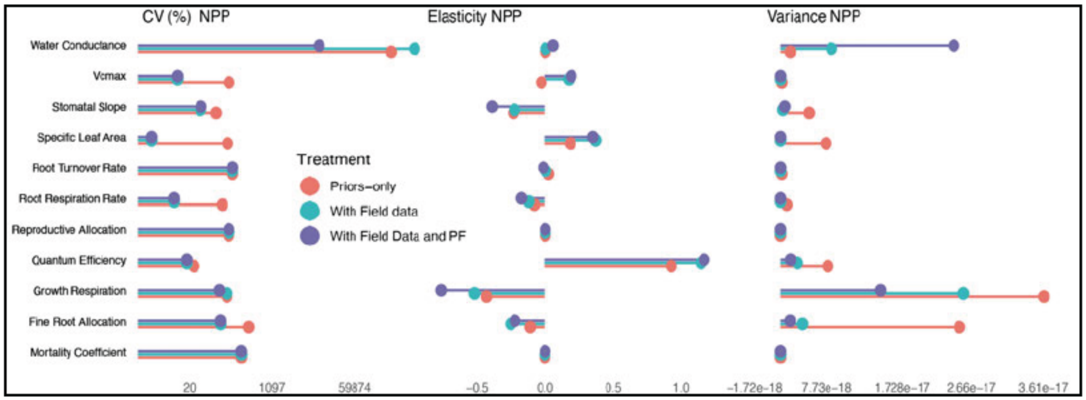

Figure 2.5: Variance of modeled Net Primary Productivity (NPP) (kgC/m^2/s) attributed to parameters, parameter elasticity, and parameter coefficient of variation (normalized parameter variance). Parameter definitions Table 2.1.

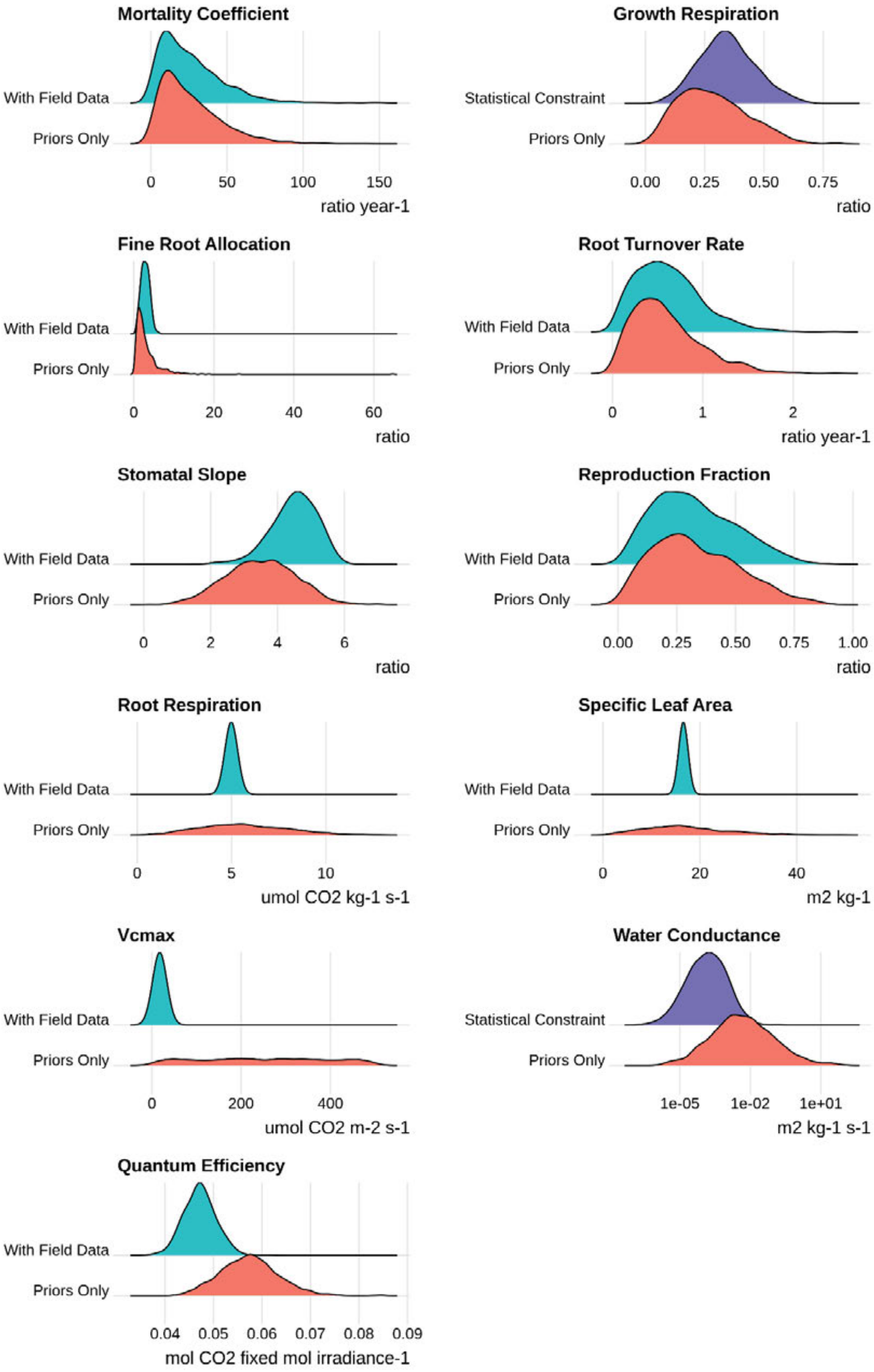
Mortality Coefficient
With Field Data
Priors Only
0
50
100
150
ratio year-1
Growth Respiration
Statistical Constraint
Priors Only
0.00
0.25
0.50
0.75
ratio
Fine Root Allocation
With Field Data
Priors Only
0
20
40
60
ratio
Root Turnover Rate
With Field Data
Priors Only
0
1
2
ratio year-1
Stomatal Slope
With Field Data
Priors Only
0
2
4
6
ratio
Reproduction Fraction
With Field Data
Priors Only
0.00
0.25
0.50
0.75
1.00
ratio
Root Respiration
With Field Data
Priors Only
0
5
10
umol CO2 kg-1 s-1
Specific Leaf Area
With Field Data
Priors Only
0
20
40
m2 kg-1
Vcmax
With Field Data
Priors Only
0
200
400
umol CO2 m-2 s-1
Water Conductance
Statistical Constraint
Priors Only
1e-05
1e-02
1e+01
m2 kg-1 s-1
Quantum Efficiency
With Field Data
Priors Only
0.04
0.05
0.06
0.07
0.08
0.09
mol CO2 fixed mol irradiance-1

Figure 2.6: Parameter distributions at different levels of constraint. Distribution widths are proportional to the CV% column in Figures 2.3-2.5. Reproduction Fraction, Mortality Coefficient, and Root Turnover Rate have no constraint. Parameters are described in Table 2.1. Distributions are described in supplemental Tables S2.1- S2.1. Distribution means are in Table S2.5.

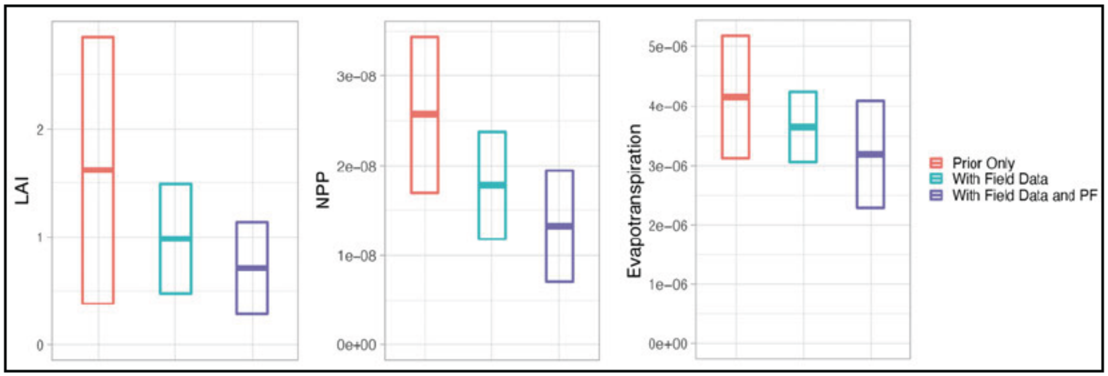

Figure 2.7: Mean and SD of Leaf Area Index (m^2/m^2), Net Primary Productivity ($kgC/m^2/s$), and Evapotranspiration ($kg/m^2/s$) from 2013-2019.

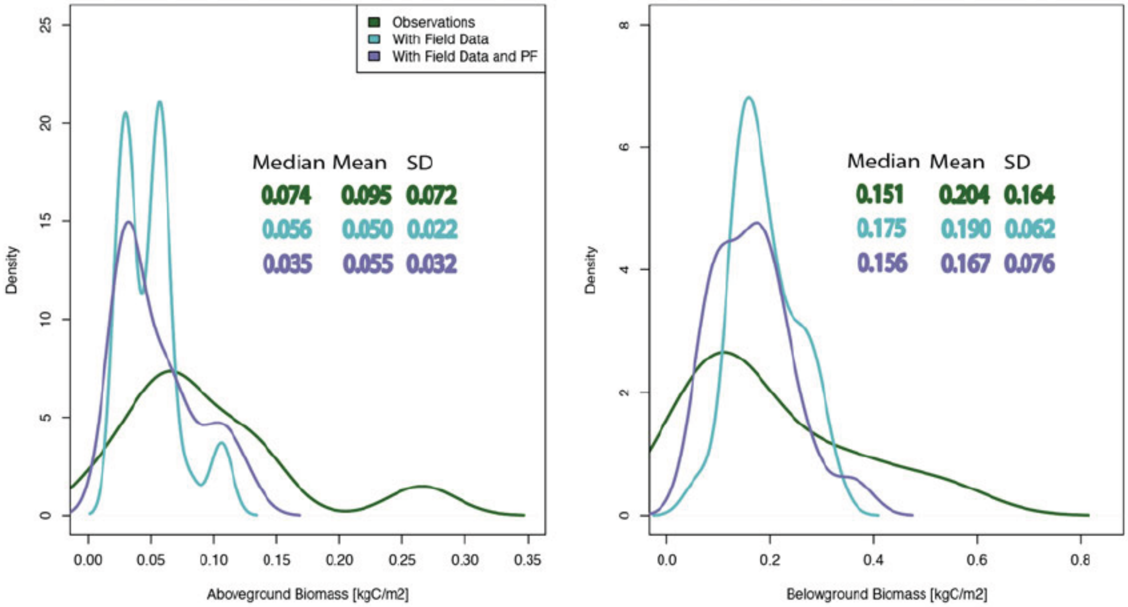

Figure 2.8: Density of observed above and belowground biomass compared to modeled above and belowground biomass with and without calibration. Modeled distributions come from 50-member ensembles with parameter distributions described in Tables S2.1-S2.3. Raw points in Figure S2.5.

Discussion

We set out to systematically constrain parametric uncertainty in an ecosystem model's representation of an invasive species. We started first by quantifying the uncertainty and sensitivity in the parameters' priors. After that, we designed a field season that targeted the largest sources of output uncertainty. Our field data constrained the overall uncertainty in LAI, NPP, and Evapotranspiration. Incorporating our field data changed the parameters the model was sensitive to – shifting sensitivity to photosynthetic control parameters, and SLA. While we were able to use our field data to indirectly constrain the partial variance attributed to growth respiration, the partial variance associated with water conductance increased. When we used a particle filter to reduce the parametric uncertainty in distributions of water conductance and growth respiration, the output uncertainty in NPP and Evaporation increased, and LAI slightly lowered. After both cycles of constraint, Cogongrass had a lower quantum efficiency and higher stomatal slope compared to priors (Figure 2.6).

We hypothesized that after constraint, cogongrasses' mean quantum efficiency value would be higher than the mean of the prior, reasoning that high quantum efficiency translates into higher productivity. We found the opposite (Figure 2.6; Table S2.5). This could be because cogongrass has some physiological aspect that makes it less light-use-efficient. Bundle sheath leakage of CO_2 has been shown to explain some variation in quantum yield in C4 grasses (Skillman, 2008). Experimentally, shading reduced cogongrass establishment, biomass, and sprouting (Estrada et al., 2016; Hamidavi et al., 2021). In contrast, we correctly hypothesized that mean stomatal slope would be higher than the prior estimate (Figure 2.6). In fact, cogongrass' mean stomatal slope is similar to LeBauer et al., (2013)'s stomatal slope estimate (mean 4.1 vs 4.5 Table 2.4) for *Panicum virgatum*, a grass used in biofuel production. These results suggest that cogongrass' photosynthesis is relatively efficient in hot and dry conditions, but has lower-light-use efficiency than other C4 grasses. It's unclear how drought tolerant cogongrass is. Greenhouse experiments found that cogongrass drought stress reduced biomass and reproduction more than nutrient stress (Hamidavi et al., 2021; B. Zhang et al., 2021), but also found that cogongrass can survive ~30 day periods without watering. A garden experiment found that precipitation exclusions had little effect on cogongrass (Alba et al., 2017; Fahey et al., 2018). Finally, we found that root-respiration had a mean similar to that of C4 grasses in general. While this was contrary to our hypothesis, our sensitivity analyses showed that cogongrass was not sensitive to root respiration (Figures 2.3-2.5). This trait seems unlikely to confer a competitive advantage to cogongrass.

We hypothesized that each cycle of constraint would reduce output uncertainty. Our first round of field-based constraint did reduce output uncertainty (Figure 2.7), but further statistical calibration increased output uncertainty despite lowering parametric uncertainty (Figure 2.6). How is it possible to narrow parameter distributions without reducing the uncertainty in the model itself? Certainly, the changes to model elasticity contributed (Figures 2.3-2.5). In addition, the data we used to construct the particle filter was belowground and aboveground biomass. The ED2 model we used only has a limited number of ways that congress could allocate biomass, which meant that linear changes to one parameter were not able to recreate the variability of observations (Figure S2.3). Much of the increased output uncertainty was attributed to water conductance, which is a parameter that measures the movement of water in terms of carbon allocated to roots (Table 2.1). With limited options for allocating roots, water conductance became more important.

Water conductance and growth respiration have been dominant sources of uncertainty in previous ED2 forest and grassland projections (Dietze et al., 2014; Raczka et al., 2018; Shiklomanov et al., 2020). One tool for decreasing the uncertainty associated with water conductance is ED HYDRO. ED HYDRO is a version of ED developed to translate water conductance into mechanistic hydraulic traits (Xu et al., 2016). ED HYDRO allows for measurement of hydraulic parameters, but could come at the cost of uncertainty around belowground carbon dynamics because of increased complexity (Cowdery, 2021). ED HYDRO is a single example of a tool addressing a common question: Should we restructure a model to reduce parameter uncertainty, if it introduces complexity? Optimizing model complexity for forecast skill is an area of active research (Famiglietti et al., 2021; Fisher & Koven, 2020). Large parameter uncertainty can trade-off with model structural error, and disguise opportunities for restructuring (Buotte et al., 2021; Famiglietti et al., 2021; Medlyn et al., 2015). Finding the perfect model complexity is still an open question, but reducing parameter uncertainty can inform restructuring decisions.

Our workflow successfully reduced parameter uncertainty to the point where structural uncertainty began to dominate. The order of our workflow highlighted the strengths of each constraint technique. Because we already knew the uncertainty and elasticity of each parameter from prios, we were able to prioritize parameters to measure during field work. By incorporating field data before statistical constraint, we fixed the modeled response to predictions that are consistent with congongrass's traits, which prevented the statistical calibration from selecting biologically implausible parameter values in later stages. It also let us collect data that we could use for statistical calibration later on.

Our workflow synthesizes the parameter uncertainty reduction strategies groups are pursuing ad hoc. The sensitivity and uncertainty analyses we conducted at each stage are already used across a swath of environmental models: from simple ecosystems (Trotsiuk et al., 2020) to radiative transfer (Meunier et al., 2022; Shiklomanov et al., 2016), aquatic food webs (Bracis et al., 2020), and climate simulations (Woodard et al., 2021). Meunier, van der Heijden, et al., (2021) first conducted a meta-analysis of literature values (Figure 2.1), and then statistically constrained the highly uncertain parameters that remained (Figure 2.1) (Meunier, van der Heijden, et al., 2021; Meunier, Verbeeck, et al., 2021). By organizing parameter-uncertainty steps into a single workflow, we demonstrate how these techniques can work together, and systematically reduce parameter uncertainty.

Deciding on an acceptable level of parameter uncertainty changes with application. Testing a hypothesis with a model may have a higher level of acceptable uncertainty than model projections for policy development. In this paper, we consider the point at which different forms of uncertainty begin to dominate a natural stopping point.

Conclusions

All process-based models need a battle plan for how they can reduce parameter uncertainty. We demonstrate a workflow for reducing parametric uncertainty. We suggest using iterative sensitivity and uncertainty analyses that begin with broad priors, incorporate literature values via a meta analysis, move to targeted measurements, and end with statistical calibration or model restructuring. We demonstrated how this played out with the calibration of parameters for an invasive grass, and found that model parameters began to dominate after incorporating targeted data, and that model structure error began to dominate after statistical calibration.

As a community, we need to actively manage parameter uncertainty. High parameter uncertainties can prohibit models from addressing pressing issues, like the future of the carbon cycle, and society's capacity to conserve and adapt (Hobbs et al., 2015; IPCC, 2014; National Research Council, 2001). Managing parameter uncertainty is a challenge for any field using process-based models (Donatelli et al., 2017; Fatichi et al., 2016; Lai et al., 2021; Tracy et al., 2018; Y. Zhang et al., 2019). Our workflow offers a practical solution to systematically reduce parameter uncertainty.

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CHAPTER THREE: HOW FUTURE CLIMATE MEDIATES COGONGRASS INVASIONS IN SOUTHEASTERN FORESTS

Abstract

Imperata cylindrica, (cogongrass) is an invasive grass spreading across the southeastern United States and into what remains of longleaf pine forests. Cogongrass outcompetes native understory vegetation, and lowers regional biodiversity. However, despite the social and economic importance of pine-oak savannas, few studies have looked at cogongrass' effect on pine-oak forests. In addition, the photosynthetic strategy of cogongrass (C4) and native trees (C3) provide different benefits under future climates, and could change the severity of cogongrass invasions under climate change. To test this, we modeled a cogongrass invasion under four climate treatments (Elevated CO_2, Elevated Temperature, Elevated CO_2 + Temperature, and Present Day), and three competition scenarios (Cogongrass alone, Trees alone, Cogongrass + Trees). We found that cogongrass did not survive past 15 years in the understory of our undisturbed model forests. We found that cogongrass had less biomass and density under hotter temperature treatments when grown alone, and faster extinction rates when competing with trees. Despite cogongrass' extinction, it changed the dominant tree species from oaks to pines. This suggests 1) pine dominance can emerge without fire from interspecies competition alone, and 2) that cogongrass can have long-term effects on community structure.

Introduction

Invasive species can upend ecosystems by changing species composition and in turn cause changes to the carbon balance of an ecosystem (Gaertner et al., 2017). But composition shifts do not always translate into changes to carbon cycling as invaders could replace functionally similar species (Castro-Díez & Alonso, 2017). Understanding how and when invaders cause changes to the biogeochemistry of a system is important both because plants are regulators of climate, but also because C cycle changes can be precursors to shifts in ecosystem disturbance regimes and vegetation structural composition (Gaertner et al., 2017).

At the same time, climate change is altering how ecosystems cycle carbon. Through the combustion of fossil fuels and land use change, humans have caused a build up of carbon dioxide (CO_2) in the atmosphere that the earth has not experienced in over 20 million years (Pearson & Palmer, 2000). Elevated CO_2 traps longwave radiation in the atmosphere, which warms the planet (IPCC, 2014). In terrestrial systems, elevated CO_2 and temperature caused plants to assimilate increasing levels of carbon globally (Le Quéré et al., 2013). Temperature changes humidity, which has physiological implications for photosynthesis (Allen et al., 2010; Grossiord et al., 2020), and has been associated with tree mortality. Temperature changes can also trigger extreme disturbance events like droughts or wildfires (McDowell et al., 2018).

Climate change shapes ecosystems globally – but so do other anthropogenic activities. In Canada, land-use change had a larger effect on species composition than climate change in the 19th century (Danneyrolles et al., 2019). Global trade and environmental change has increased the number of biological introductions (Seebens et al., 2018). Biological introductions can alter evolutionary trajectories, and upset ecosystem processes (Antonio & Vitousek, 1992; D'Antonio & Vitousek, 1992;

Ehrenfeld, 2010). Human introduction of novel species and altered climate regimes are both intensifying forces of global change. Understanding how they interact with each other is essential to understanding future ecosystems.

We aim to test if an invasive grass changes biogeochemical cycling when it invades, and to assess how future climate affects cogongrass invasions. *Imperata cylindrica* (cogongrass) has infested the southeastern United States since its introductions in 1912 and 1920s (Estrada & Flory, 2015). Cogongrass is predicted to spread (Bradley et al., 2010) to the majority of US timberland, including much of the remaining old-growth Longleaf pine forests (Kirkman & Mitchell, 2006). Pine-oak woodlands and savannas are culturally and economically significant (Dezember, 2018; Nordman et al., 2021); If cogongrass invasions decrease forest productivity this could have important cumulative effects on economic yields and forest use, in addition to impacts on carbon cycling.

We currently have conflicting evidence about the impacts of cogongrass on pine forests. When invading, cogongrass outcompetes native-understory vegetation, becoming a taller, denser, monoculture (Brewer, 2008; Fahey et al., 2018). Cogongrass could shift pine forests demographically by preventing seedlings from establishing. Daneshgar et al. (2008) and NeSmith et al. (2017) found cogongrass reduced pine sapling survival. However, NeSmith et al. (2018) also found temporary facilitation between pine saplings and cogongrass during drought treatments, even though overall survival was reduced. NeSmith et al's study hints that cogongrass' effect on trees could be mediated by climate. Cogongrass could also change the landscape by lowering the productivity of adult pines.

Cogongrass has been a part of the landscape for ~100 years, but there are no studies that quantifies how cogongrass changes productivity in pine-oak savannas.

The next 100 years will subject the Southeast to an unprecedented climate regime. Because the Southeast is one of the United States' largest regional sinks of carbon (Crevoisier et al., 2010; Lu et al., 2015), there are several modeling studies that tried to capture how southeastern forests will respond biogeochemically to climate change. They agree that the Southeast will likely remain a carbon sink, but disagree on if the size of the sink will decrease (Luo et al., 2008; Miller et al., 2016; Thomas et al., 2017; Zhao et al., 2010, 2013), or increase (Hatch et al., 1999). They also disagree about the drivers of the forest-based carbon sink, with candidates including droughts, elevated CO_2, land use change, management techniques, disturbances, and nutrient limitation. Free-air CO_2 enrichment experiments, which exposed ecosystems to artificially elevated levels of CO_2, found that elevated CO_2 increased plant growth and that the effect was more dramatic in trees than in grasses (Ainsworth & Long, 2004). Thus there is reason to believe that future climate regimes will change how forests cycle carbon, and that it will affect C3 pines and oaks, and C4 grasses differently.

The different photosynthetic strategies of trees and cogongrass could control how climate interacts with invasion. As atmospheric CO_2 increases, managing for cogongrass could get cheaper as C3 pines experience CO_2 fertilization (McCarthy et al., 2010). Conversely, elevated temperatures could cause invasions to worsen in their effects or hasten in their timing, as C4 plants are more water-use-efficient (Still et al., 2003). Experimental work by Chuine et al. (2012) found that the invasive C4 grass *Setaria* *parviflora* had higher biomass and fecundity under warmer and dryer conditions (Chuine et al., 2012). Photosynthetic strategy can interact with climate to dictate competitive interactions between grasses and trees. For example, Pau et al., (2013) found that C3 and invasive C4 grasses in Hawaii inhabited areas with distinct climates and different levels of tree-cover (Pau et al., 2013). By contrast, cogongrass outcompetes native C4 grasses, saplings, crops, and other invasive-plants across a range of land cover types (Estrada & Flory, 2015; Fahey et al., 2018). But understanding how future climate mediates cogongrass-pine competitions targets the interaction that defines the landscape as a savannah: trees vs grasses.

To determine if cogongrass changes productivity in the southeast, we modeled cogongrass invasions into mixed oak and pine stands and estimated its effect on Southeastern forests both now and under future climate and CO_2 treatments (Figure 3.1). First, we hypothesize that when grown in competition with pines and oaks, that cogongrass will establish in the understory, because it is a successful invasive species. Second, we hypothesize that cogongrass will have larger biomass and more individuals under hotter climate treatments when simulated in a monoculture, and when simulated competing with trees. We hypothesize this because cogongrass appears to be drought adapted. Cogongrass survives droughts (Zhang et al., 2021), withstands high temperatures (Hamidavi et al., 2021), and has drought-optimized traits (Chapter 2). Because cogongrass's C4 photosynthesis strategy uses water efficiently, we hypothesize that cogongrass will have the largest competitive advantage over C3 trees under hot temperature treatments. Even in monoculture, we hypothesize that cogongrass's biomass will be larger under hotter treatments because cogongrass's photosynthetic machinery requires lower activation energy in hotter temperatures (Jones, 2013; Longo et al., 2019). Third, because cogongrass decreases seedling survival and competes with adults, we hypothesize that oaks and pines grown with cogongrass will have lower biomass levels, and sparser density compared to oaks and pines grown alone. Finally, because elevated CO_2 benefits C3 species more than C4 species, we hypothesize that that cogongrass will have less biomass and fewer individuals when competing with C3 oaks and pines under elevated CO_2 treatments.

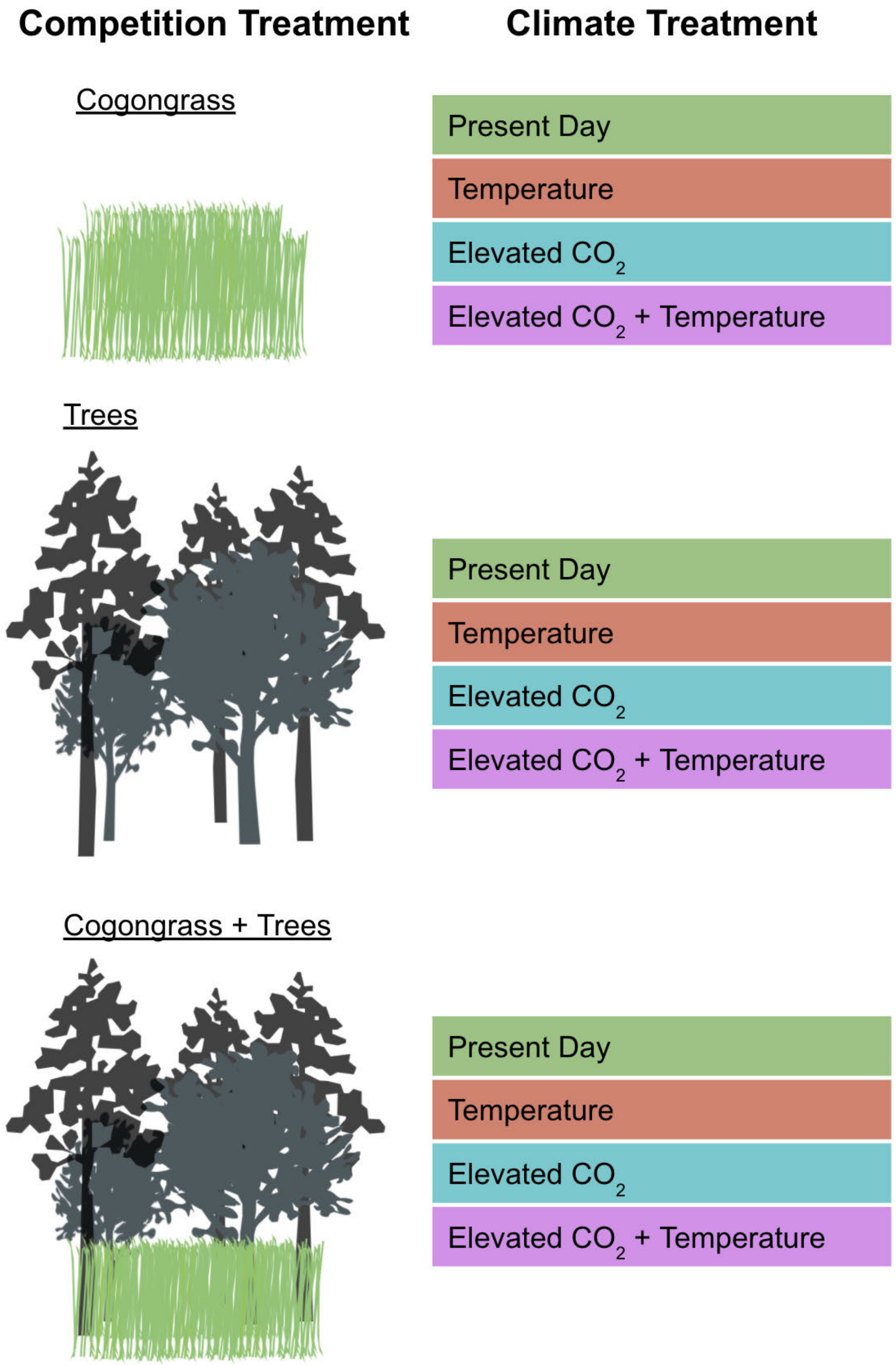

Figure 3.1: Illustration of competition treatments and meteorology treatments. Elevated CO_2 + Temperature levels are based on radiation and CO_2 levels from RCP 8.5. Present

day meteorology is generated from cycling the climate and CO_2 levels from 2006-2026. Temperature has RCP 8.5 temperature and other climate increases while CO_2 is held constant. Elevated CO_2 has RCP 8.5 -level CO_2 increases and temperature and climate resampled from 2006-2026. See Figure S3.1 for more information.

Methods

The Ecosystem Demography 2 (ED2) model

We used Ecosystem Demography 2 (ED2) model to predict ecosystem responses to cogongrass invasions, because it both represents competitive interactions and has a fully dynamic energy, water, and carbon budget (Longo et al., 2019; Medvigy et al., 2009). It has previously been used to model southern pine forests under climate change treatments (Dietze et al., 2014; Miller et al., 2016;De Kauwe et al., 2014; Medlyn et al., 2015; Walker et al., 2014). ED2 is described generally in the methods section of Chapter 2, and in detail in Longo et al., (2019). Broadly, ED2 similates cohort-level processes like photosynthesis, respiration, and transpiration and allocates any net carbon to biomass pools (i.e. roots, leaves, wood). These biomass pools then control plant-cohort access to water, light, and CO_2. Light competition is simulated by treating each cohort's canopy as an infinitely thin-flat layer arranged by cohort height, where the amount and type of radiation changes at each layer, according to the modeled cumulative leaf area at each height.

Within ED2, grasses have no wood pool, have a maximum height of 1.5 m, and grass-heights are estimated from an allometry relating biomass to height as modified by specific-leaf-area. Tree heights come from two diameter-at-breast-height (DBH) based allometries (biomass to DBH, DBH to height), and trees allocate carbon to leaves, fine roots, sapwood, and storage, and from storage to wood and reproduction. Different types of grasses and trees are simulated by calibrating Plant Functional Types (PFTs). Parameters associated with PFTs start with priors for PFT traits based on broad categories (i.e. “plants”, “trees”), which are narrowed by including PFT-specific trait measurements into a Hierarchical Bayesian meta-analysis (LeBauer et al., 2013). We used three PFTs: “Temperate Southern Pines”, “Temperate Southern Mid-successional Hardwood” and a cogongrass PFT (Chapter 2). Temperature Southern Pines, and Temperate Southern Mid Hardwoods have been both used to simulate southern forests, and forests under elevated CO_2 (Dietze et al., 2014; Miller et al., 2016;De Kauwe et al., 2014; Medlyn et al., 2015; Walker et al., 2014). Full details of parameters associated with PFTs are available via https://www.betydb.org/.

Modeling experiments

To test our hypothesis that cogongrass would have higher biomass and density under higher temperatures, we ran cogongrass alone under 4 climate scenarios from 2006 to 2100 (Figure 3.1). The four meteorological treatments were based on the Coupled Model Intercomparison Project phase 5’s Representative Concentration Pathway 8.5 (RCP8.5) (Pchauri; Rajendra K. et al., 2014), and the Global Fluid Dynamics Laboratory’s CM3 model, ensemble member r1i1p1 (Geophysical Fluid Dynamics Laboratory, 2017). This model and ensemble member combination was chosen to represent approximately the central tendency of climate projections under scenario 8.5 (Jiang et al., 2012; Yin et al., 2013). Under the 8.5 scenario, simulated climate variables like temperature, and humidity, change in response to elevated CO_2. Notably, temperature increases. In our four meteorological treatments, we separated the effects of elevated CO_2 and climate responding to elevated CO_2. Our "Elevated CO_2 + Temperature" treatment is equivalent to RCP8.5. Our "Temperature" treatment is to simulate future climate without increasing CO_2 , and our "Elevated CO_2" is increasing CO_2 without future climates. In our "Present Day" treatment, the CO_2 and climate from 2016-2026 are resampled (Figure 3.1; Figure S3.1).

In our cogongrass only runs, each meteorological treatment included 50 ensemble members to estimate parameter uncertainty. Each member within the 50 ensembles had parameter values randomly sampled from ± 1 SD around the joint parameter posterior. Parameter distributions match those described in Chapter 2.

To test how cogongrass performed against forests, the same four climate scenarios were repeated for a tree-only treatment and a cogongrass + tree treatment (Figure 3.1). In these experiments we ran single ensemble-member runs with parameters held at their mean value. These experiments were repeated twice. In the first round, we ran 4 climate treatments by 3 competition treatments, allowed to grow from 2006 until 2100. Because cogongrass was unable to persist past the point where our climate treatments diverged (Figure 3.4), we ran a second round of experiments from 2085 until 2100 with the addition of a simulated external propagule pressure (i.e. seed rain from outside the stand).

Model Initialization

The ED2 initial conditions for cogongrass were fixed at the initial planting biomass and density used in Alba et al.'s cogongrass experiment (Alba et al., 2017). For trees, and cogongrass + trees competition treatments we initialized ED2 using forest inventory data (See below) from an existing site, specifically a site from Moody Air Force Base (AFB). We chose a site within Moody AFB because Moody AFB is centrally located in the Southeastern US (lat 30.984, lon -83.175), and it represents a midpoint along a temperature and precipitation gradient (Figure S3.2; Figure 4.2). We then chose the site within Moody AFB that had a tree density closest to the mean density across a dataset of 115 sites, from across the Southeastern US (Figure S3.3; Figure 4.2). Our site had gone ~ one year without a prescribed burn at the time of sampling (Allan et al., 2021).

Our site was a 500 m^2 circle, with trees >3cm Diameter at Breast Height (DBH) recorded. Our site had a total of 71 trees with a mix of *Pinus clausa* (N=3, DBH =12-32.5 cm), *Pinus palustris* (N=40, DBH = 3.4-22.9 cm), *Quercus nigra* (N=24, DBH = 3.3-14.5 cm), and the family *Asteraceae* (N=4, DBH = 3.6-7 cm) (Figure S3.4). *Pinus clausa* and *Pinus palustris* both were represented in ED2 by the Temperate Southern Pines PFT. *Quercus nigra* was represented by the Temperate Southern Mid Hardwood PFT. We excluded the *Asteraceae*. The site had loamy sand soils. Soils texture was estimated from the Soil Survey Geographic Database (SSURGO) accessed through the soilDB R package (Beaudette et al., 2022; Soil Survey Staff, 2022).

Results

Cogongrass by Climate Treatments

We found that cogongrass's biomass and density over a century was not dramatically altered between climate treatments, but that treatments with elevated temperature had lower biomass and density (Figures 3.1-3.2). In the final decade of model simulation (2090-2100), Cogongrass under elevated Temperature had a mean density of 7.97 plants/m^2 (SD 4.56), Elevated CO_2 + Temperature 11.6 plants/m^2 (SD 8.08). Present Day had a mean of 15.8 plants/m^2 (SD 7.95), and Elevated CO_2 had a mean of 18.0 plants/m^2 (SD 9.52). Biomass was lowest under the Temperature treatment (2090-2100 mean 0.056 kgC/m^2, SD 0.024), second lowest under Elevated CO_2 + Temperature 0.070 kgC/m^2 (SD 0.019), followed closely by Present Day 0.084 kgC/m^2 (SD 0.018). Biomass was highest under Elevated CO_2 0.093 kgC/m^2 (SD 0.013). The treatment scenarios fell within overlapping 95% confidence intervals (Figures 3.1-3.2).

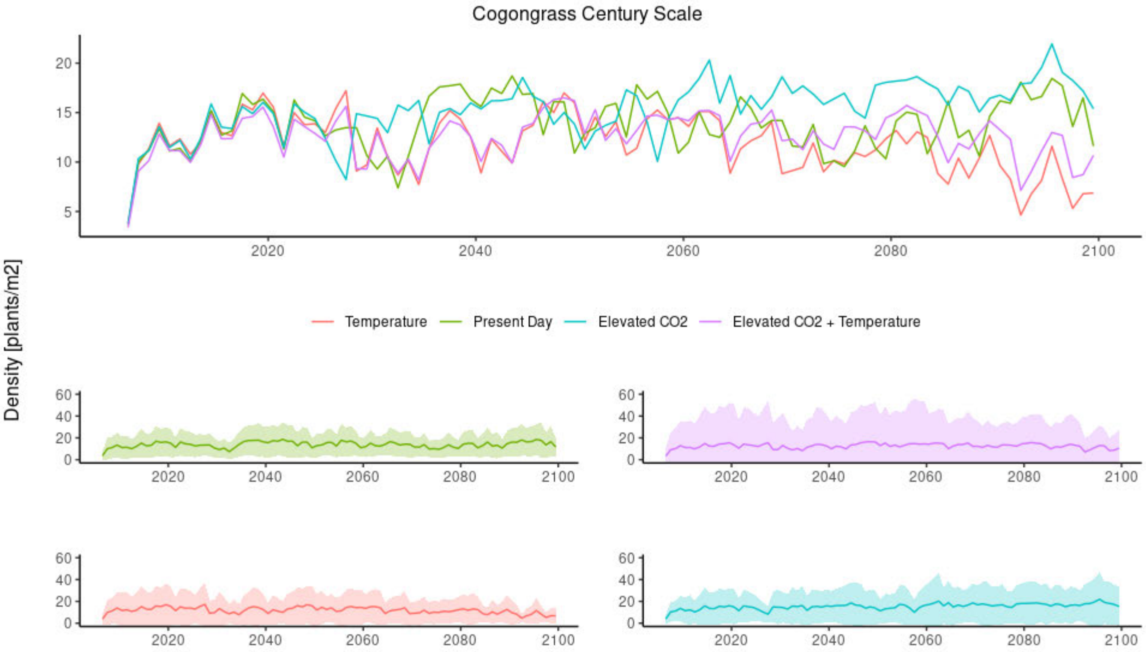

Figure 3.2: Number of cogongrass plants over century, Upper panel shows mean quantile value. Lower panels show the mean quantile of each climate treatment against a 95% CI. Climate treatments diverge after 2026.

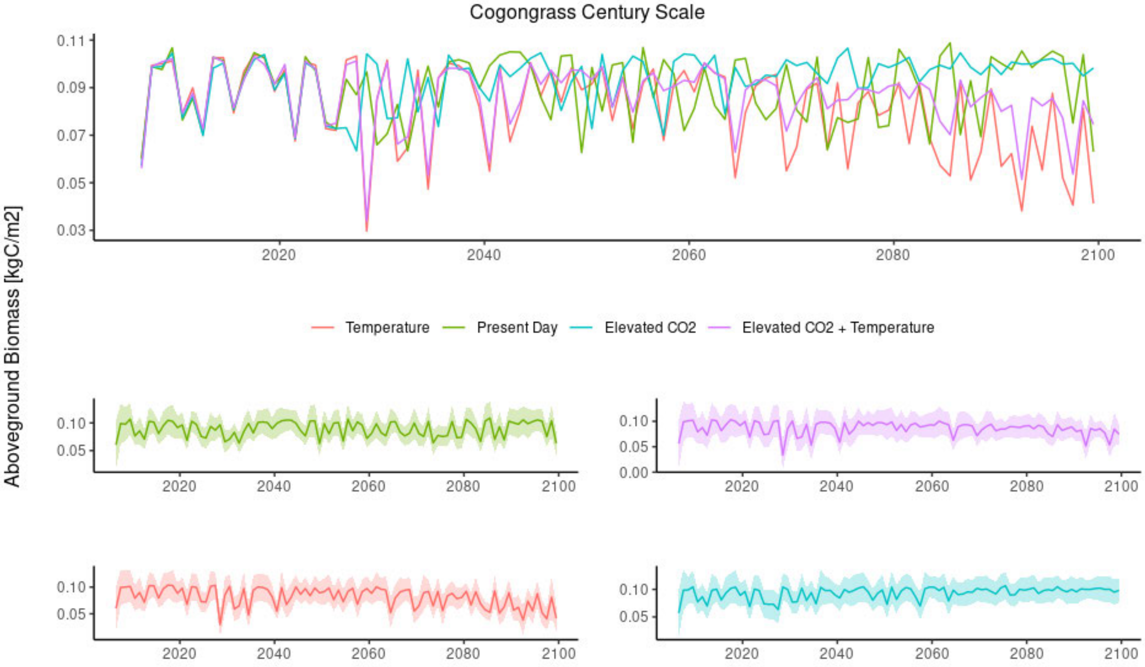

Figure 3.3: Cogongrass aboveground biomass over century, Upper panel shows mean quantile value. Lower panels show the mean quantile of each climate treatment against a 95% CI. Climate treatments diverge after 2026.

Competition Treatments

When we modeled cogongrass competing with a pine-oak stand, we found that pines dominated the stand within 10 years, reduced oak abundance and biomass, and caused cogongrass to reach extinction (Figure 3.4; Figures 3.5-3.6 Top). This was true in both our century-long runs of cogongrass and trees competing, and our 15-year runs from 2085-2100. Despite congongrass's inability to thrive in the ED2 modeled understory, we can still assess impacts of climate change induced stress on cogongrasses' demography and biomass by assessing the impacts of the different climate treatments on the timing of extinction. Cogongrass was slowest to decline under Elevated CO_2 and Present Day treatments, which had positive biomass and density 4-8 years after other treatments hit zero (Figures 3.5-3.6 Top). Trees suppressed cogongrass' cumulative biomass and cumulative density most dramatically under Elevated CO_2 (-12.5 kgC/m^2 , -2259 $plants/m^2$), then Present Day (-11.1 kgC/m^2 , -2095 $plants/m^2$), and Elevated CO_2 + Temperature (-10.6 kgC/m^2 , -1616 $plants/m^2$). Temperature had the smallest cumulative reduction (-8.4 kgC/m^2 , -1166 $plants/m^2$) (Figures 3.5-3.6 Bottom Right). Cogognrass' density and biomass both responded to climate and competition treatments in the same direction, but they did not scale directly, and their relationships were different across treatments (Figure S3.5).

Cogongrass affected the trees as well. When the pine-oak stand was run without cogongrass, oaks had larger biomass and density, and pines had low biomass and density

(Figure 3.4, Figures 3.7-3.8). We estimated that cogongrass had a negative effect on overall tree biomass and density for most climate treatments (Figure 3.8 Bottom Left), but the pine PFT saw a substantial increase in biomass and density when grown alongside cogongrass (Figures 3.7-3.8). When dominant, oaks were more numerous and productive than pines in all climate treatments except present day (Figures 3.7-3.8 Bottom). Trees saw the largest biomass and densities under the Elevated CO_2 treatment, regardless of PFT (Oaks: 5.99 kgC/m^2 309 plants/m^2, Pines: 4.98 kgC/m^2 268 plants/m^2) (Figures 3.7-3.8), and the lowest densities and biomasses under the temperature treatment (Oaks: 0.238 kgC/m^2 9.42 plants/m^2, Pines: 0.498 kgC/m^2 12.2 plants/m^2).

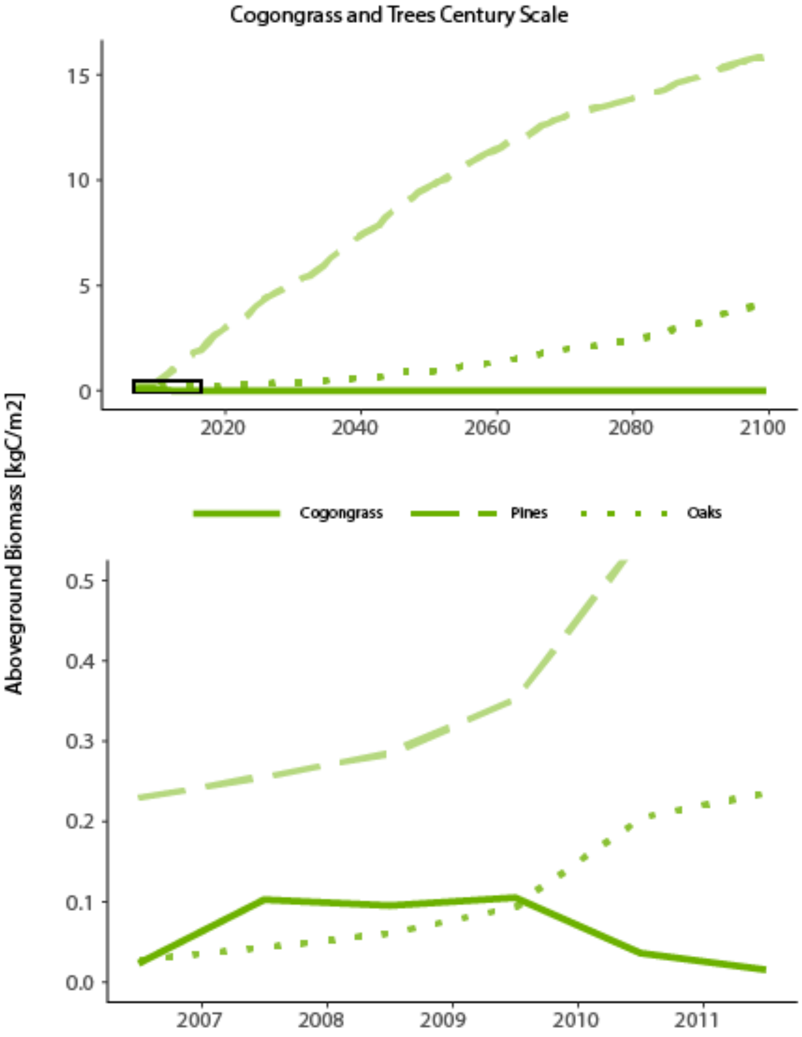

Figure 3.4**:** Cogongrass competing with Pines and Oaks from 2006–2100. Figure shows results from the present-day climate treatment. Modeled cogongrass reached extinction before climate treatments diverged. Bottom panel is the data from the boxed-section of the top panel

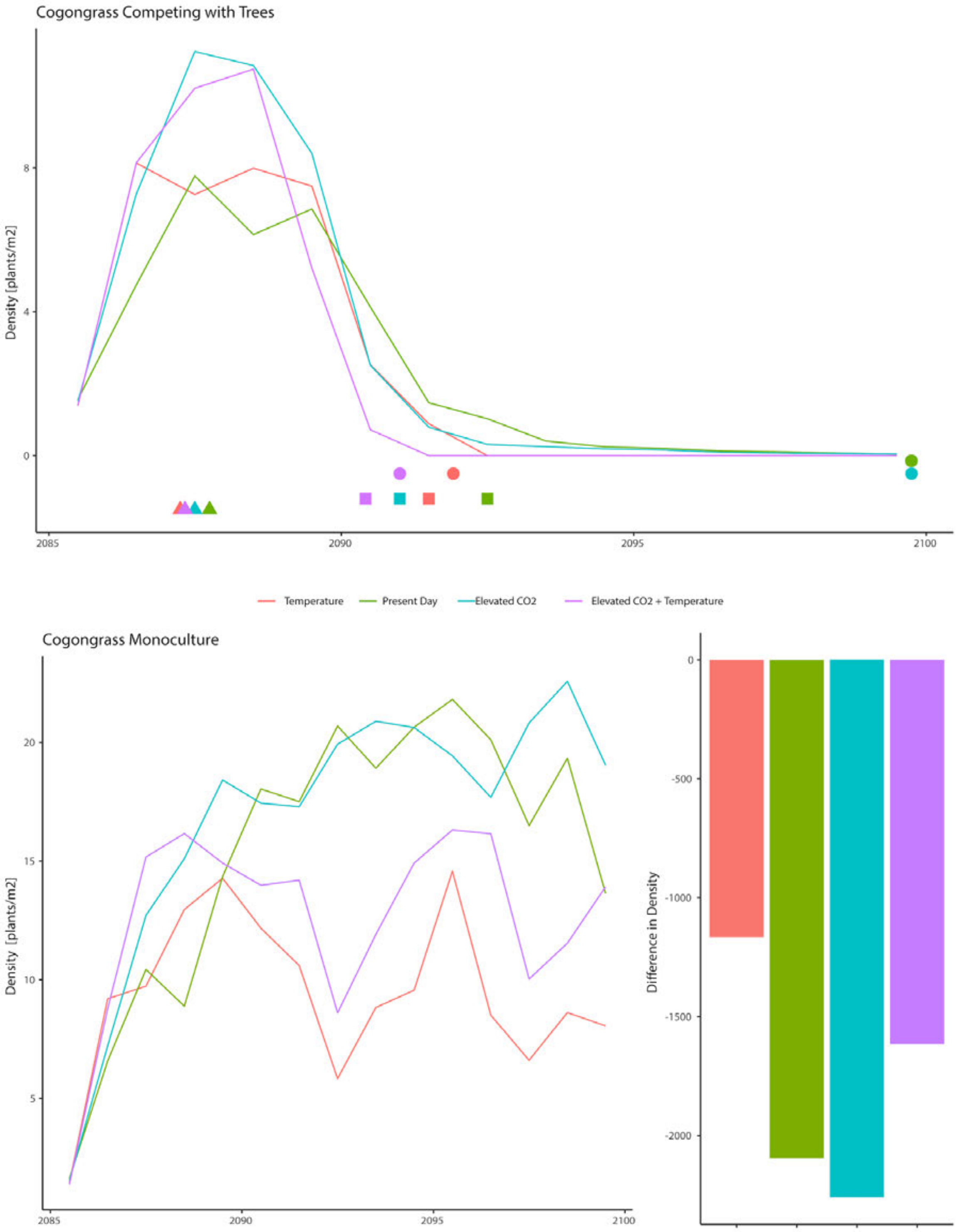
Cogongrass Competing with Trees
Density [plants/m2]
0
4
8
2085
2090
2095
2100
Temperature
Present Day
Elevated CO2
Elevated CO2 + Temperature
Cogongrass Monoculture
Density [plants/m2]
5
10
15
20
2085
2090
2095
2100
Difference in Density
0
-500
-1000
-1500
-2000

Figure 3.5: *Top* - Annual July density of Cogongrass grown with trees from 2085–2100. Ticks designate timing of events. Triangles are when cogongrass hits its maximum number of plants. Squares are when cogongrass number of plants falls below its initial value, and circles are when cogongrass hits its minimum number of plants. Temperature and Elevated CO_2 + Temperature hit zero, but Elevated CO_2 and Present Day did not. *Bottom Left* - annual July density of Cogongrass grown alone from 2085–2100. *Bottom Right* - Cumulative sum of the difference between the Cogongrass and Trees treatment and Cogongrass-monoculture treatment.

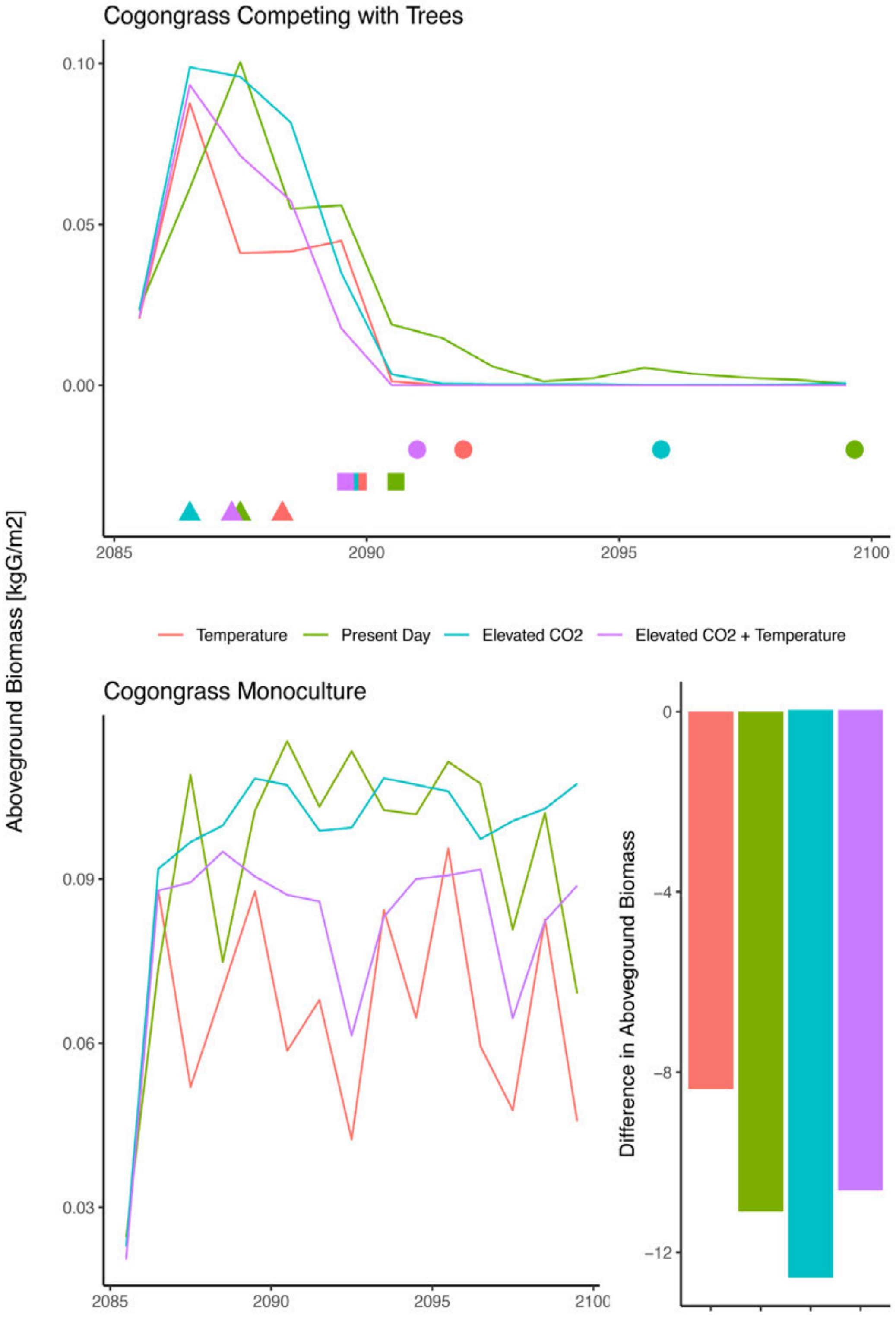
Cogongrass Competing with Trees
0.10
0.05
0.00
2085
2090
2095
2100
Aboveground Biomass [kgG/m2]
Temperature
Present Day
Elevated CO2
Elevated CO2 + Temperature
Cogongrass Monoculture
0.09
0.06
0.03
2085
2090
2095
2100
0
-4
-8
-12
Difference in Aboveground Biomass

Figure 3.6: *Top* - Annual July aboveground biomass of Cogongrass grown with trees from 2085–2100. Ticks designate timing of events. Triangles are when cogongrass hits its maximum biomass. Squares are when cogongrass biomass falls below its initial value, and circles are when cogongrass hits its minimum biomass. Temperature, Elevated CO_2 + Temperature, and Elevated CO_2 hit zero. Present Day did not. *Bottom Left* - annual July aboveground biomass of Cogongrass grown alone from 2085–2100. *Bottom Right* - Cumulative sum of the difference between the Cogongrass and Trees treatment and Cogongrass-monoculture treatment.

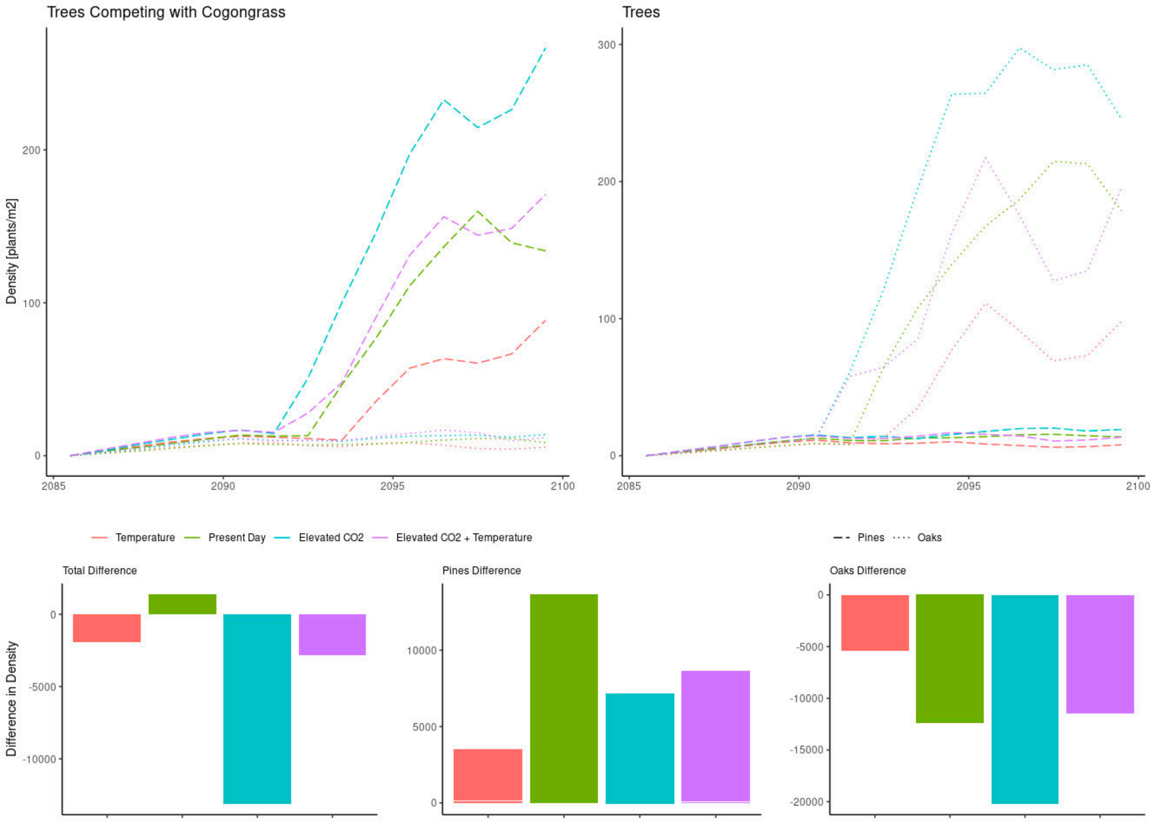

Figure 3.7: Effect of competition on tree density. *Top Left*- Oaks and pine PFTs grown with cogongrass from 2085-2100. *Top Right* - Oaks and pine PFTs grown without cogongrass from 2085-2100. *Bottom* - Difference in tree density between trees-only and

cogongrass + trees competition treatments summed from 2085-2100.

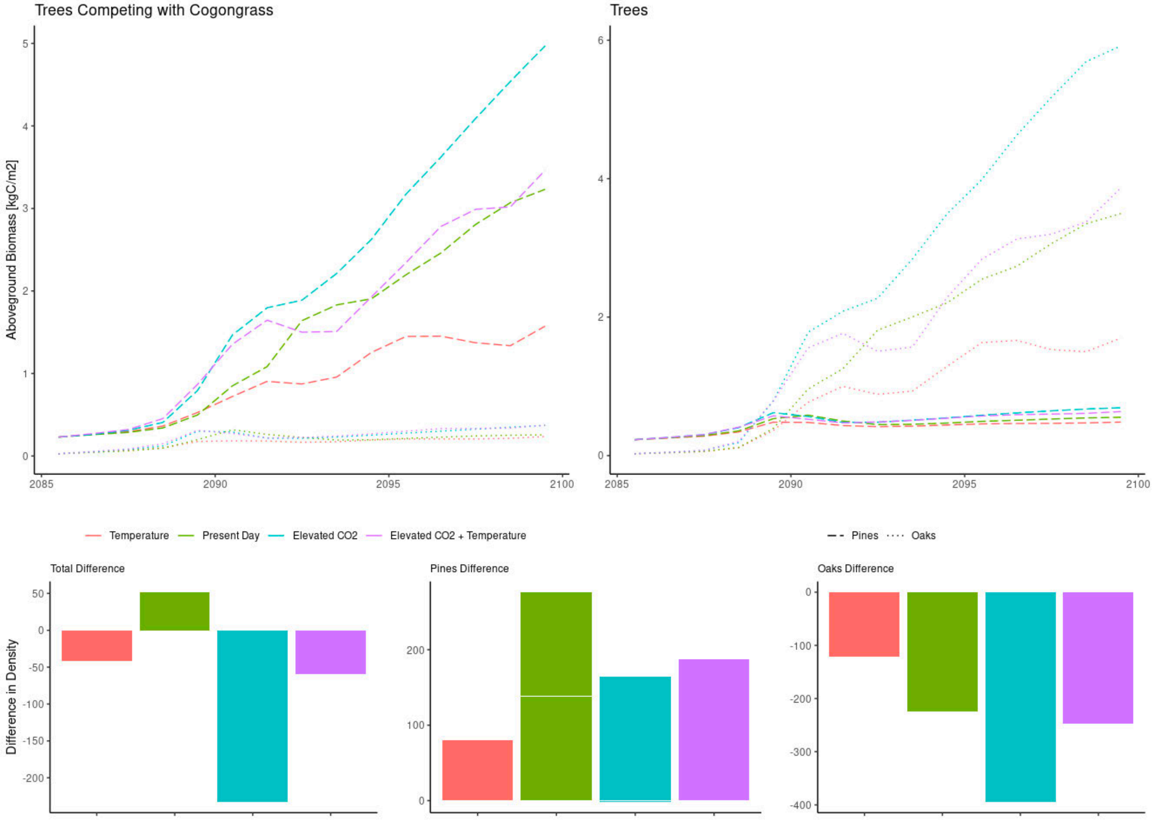

Figure 3.8: Effect of competition on tree biomass. *Top Left* - Oaks and pine PFTs grown with cogongrass from 2085-2100. *Top Right* - Oaks and pine PFTs grown without cogongrass from 2085-2100. *Bottom* - Difference in tree biomass between trees-only and cogongrass + trees competition treatments summed from 2085-2100

Discussion

We aimed to quantify the effect of cogongrass invasions on southeastern forests, and see if future climate mediates the severity of those effects. We found that cogongrass monocultures performed poorly under hotter climate treatments. When modeled in competition with trees, cogongrass was unable to persist past 20 years into the simulation, but facilitated pine dominance over oaks.

Cogongrass's extinction when grown with trees was surprising. Cogongrass is a successful invader across the southeastern United States. Cogongrass' extinction could be an artifact of ED2's light competition implementation (Fisher et al., 2018) as ED2 is known to over-predicted understory tree mortality due to shading in highly productive sites (Medvigy & Moorcroft, 2012). Uncertainty around NPP has been attributed to leaf transmittance and clumping parameters (Meunier et al., 2022; Viskari et al., 2019). Alternatively, cogongrass may survive and compete in understories via mechanisms not present in ED2. Cogongrass practices allelopathy (Estrada & Flory, 2015), and has been shown to redistribute photosynthate along clonal networks to compensate for shading (Estrada et al., 2020). Cogognrass' traits may change quickly to adapt to new situations (Hiatt & Flory, 2020). Extinction in a shaded stand may also be a realistic finding. Experimentally, cogongrass tillers have failed to survive in shaded forest plots (Estrada et al., 2017). Cogongrass' low quantum efficiency (Chapter 2) is consistent with low-performance in the understory. Disturbances like agriculture and development are mechanisms that drive cogongrass' success as an invader (Estrada et al., 2017; Estrada & Flory, 2015), but our forests were simulated with only climate and cogongrass as disturbances. Southeastern forests are also frequently burned (Flannigan et al., 2009; Kirkman et al., 2013; Mitchell et al., 2006). Cogongrass might realistically not survive the shade of a 15-year undisturbed forest, and cogongrass may be common across the southeast because 15-year undisturbed forests are rare.

We found that cogongrass had the lowest biomass and density under elevated temperatures. We hypothesized cogongrass would thrive under elevated temperatures.

While higher temperatures can facilitate metabolically controlled processes like photosynthesis, plants have a threshold at which respiration grows, and temperature has a negative effect on net photosynthesis (Bonan, 2008; Jones, 2013). Cogongrass may be able to survive high temperatures, but still perform better under cooler treatments. Tees suppressed the least amount of cogongrass biomass and density under elevated temperature treatments, but that may be because cogongrass had less biomass and density in those treatments, not because cogongrass had a competitive advantage. Photosynthetic strategy may have made a difference. Temperature had an effect on cogongrass, but for trees CO_2 and temperature had an effect. This is consistent with experimental findings. In free-air CO_2 enrichment experiments, trees increase their biomass under elevated CO_2 until nutrient limitation (Ainsworth & Long, 2004). In open-top CO_2 enriched field chambers, cogongrass grew taller and had greater water-use-efficiency under elevated CO_2, but the effect varied by ecotype (Runion et al., 2016).

We hypothesized that cogongrass invasions would decrease the biomass and density in trees. Our hypothesis was supported in all climate treatments except present day, but not for the reasons we expected. Cogongrass facilitated pine dominance over oaks. Because oaks were more productive and numerous, cogongrass decreased tree biomass and density overall. But pine biomass and density increased with a cogongrass invasion. We know that cogongrass can interact with pines in complex ways. For example, two years into the drought by invasion experiment described by Alba et al., (2017), cogongrass reduced seedling survival, but offset drought stress for pine seedlings (Alba et al., 2017; Fahey et al., 2018). After three years, cogongrass began shading out pines, and pines experienced dual stressors of invasion and drought (NeSmith et al., 2018). After five years, pines experiencing a single stressor (drought or invasion) were larger than either pines grown under none or both because of a filtering effect (Alba et al., 2019). Cogongrass may be acting in a similar role in our modeled pine-oak system; providing temporary facilitation with long-term implications for community structure.

We found that without cogongrass, our forests became oak-dominated, a result supported by the literature. Studies of old-field succession in the North Carolina piedmont found that without perturbations, oaks began to have larger densities than pine species 20-40 years after forests developed a broadleaf understory (Billings, 1938; Bonan, 2008; Oosting, 1942). We began our runs with an oak understory (Figure S3.3), and found that oak-density surpassed pine density in ~10-12 years. While not identical to the timing described by Billings (1938) and Oosting (1942), our model runs are consistent with the progression described by Billings (1938) and Oosting (1942), which is encouraging given that we initialized not from an old-field, but based on a community of trees that developed from active fire management.

We found that with cogongrass, pines were able to dominate over oaks. Classically, fires maintain pine overstories in the southeastern US. Both Clements (1936) and Odum (1969), pointed to Southeastern pine forests as a “fire climax”, when defining the concept of succession (Clements, 1936; Odum, 1969). Fires are a common and effective management tool to maintain pine overstories, particularly those of longleaf pine (Kirkman & Mitchell, 2006; Starr et al., 2015). Pines have a long evolutionary history with fire, and have developed distinct traits like thick bark and life-stages to survive fires (Schwilk & Ackerly, 2001). Our results suggest that pines can dominate without fires; that pine dominance can come from interspecies competition alone, and that transitory understory species can change which trees dominate. Fire may lead to pine dominance, but pine dominance might not require fire. This is a mixed result for pine conservation goals if prescribed fires become less safe under climate change (Kupfer et al., 2020; Mitchell et al., 2014). While cogongrass itself is a clear detriment to biodiversity and conservation (Chapter 4), our results suggest that pines may be competitive in some fire-free contexts.

Conclusion

Cogognrass is an invasive grass affecting the southeastern US. Because of cogongrass' photosynthetic strategy (C4), we hypothesized that hotter temperatures and higher CO_2 under climate change would alter how cogongrass competed with (C3) oaks and pines. Cogongrass was unable to persist in our modeled forests, and reached extinction in ~ 20 years. We found that cogongrass had lower biomass and density under elevated temperatures, and that hotter temperatures caused faster extinctions. Oaks grew to dominate pine-oak forests simulated without cogongrass, but pines dominated when cogongrass was present. This suggests that pine-dominated forests can emerge without fires, and that understory species can mediate which species dominate. This demonstrates that invaders -even when they are temporarily on a landscape- can alter forest composition for decades.

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CHAPTER FOUR: PRESCRIBED BURNING TO CURB TICK POPULATIONS: A DECISION SUPPORT TOOL FOR SOUTHEASTERN DEPARTMENT OF DEFENSE INSTALLATIONS

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Abstract

Tick Borne Diseases (TBD) are a persistent and intensifying threat to human health. Vegetation structure and climate change can impact tick populations by creating tick habitat or preferred tick microclimate. In the Southeastern US, prescribed burning has historically been effective at reducing tick populations, but invasive species and climate change could make prescribed burns less effective or feasible. We built a Decision Support Tool to help partners from nine Department of Defense installations navigate the interactions between prescribed fire, climate, vegetation, and tick borne disease risk. We began by interviewing partners about management priorities. We then built a R Shiny web application that communicated metrics of TBD risk and pathogens detected. We also developed interactive projections exploring how hypothetical changes to environmental variables affect tick populations. We found that tick populations are most sensitive to leaf litter and humidity changes. This knowledge provides managers with alternative control strategies beyond prescribed burns.

Introduction

Reported human cases of Tick Borne Diseases (TBD) more than doubled from 2004–2016 (Rosenberg et al., 2018). Reasons for this increase are complex and varied, but include ecosystem changes and climate change (Caminade et al., 2019). Climate and vegetation both mediate tick borne disease risk in direct and indirect ways. Tick survival is directly affected by micro-climate variables like humidity, precipitation, and heat (Rosendale et al., 2016), and climate can also impact tick population size, host-seeking behavior, and population timing (Berggoetz et al., 2014; Eisen et al., 2018; Levi et al., 2015). Additionally, climate affects ranges, and can drive range expansions (Colwell & Rangel, 2009). This paper focused on the Southeastern US, where the Gulf Coast tick and the Lone-star tick have both had dramatic range expansions in the last 50 years (Sonenshine, 2018). This range expansion could be driven directly by changes in temperature or humidity, which effect tick survival, but are also fueled by climate-driven changes to host population and ranges, especially white tailed deer, feral hogs, and mice (Mowry et al., 2019; Sonenshine, 2018; Weiskopf et al., 2019).

Similarly, vegetation can directly and indirectly affect TBD prevalence. Vegetation directly affects tick survival via the microclimate, and provides tick habitat in the form of litter and low structure vegetation (Jordan & Schulze, 2020; Linske et al., 2019; Mathisson et al., 2021). In the Southeast, pine dominated systems were hotter and drier at ground-level than broad-leaf systems, and altered several tick species' questing behavior (Schulze & Jordan, 2005). Mast-producing trees and climate interact to alter host abundance, in turn altering tick abundance (Ostfeld et al., 1996).

Although ticks and TBDs are an increasing problem, many broadly-effective management strategies for reducing TBDs have emerged. TBDs can be prevented by management practices that cull tick populations, such as the removal of invasive species associated with ticks (Allan et al., 2010). In the Southeastern US specifically, prescribed burning is a common management practice that decreases tick populations in the short and long-term, and reduces TBD risk (Gleim et al., 2014). Allen et al., (2021) found that woody-litter and tree density increased tick populations, and ticks are affected by vegetation-mediated microclimate. Specifically, ticks survived longer in stands of the invasive grass *Imperata cylindrica,* or Cogongrass. Outside the Southeast, Pascoe et al., (2020) similarly found that wildfires significantly reduce tick populations two years post-burn, but attributed the difference to direct loss and vegetation changes, and noted that vegetation would likely return. These studies suggest that frequent prescribed burning is an effective strategy to combat tick populations for three reasons: fire culls tick populations, destroys litter habitat, and shifts the ecosystem to a less-hospitable pine understory.

However, burns can create canopy gaps that promote vegetation that ticks favor, such as fast-growing understory species and invasive species (Guthrie et al., 2016; Huebner, 2005). There are also a handful of studies that have found that infrequent burns may not affect tick populations, or may even increase tick populations as vegetation recovers (Padgett et al., 2009). For example, prescribed burns accelerate cogongrass spread, as cogongrass burns hotter and recovers faster than native vegetation (Flory et al., 2022). In turn, ticks survive longer in cogongrass stands than on native grasses.

These findings together suggest a range of possibilities: Future climate could make the risk of wildfires higher, and the regular use of prescribed burns more difficult, increasing tick populations (Flannigan et al., 2009; Mitchell et al., 2014). Climate may shift the understory to favor ticks independent of disturbance regime, or cogongrass invasion (Chapter 3). Prescribed fire could reduce tick populations, or accelerate invasive species and tick survival (Fusco et al., 2019). It's unclear how vegetation, climate, overstory, and frequent burning interact to deplete or sustain tick populations (Allan et al., 2021).

Future vegetation interactions are becoming important land management priorities. In a survey of land-managers in the Southeast roughly half listed the abundance of invasive species as important to them (Martin, 2019). We are unaware of similar studies about the relative importance of tick population management to regional land managers, nor how these goals intersect with the interacting challenges of climate change, invasive species, and fire (Chapter 3).

A number of Decision Support Tools (DSTs) exist already pertaining to the implementation of prescribed fire, such as: FARSITE (Finney, 2004), SPITFIRE (Thonicke et al., 2010), First Order Fire Effects model (Hood & Lutes, 2017), FFI (Lutes et al., 2009), and Interagency Fuels Treatment Decision Support System (Wells et al., 2009). However, these management decisions are made in isolation from decisions concerning efforts to control plant invasions or mitigate tick-borne disease risk, for which there are no established DSTs at present to our knowledge. Therefore, we developed a DST designed to integrate across multiple environmental management decisions. While this tool potentially has applications to land managers across the Southeast, it was specifically developed in partnership with land managers at nine U.S. Department of Defense (DoD) installations. Therefore before designing this DST we conducted structured interviews with different installations to establish management priorities. This paper has three goals:

1) Report on the DoD management priorities identified through these structured interviews
2) Report on the development of our tick management DST
3) Illustrate how this DST can be used to explore each installation's tick-borne disease risk and how alternative fire and management scenarios may affect tick populations

This decision support tool is based on field data collected from Department of Defense (DoD) sites. However, the DoD installations represent a large range of latitudes, soil types, and forests of the southeastern US. Estimates of tick-borne disease risk, may not correspond to levels of disease risk nearby. However, the underlying relationships between prescribed burns and ticks may be useful to public and private land managers to explore how burn frequency affects ticks (Goal 3).

Methods

This decision support tool relies on the field data, pathogen analysis, and path analyses done as part of a larger research project investigating the interacting impacts of invasive species, climate, fire, and management on tick populations and TBD disease prevalence for the Strategic Environmental Research and Development Program (SERDP) grant number 2636 . Here we briefly review the study system, field data collection, laboratory pathogen analyses and statistical path analysis that we take as inputs into our DST. Full descriptions can be found in Allen et al (2021) and the SERDP-

2636 report available for download at https://www.serdp-estcp.org/Program-Areas/Resource-Conservation-and-Resiliency/Natural-Resources/Species-Ecology-and-Management/RC-2636.

Field Data Collection

We collected field data from nine DoD installations across the southeastern United States (Figure 4.1) that were selected to capture a range of temperature and precipitation gradients across the southeast (Figure 4.2). Field data included vegetation data like overstory composition, percent canopy cover, litter depth and percent litter cover. Field data was collected from 500m^2 plots within each installation. Installations had a range of sampling effort from 3 plots at Moody AFB to 13 at Camp Shelby, Fort Jackson, and Camp Blanding. 92 plots were sampled in total. Each plot had four tick traps, four 50m dung transects, and four 1m^2 and 25cm^2 quadrats. Within each 500m^2 plot all trees with a DBH of over 3cm were mapped, identified to the species level, and had their DBH measured. Ten trees within the plots had their heights recorded. Percent Canopy Cover was estimated with a spherical convex densiometer (Forestry Suppliers, Jackson, MS). Within the 1m^2 quadrat, percent litter was estimated, along with three measurements of litter depth from the top litter level to the mineral soil surface. Within the 25cm^2 quadrat, all vegetation and litter biomass was collected, dried, and weighed to estimate standing biomass.

Host Abundance of large mammal host species (e.g. white tailed deer, *Odocoileus virginianus*) was measured based on four 50m dung transects at each plot. Dung was recorded <1m away from the transects. Tick populations were sampled using dry-ice baited traps set at sites for 24 hours (See Table 4.1 Trapping Effort).

Tick pathogens were detected by using a Fluidigm Access Array combined with Illumina sequencing individual ticks. Fire history was obtained from the installations at a management compartment level and includes information about the timing and extent of both prescribed burns and wildfire. Time Since Last Fire, also called Days Since Fire, are the number of days since the plot was burned. Fire regime – 15 yr FRI is the fire return interval averaged over 15 years for each plot (average number of years between fires), calculated in GIS using data provided by installations. Climate data comes from Daymet (Thornton et al., 2016; https://daymet.ornl.gov/). 1 year vapor pressure deficit was estimated as the average vapor pressure deficit for the last 365 days leading up to the sample date. Climate – 30yr CV fire days is a 30-year average of annual coefficient of variation of fire days defined as having <6 mm of recorded precipitation.

Structured Interviews with Installation Decision Makers

To better understand installation needs for decision support surrounding tick-borne disease, invasive species, and fire, and how these fit into forest management goals more broadly, we designed interviews and reached out to contacts at DoD installations via email and phone. Within the nine participating DoD installations (Figure 4.1), we targeted six installations where we had established contacts from field sampling (Tyndall AFB, Moody AFB, and Camp Shelby were not included). We successfully completed 30-min structured interviews with a representative from five of these installations (Avon

Park AFR, Camp Blanding, Eglin AFB, Fort Jackson, and Fort Benning), while the sixth was unavailable for an interview. Representatives had varying titles, but were all tasked with implementing their installations environmental management goals. Interviews were organized around a script that began with broad questions on the installation's decision-making process, and moved to specific questions about how the installation could use data from our project (Figure S4.1). We asked questions about installation priorities, evaluation metrics, and timelines of operation. We inquired about how each installation might value datasets from different aspects of the project: cogongrass invasions, tick borne disease metrics, and climate projections. We often ended interviews asking managers to describe their ideal DST tailored to their installation (Figure S4.1). Responses were recorded for reference. We summarized interviews by identifying areas where managers had consensus and areas of contrast for each of the interview themes. These responses highlighted what aspects of this project installation managers valued, how installation managers envisioned using a DST, and potential challenges and opportunities associated with DST implementations. Findings from these interviews allow us to tailor the design of our DST to shared priorities across installations.

This project was reviewed by the Boston University Institutional Review Board (IRB) and was determined to not meet the definition of human subject research and therefore did not require further IRB review and approval (Figure S4.2).

R Shiny Web Application

We elected to build our DST as a R Shiny web application (Chang et al., 2019; R Core Team, 2019), because 1) most of the underlying analyses performed for this project were conducted in R making for straight-forward harmonization of data, and 2) R Shiny is user-friendly and can perform complex data visualizations. We chose a web application because they are more intuitive to use by non-experts, can be updated with new data and features, and are not tied to specific software requirements. PINEMAP, a research project that focused on the restoration of the same southeastern longleaf pine ecosystems in which we performed this research, had success implementing their decision support system as a web application (Martin, 2019). Calculations underlying the TBD risk map are found at https://github.com/whalend/SERDP_Project/blob/master/R_scripts/ticks_tbo_mapping.R. The interactive map code is at https://github.com/mccabete/SERDP_shiny.

Summary of Features

Our DST content is sorted into tabs. Below is a list of tabs in the DST and the content associated with those tabs.

Tick-Borne Disease

- Disease Risk Map: Map of Tick-Borne Disease risk (Risk of pathogen exposure per 24 hours), Tick abundance in counts, and Pathogen prevalence at each of the DoD installations. Data available for download.
- Tick Pathogens: Searchable & downloadable database of pathogens that were detected at each base, and a key to diseases the pathogens cause.
- Tick Hosts: Searchable & downloadable database of animal hosts detected at each installation.

Vegetation

- Litter: Summary figures of litter depth and percent cover per installation.
- Canopy cover: Summary of figures of percent canopy cover per installation.

Exploring Hypotheticals

- Predictors of Tick Populations: Project tick populations with new fire regimes, climate, levels of vegetation biomass, canopy cover, and leaf litter.

Access and Installation Instructions

To see the app navigate to: https://serdp2636.shinyapps.io/serdp2636/

The underlying code that generates the app is at:

https://github.com/mccabete/SERDP_shiny/tree/main/code

Our tool requires an internet browser to access, and no other software to run. Graphics can appear differently depending on the browser. Data downloaded from our tool may require software to be opened or edited. We provide the options to download .csv files and .pdf files.

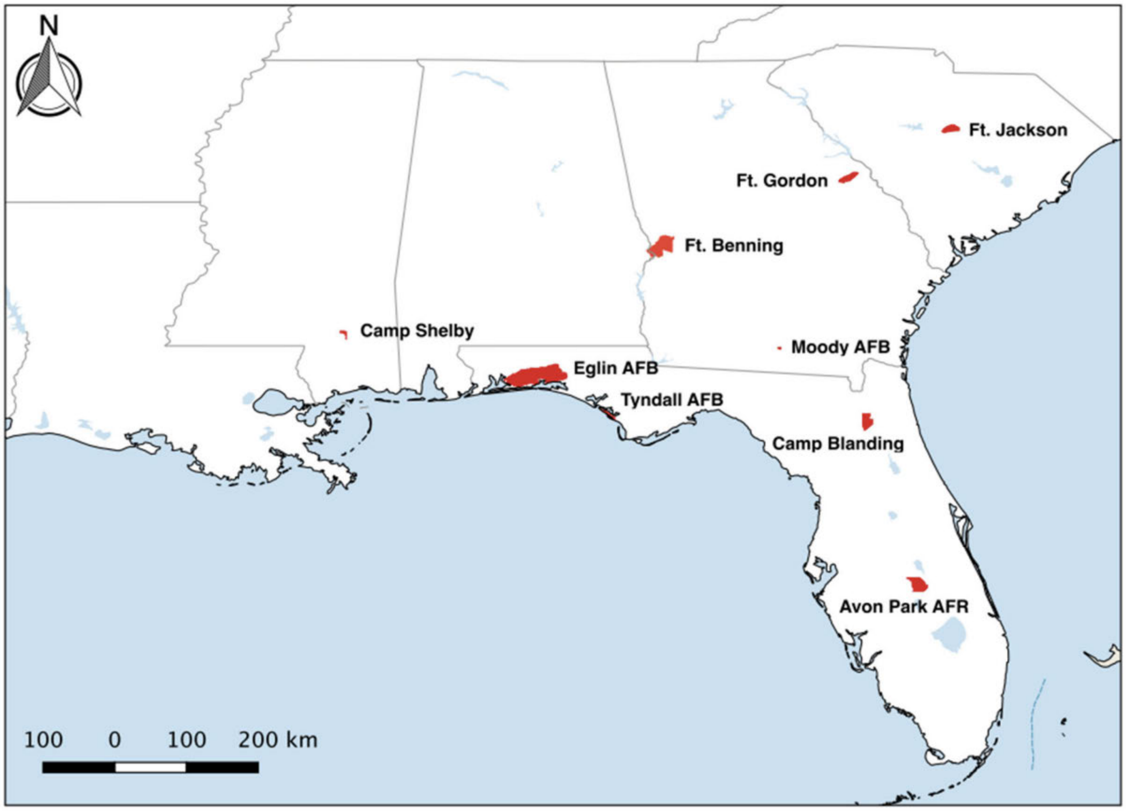


Figure 4.1: Study area with the location of each Department of Defense (DoD) installation sampled.

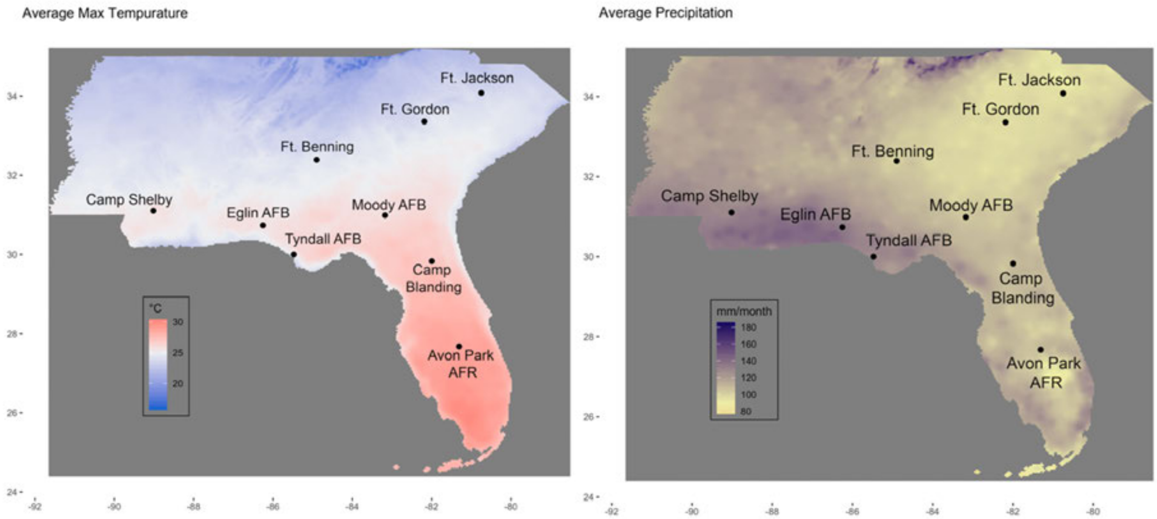


Figure 4.2: Average maximum temperature (left) and average monthly precipitation (right) from (1980-2018) Daymet climate variables.

Tick Borne Disease Risk Map

Our DST contains an interactive map of tick-borne disease risk as estimated by tick population sampling and pathogen analysis. It depicts three different estimates of TBD exposure risk based upon 1) tick abundance, 2) human pathogen prevalence, and 3) the product of tick abundance and pathogen prevalence, pathogens per trap, which is our best overall estimate of TBD exposure risk (Table 4.1). Traps were left at sites for 24 hours, so final risk numbers are presented in units of human pathogens per 24 hours.

$$Ticks\ Per\ Trap\ = Total\ Ticks\ /\ Trapping\ Effort$$
$$Human\ Pathogen\ Prevalence\ Per\ Tick\ =\ Pathogen\ Abundance\ /\ Total\ Ticks$$
$$Pathogens\ Per\ Trap =\ Ticks\ Per\ trap\ \times\ Human\ Pathogen\ Prevalence\ Per\ Tick$$

Installa-tion	**Pathogen Abun-dance**	**Total Ticks**	**Human Pathogen Prevalence Per Tick**	**Trapping Effort**	**Ticks Per Trap**	**Pathogens Per Trap**
Avon Park	0	6	0.00	28	0.214	0.00
Camp Blanding	129	318	0.173	75	4.24	0.733
Camp Shelby	10	25	0.16	39	0.641	0.103
Eglin AFB	42	89	0.146	42	2.119	0.310
Ft. Benning	2	25	0.04	31	0.81	0.0324
Ft. Gordon	20	71	0.113	26	2.73	0.308
Ft. Jackson	3	7	0.143	31	0.2265	0.0326

Moody AFB	3	7	0.143	16	0.43800	0.0630
Tyndall AFB	126	165	0.212	48	3.4380	0.7297

Table 4.1**:** Data used to calculate tick borne disease risk per installation. Because traps were left for 24 hours, the units on pathogen abundance, total ticks, and pathogens per trap are per day. Trapping effort is in units of the number of traps set.

The DST includes histograms of the number of ticks observed per trapping effort sampling event, and total number of ticks per species.

Exploring Hypotheticals

The scenario exploration tool aims to visualize predictions of how tick populations are likely to change in response to changes in input variables related to climate, fire, and vegetation. The scenario exploration tool builds off of the path analysis (a.k.a. structural equation model) described in Allen et al. (2021) and Dillon et al (*in prep*) . The component linear models from the path analysis defined relationships between environmental variables (Figure 3). For the DST we focused on the environmental variables affecting tick abundance (Figure 3, pink). Information on hosts (Figure 4.3, yellow) was not included in the DST. 30yr CV fire days and 15 yr FRI were not found to have direct effects on tick abundance, and were excluded from the DST. Neither Time since fire nor canopy cover had a significant direct effect on tick abundance, but were included in the DST because they had a significant effect on litter cover. Significant connections to ticks included litter depth, litter cover, standing biomass and vapor pressure. Predicted tick abundance was greater with increasing litter cover, litter depth, standing understory biomass, and vapor pressure.

We used ggpredict from the R package ggeffects as a wrapper for the predict function (Leeper, 2019; Lüdecke, 2018). The ggpredict function uses the component linear models of the path analysis, which was conducted using the R packages glmer and piecewiseSEM, and computes an out-of-sample confidence interval (integrating over random effect variances) based on the terms passed to the function (Bates et al., 2015, p. 4; Lefcheck, 2016). Unlike other parts of the DST, these results are not tailored to a specific installation. Our scenario exploration tool lets users select one or two variables, and will predict the change in tick population conditional on the variable being held at set levels. For a single variable, the tool will show the predicted number of ticks across the range of the variable. For two variables, the tool will show how ticks change across the range of the first variable, with three lines representing the second variable at representative levels. By default, the tool will select the mean +/- one standard deviation. Users can control the range of the first variable (to do projections) and the levels of the second variable (to explore the extent of interactions). Some of the underlying data driving the path analyses can be explored by installation via the Vegetation tab.

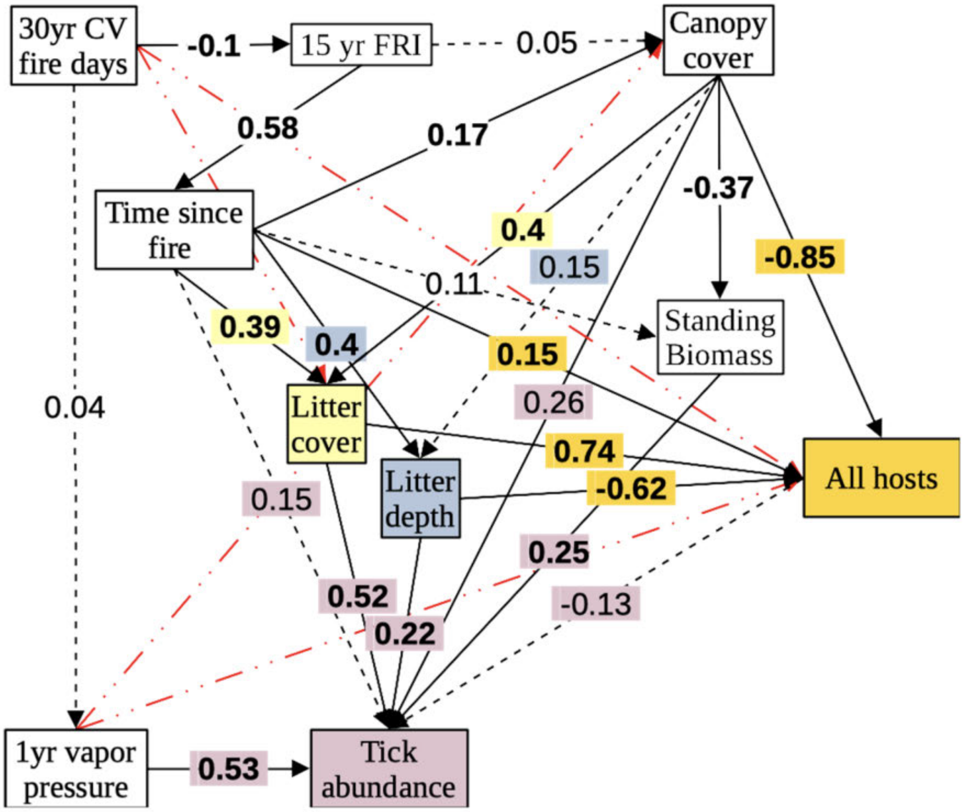


Figure 4.3: Path analysis and figure from (Allan et al., 2021). Numbers of standardized path coefficients that correspond to relative strength of effects. Color indicated response variable. *Bold coefficient values = P<0.05. Values on dashed paths = P>0.1. Normal text on solid paths = 0.05<P<0.1. Red dash-dot-dot lines are "missing" paths identified during model fitting.*

Results

Structured Interviews with Installation Managers

Interviews with installation managers revealed that while most installations have similar goals, how those goals are prioritized varied by installation. Overall, common natural resource management goals were: accommodate military training, wildfire risk reduction, habitat and species conservation, and silviculture. All of the installations relied on prescribed fire as a primary management strategy, and managers structured burn schedules to maintain a frequent fire-return interval for priority areas. Most interviewees characterized conservation, silviculture, and reduction of wildfire risk as long-term goals, with evaluations happening at yearly, five-year, decadal and multidecadal timescales. Several spoke about multidecadal changes in Red Cockaded Woodpecker (*Leuconotopicus borealis*) populations, pine populations (particularly longleaf pine), and anticipated changes to forest composition in the future.

In general, when asked about investment in major themes of our project - ticks, invasive species, and climate projections - managers typically indicated they would value each theme based on how closely it mapped onto these central priorities (training, wildfire, conservation, silviculture). However, there was quite a bit of variation among managers in how they weighed these priorities. For example, not all installations interacted with military training in the same way. At some installations military training and ground exercises dictated the day-to-day scheduling of prescribed burns. One interviewee suggested that a DST would only be useful if it incorporated military training activity. Some installation managers characterized military training as important but happening in parallel with natural resource management. One interviewee said that military training was largely independent from natural resource management. Of the installations that worked closely with military training personnel, interviewees said that military-motivated burns took priority unless there was a safety issue that needed to be addressed. One interviewee provided an example where conservation goals outweighed military goals: the military was considering clear-cutting a stand of longleaf pines to create a site to simulate desert conditions, and the natural resource team countered that the time it would take to regrow the longleaf population offset the gains of a new training site. However, this example was described as rare. On the whole, each installation shaped its long-term thinking around a varied military presence.

Another source of contrast was how each installation handled management of invasive plant species. All of the installation managers considered invasive species a management problem, and that controlling them was essential to their conservation goals. Our questions focused on cogongrass, but it was by no means the only invasive species that installations were grappling with – or even the most difficult species to eliminate. Two other species mentioned as difficult to control were Japanese climbing fern and kudzu. Some installation managers were optimistic about their successful control of cogongrass. As one interviewee stated, "Our longest running feud has been with cogongrass … and we are doing fairly well. We finally turned a corner". However, others felt that it was a "losing battle" and that even if our project offered an insight into cogongrass control, they were "already at capacity" on cogongrass control, and would struggle to implement additional changes. Not all the installation managers we spoke to had cogongrass invasions, but all were monitoring for it. One interviewee said that our project could be a useful way to anticipate the effects of cogongrass when it reached their installation. Installations actively controlling cogongrass used some combination of burning and herbicides, and sometimes physical management techniques.

Installation managers agreed that data on tick populations and tick-borne pathogens were useful. Four out of five interviewees listed it as the most valuable topic our project covered. Most said that monitoring tick populations and pathogens would be helpful for the safety of their staff or the safety of installation personnel. As one interviewee stated, “To me, tick-borne disease is not a management goal but a health and safety goal”. Another interviewee suggested that connecting invasive species to health outcomes like tick-borne diseases could better motivate invasive plant control. Most managers felt that prescribed burns were effective at controlling tick populations, but were still concerned about tick bites originating from infrequently burned areas, and about the illnesses associated with tick bites. Only one interviewee listed tick research as low-priority, citing the efficacy of permethrin-treated uniforms.

Climate projections were considered valuable when they were able to extend understanding of other important datasets into the future, but were considered lower-priority than other aspects of the project by four out of five interviewees. One interviewee listed it as most important, because they could inform demographic shifts in the forests over time. This interviewee was also interested in using climate projections to inform tree planting decisions, and ensuring that trees planted today would be able to tolerate future climates.

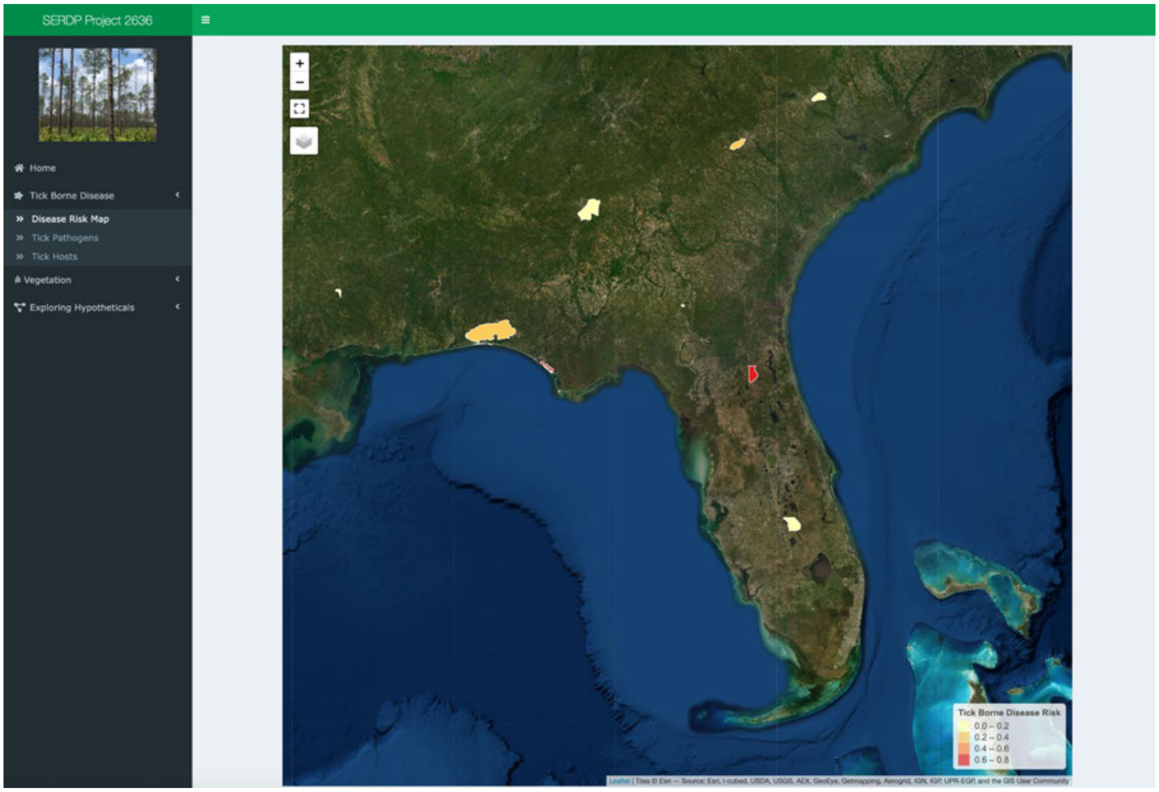
While many of our interview questions focused on the content of a DST from this project, we also asked about what forms of implementation would be effective. We learned that two installations already use a DST or ecosystem modeling in their planning. For example, Fort Benning uses a combination of monitoring plots and LANDIS-II modeling (Martin et al., 2015), and Eglin AFB uses a burn prioritization model that is maintained by a GIS specialist (Hiers et al., 2003). In general, GIS was the type of software most installations utilized. That said, two interviewees warned against designing a tool that required a specific operating system to run, or that needed to be run locally on a computer. This sentiment was echoed by others who explained that a variety of common software is not approved for use on installation computers, and that even approved software can be difficult to maintain locally because of access restrictions. One interviewee offered online tools, specifically QGIS, as a solution. One manager also cautioned that time-limited personnel may be slow to adopt a new tool, but suggested that an installation-specific demonstration could help.

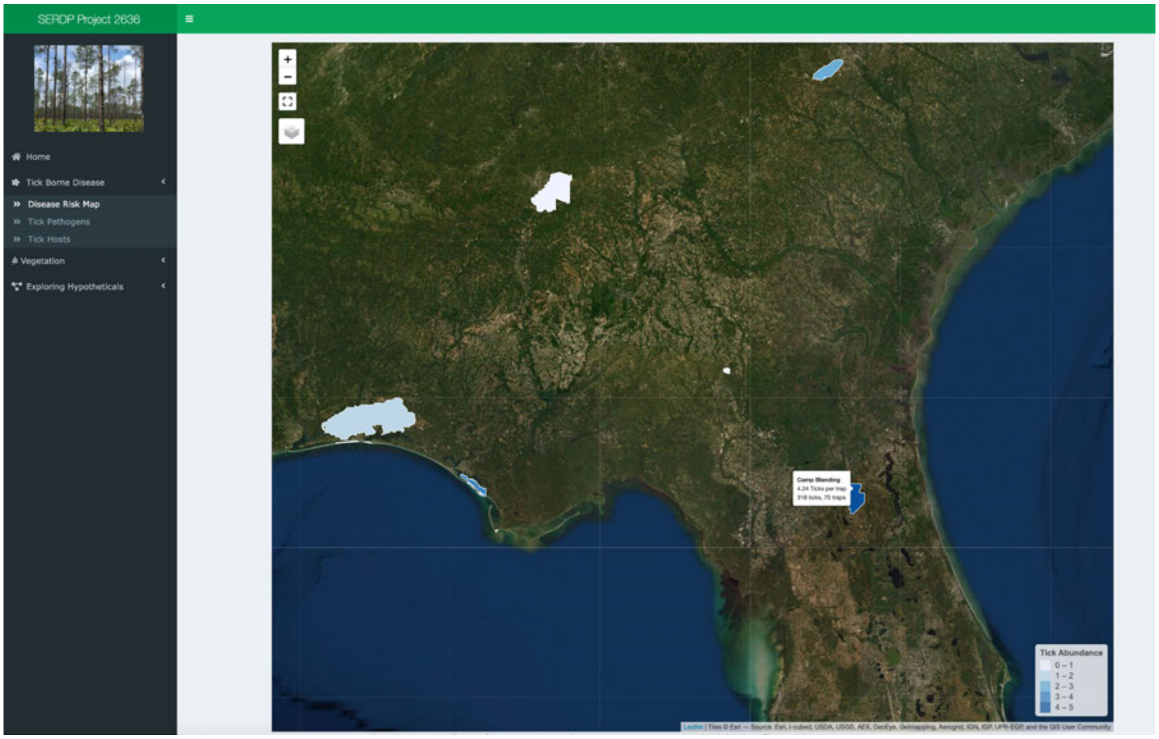
Taken together, these conversations highlight that while the mechanics of management at each installation are different, all of the installations have similar objectives, challenges, and interests. We learned that installations differ enough in their on-the-ground operations that even with perfect information, it would be challenging to design a tool that met the everyday logistical needs of each installation. However, we also learned what information would be valuable for broad decision-making. Managers expressed interest in connecting management decisions to health of personnel, TBD risk monitoring, insights into cogongrass invasion prevention and quantifying cogongrass effects, and forest demographic changes. Existing DSTs used by installations offer concrete examples to draw from and complement. Finally, we were reassured that a web-based DST was the best method to host and share our findings. These insights will help us shape the features and dissemination of our DST.

Tick Borne Disease Risk by Installation

Camp Blanding and Tyndall both had the highest rate of tick borne disease risk (Table 4.1). Camp Blanding reported 0.73 pathogens per trap per day, and Tyndall 0.72

pathogens per trap per day. Ft. Gordon, and Eglin AFB had mid range rates of 0.25 pathogens per day. Moody AFB and Camp Shelby had lower levels at 0.063 and 0.06 respectively, and Ft. Benning, Ft. Jackson and Avon Park had the lowest levels at 0.025, 0.019, and 0 respectively. For all sites, the level of tick borne disease risk was driven by the number of ticks collected more than than the number of pathogens detected per tick (Figure 4.1). Camp Blanding and Tandall's high numbers are likely driven by a few sampling events with a high number of ticks (Figure 4.5). Tick borne disease risk was calculated as a function of human pathogen presence. Many managers stressed that they value data that would describe possible health effects of tick populations. To accommodate this need, we included a search functionality for installations to have detailed information about the pathogens detected, and the possible diseases they cause. For example, at Camp Blanding, 19 different pathogens were detected, five of which have associations with human TBD (Figure 4.6). Finally, we included a search of the host populations we detected at each installation (Figure 4.7) . We did this because tick populations are tied to host populations, and because several managers we spoke to had management interests in vertebrate populations on their installation. Host population descriptions provide managers with the likely source of ticks on their installation, which could inform decision making.


SERDP Project 2636
≡
Home
Tick Borne Disease
Disease Risk Map
Tick Pathogens
Tick Hosts
Vegetation
Exploring Hypotheticals
+
−
Tick Borne Disease Risk
0.0 – 0.2
0.2 – 0.4
0.4 – 0.6
0.6 – 0.8
Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community


SERDP Project 2636
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Home
Tick Borne Disease
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+
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Camp Blanding
4.24 Ticks per trap
318 ticks, 75 traps
Tick Abundance
0 – 1
1 – 2
2 – 3
3 – 4
4 – 5
Leaflet | Tiles © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

Figure 4.4**:** Two sample screenshots from decision support tool. Top panel shows pathogen exposure per trap per 24 hours. Bottom panel shows tick abundance per installation.

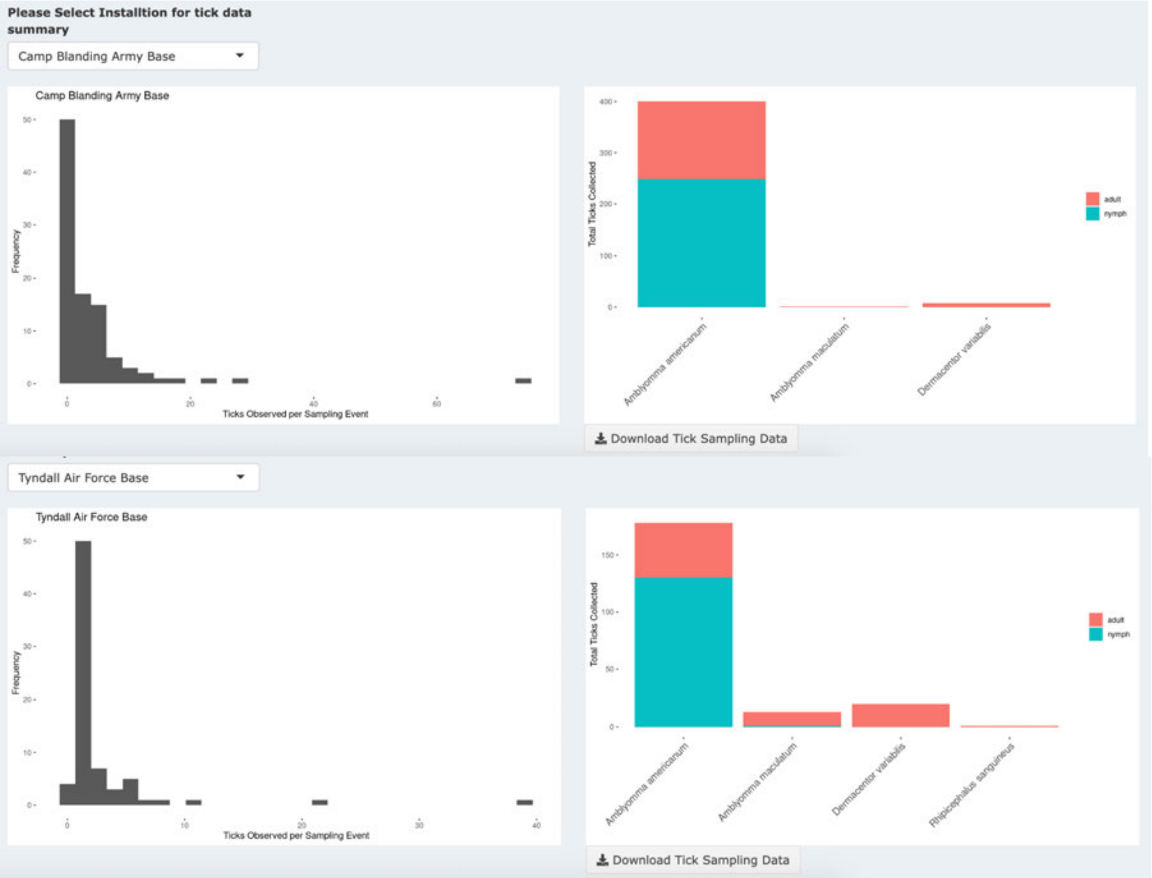
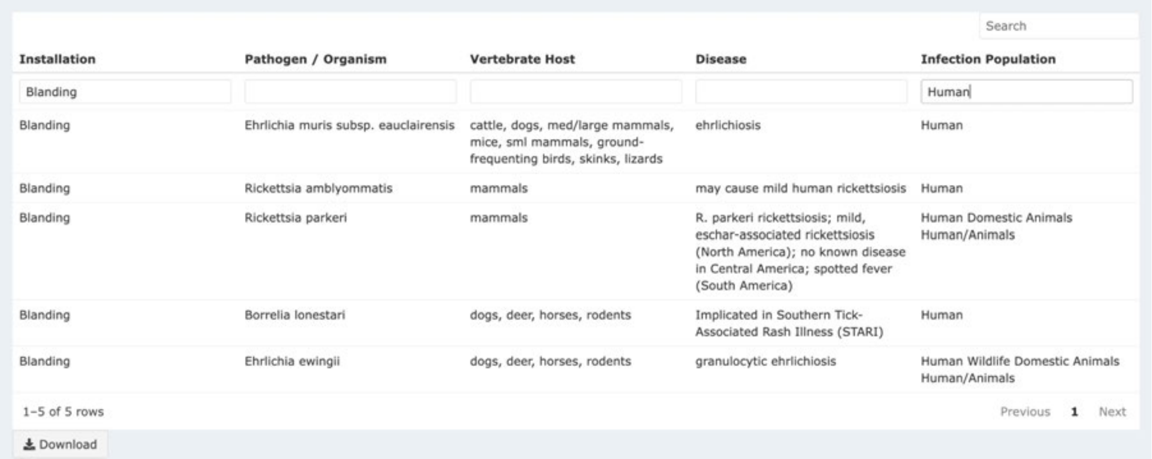
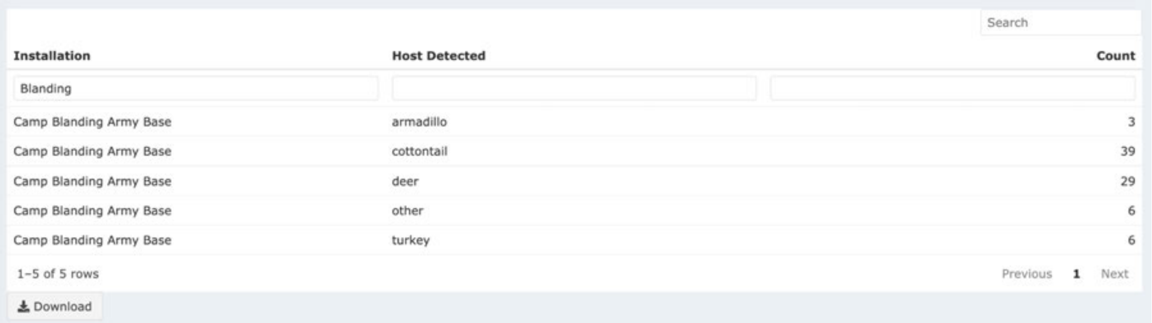


Figure 4.5**:** Frequency of Ticks Observed per sampling event, and tick species and life stage for Tyndall and Camp Blanding.



Installation	Pathogen / Organism	Vertebrate Host	Disease	Infection Population
Blanding				Human
Blanding	Ehrlichia muris subsp. eauclairensis	cattle, dogs, med/large mammals, mice, sml mammals, ground-frequenting birds, skinks, lizards	ehrlichiosis	Human
Blanding	Rickettsia amblyommatis	mammals	may cause mild human rickettsiosis	Human
Blanding	Rickettsia parkeri	mammals	R. parkeri rickettsiosis; mild, eschar-associated rickettsiosis (North America); no known disease in Central America; spotted fever (South America)	Human Domestic Animals Human/Animals
Blanding	Borrelia lonestari	dogs, deer, horses, rodents	Implicated in Southern Tick-Associated Rash Illness (STARI)	Human
Blanding	Ehrlichia ewingii	dogs, deer, horses, rodents	granulocytic ehrlichiosis	Human Wildlife Domestic Animals Human/Animals

Figure 4.6**:** Pathogens detected at Camp Blanding that cause diseases in humans. Hosts known to be reservoirs of pathogens are listed.



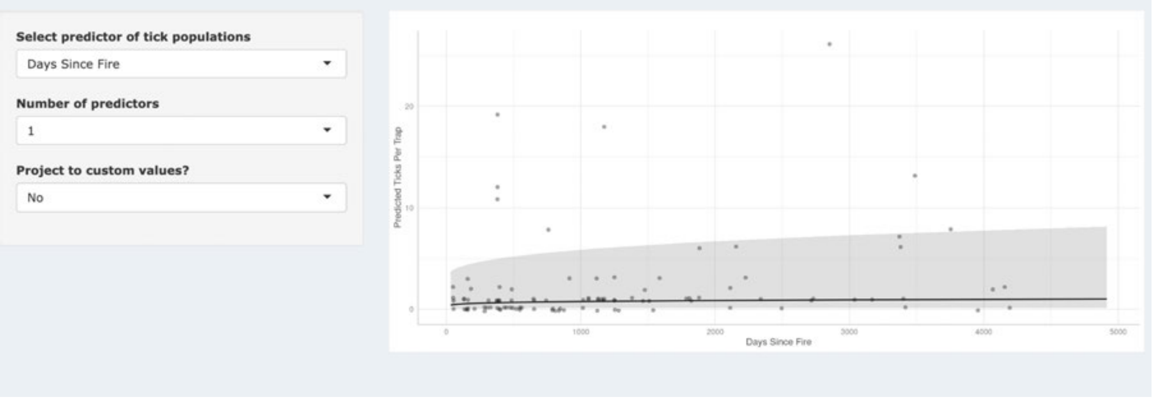
Installation	Host Detected	Count
Blanding		
Camp Blanding Army Base	armadillo	3
Camp Blanding Army Base	cottontail	39
Camp Blanding Army Base	deer	29
Camp Blanding Army Base	other	6
Camp Blanding Army Base	turkey	6

1–5 of 5 rows

Figure 4.7**:** Installation, host type, and dung-count for each host.

Exploring Hypotheticals

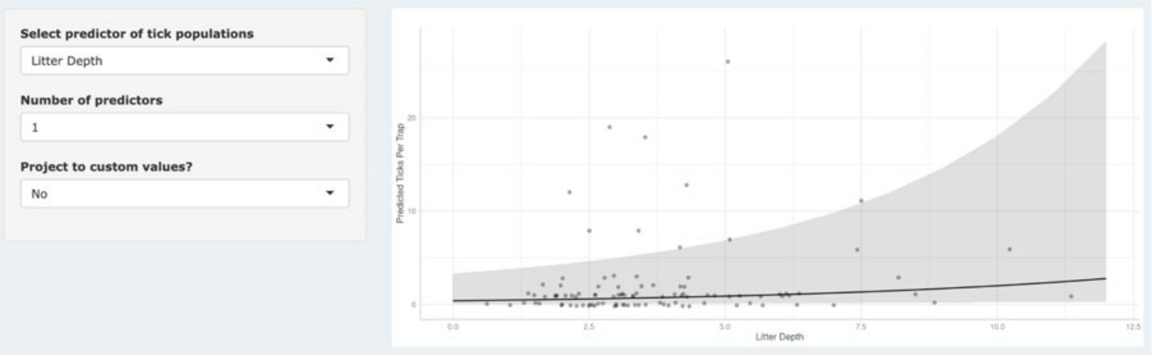
The second goal of our DST was to allow installations to explore how alternative fire and management scenarios might affect tick populations. This goal can be reframed as the question, what variables are tick populations sensitive to? The exploring hypothetical tools separates the direct and indirect effects of environmental variables on tick populations. For example, the direct effect of days since fire on tick abundance is small (Figure 4.8 Top), with the expected number of ticks remaining close to one tick per trap per 24 hours. Tick population is similarly insensitive to the direct effects of standing biomass and percent canopy cover, but is more sensitive to litter depth (Figure 4.8 Bottom), yearly vapor pressure deficit, and % litter cover.



Select predictor of tick populations
Days Since Fire

Number of predictors
1

Project to custom values?
No



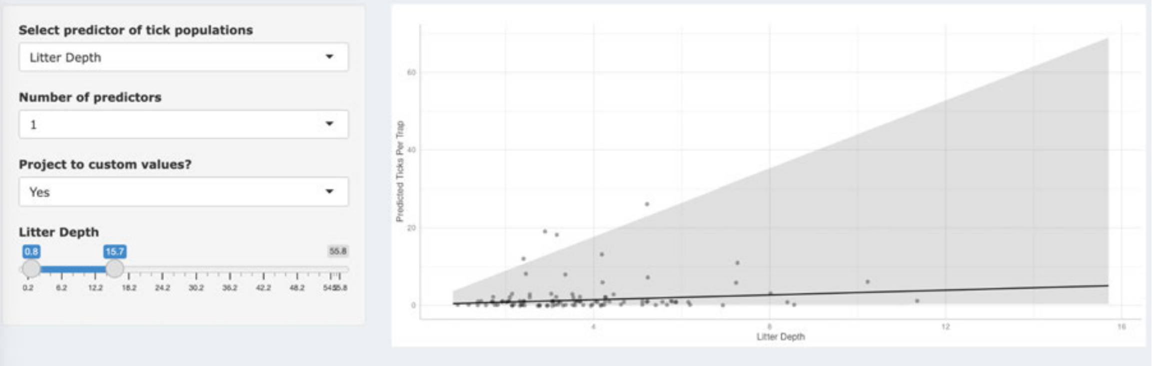
Select predictor of tick populations
Litter Depth

Number of predictors
1

Project to custom values?
No

Figure 4.8**:** Ticks per Trap as a function of Days since fire, and ticks per trap as a function of Litter Depth (cm). Line is predicted number of ticks, points are ticks per trap observed across all installations. Gray shading shows 95% confidence interval.

Users can explore how these relationships project into out-of-sample values using the “Project to Custom Values” menu. For example, litter depth increases the expected number of ticks by ~3 ticks with 3.5 cm of leaf litter (Figure 4.9).



Select predictor of tick populations
Litter Depth

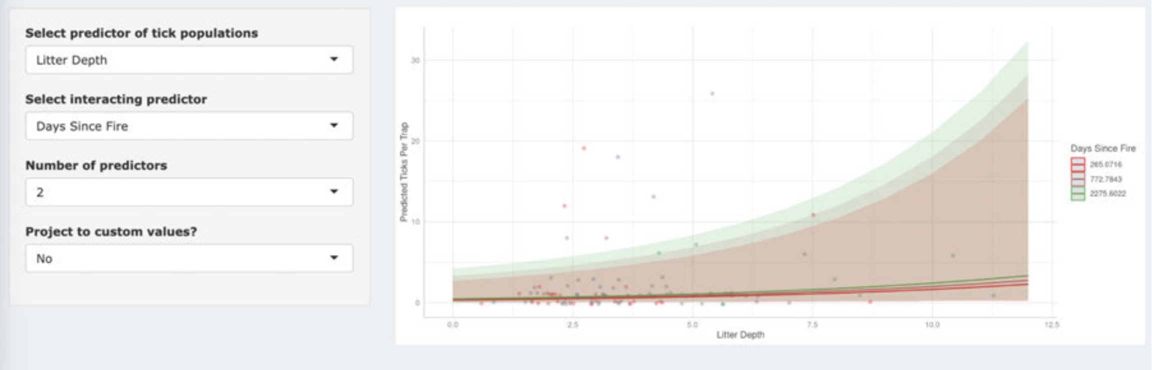
Number of predictors
1

Project to custom values?
Yes

Litter Depth
0.8 – 15.7

Figure 4.9: Ticks per Trap as a Function of Leaf Litter (cm). Line is the predicted number of ticks, and points are ticks per trap observed across all installations. Gray shading shows 95% confidence interval.

Setting the number of predictors to two allows a user to see how sensitive tick populations are to an interaction between two terms. For example, tick populations are not very sensitive to the interaction between litter depth and days since fire (expected value range of 2.5–3.5 ticks) (Figure 4.10 Top), but are sensitive to the interaction between litter depth and vapor pressure deficit (expected value ranges form ~ 3–7 ticks (Figure 4.10 Bottom). The largest sensitivity we found was the interaction between litter cover and vapor pressure deficit.

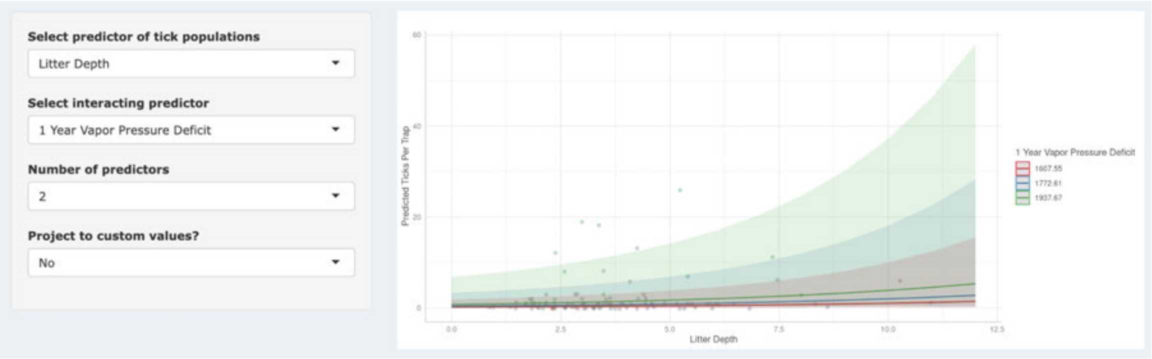


Select predictor of tick populations
Litter Depth

Select interacting predictor
Days Since Fire

Number of predictors
2

Project to custom values?
No



Select predictor of tick populations
Litter Depth

Select interacting predictor
1 Year Vapor Pressure Deficit

Number of predictors
2

Project to custom values?
No

Figure 4.10: The interaction of litter depth and days since fire, and litter depth and vapor pressure deficit. Note the change in scale on the Y axis.

Discussion

Designing a DST around Interviews with Installation Managers

Our structured interviews with land managers forewarned us that designing a tool that would align with the varied needs of all participating DoD sites would be challenging. There were a few themes that resonated with the majority of our partners. The largest resonating theme was information about tick borne disease risk at each installation. This theme ended up being the central focus of our DST. Other themes, like the control of invasive species and forest demographics changes, are not the focus of our tool, and are present in our DST only in their capacity to affect tick populations. Part of that design choice came from practicalities. All installations were monitoring for cogongrass, and several were actively suppressing cogongrass. This meant that finding instances of cogongrass invasions on DoD sites to measure was challenging. We could not build a tool to measure the effects of cogongrass because many of our partners had already prioritized suppressing it. In addition, cogongrass was never the only invasive species managers were concerned about. With both cogongrass and forest demographics, land managers were already familiar with trends on their installations. With tick populations and TBD monitoring, our group was offering new insights and data to managers. Our choice to build an online tool was directly in line with partner recommendations. By incorporating structured interviews, we were able to narrow in on a topic that was of interest to the majority of our partners.

In many ways, DoD management goals echo regional conservation goals. DoD land managers emphasized the need for prescribed fires to preserve open pine ecosystems, suppress invasive species, and conserve threatened species. These are goals shared by a network of public and private conservation organizations. For example, Natureserve, the Gulf Coastal Plain and Ozarks Landscape Conservation Cooperative, U.S. Fish and Wildlife, and East Gulf Coastal Plain Join Ventrue collaborated making metrics to judge open pine ecosystem quality, with an eye towards more frequent burns to preserve bird species, longleaf pine and shortleaf pine species (Nordman et al., 2021). The cross-institution organization, America's Longleaf Restoration Initiative, highlighted the need to control cogongrass and climbing ferns in their 2022-2024 Strategic Priorities and Actions report, in addition to emphasizing the need for prescribed fires (McIntyre et al., 2022). The unified goals of conservation groups across the Southeast gave us confidence that while TBD was not a stated priority of non-DoD sites, all conservation groups were planning around prescribed burns, and could benefit from knowing additional benefits or trade-offs that prescribed burning could cause.

Tick Borne Disease Risk By Installation

High rates of tick borne disease found at Camp Blanding and Tyndall are likely driven in part by the strong heterogeneity in tick population sampling. Part of that was likely exacerbated by changes in tick phenology along the field season, although installations were sampled over multiple years, at different times each year. It is also likely that lifestage affected results because nymphs were more likely to be encountered in a dense cluster than adults. Estimates of possible exposure in units of time is a useful way to present pathogen exposure to installations. It allows for incorporating estimates of exposure in field campaigns, and can help justify the cost of preventative measures like protective outerwear and insect repellents. By including the pathogens and diseases they could cause, we can put installations on alert for possible illnesses. Staff at Blanding, for example, might familiarize themselves with the symptoms for ehrlichiosis, richettotsis, and Southern-Tick Associated Rash Illness (STARI) (Figure 4.6). By including host data, we provide installations with the most likely reservoirs of pathogens, which might better inform decisions about how those host populations are managed.

Exploring Hypotheticals

Despite multiple lines of experimental evidence that prescribed burning reduces tick populations (Gleim et al., 2013, 2019), we found that ticks population projections were insensitive to the direct effects of fire. This suggests that fires may cull tick populations more through consuming leaf litter and by maintaining a forest structure that has lower leaf litter, rather than through direct fire mortality. We also found that predictions were most sensitive to the interactions between vapor pressure deficit and litter depth, which suggests that ticks are controlled by available habitat. These distinctions are useful because of the pragmatic solutions they open up. If prescribed burns become infeasible because of changes to the fire season (Mitchell et al., 2014), or because of scheduling conflicts, removing the leaf litter via other techniques will likely have a similar effect on tick populations. Knowing that leaf litter effects interact with vapor pressure deficit suggests that if the climate becomes drier, tick populations may decrease. It also allows for prioritization; if it is only possible to remove the litter from a fraction of the sites, managers should prioritize wetter sites. Finally, by creating a tool that puts the change of one environmental variable in terms of ticks per trap, we can justify management choices in units of ticks reduced. These analyses were based on the full range of installations across the southeast, which captures a range of temperatures, precipitation levels, and sites. This suggests that land managers in the southeast should see similar relationships between tick populations, litter, and climate.

Conclusion

We conducted five interviews with managers at participating installations, and learned that day-to-day decision making varied strongly between installations. However, installations have shared decision-making interests, and valued new insights from tick population and pathogen data and environmental effects data. We have developed a DST using R Shiny web application and it depicts three metrics of TBD exposure risk across nine installations. We report on the pathogens detected and on diseases those pathogens cause. We developed a tool that predicts how changes in environmental variables translate into changes in tick abundance, and found that tick populations are most sensitive to leaf litter and humidity. This sensitivity could be useful to find alternative management strategies if prescribed burns become less logistically feasible under climate change.

Acknowledgements

LF, BA, AG, and MCD conceived of the project and acquired the funding. WD, AG, DH, designed data collection. WD, DH, SC, collected data at DoD installations. BA and LPF conducted pathogen analyses. BA and TDM interviewed partners to inform the design of this app. WD conducted statistical analyses. MCD advised statistical implementation of the app. TDM designed and implemented the app.

License

The datasets that are downloadable from this tool are summarized versions of the datasets we collected. We ask that publications only incorporate the data from this tool with explicit permission from the RC-2636 team. Please contact Tempest McCabe tmccabe@bu.edu or Brian Allan ballan@illinois.edu if you are interested in collaboration. Our data license reflects this, and allows third parties to share and copy data, but may not so without attribution, and may not create derivatives from the data (ie future publications).

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CONCLUSIONS

Key findings

In this dissertation, I had two goals. The first was to incorporate disturbances into an ecosystem model. In my first chapter, I discussed a theoretical technique for including contagious disturbances into dynamic vegetation models. In my second chapter, I layed out a workflow for reducing parameter uncertainty in an invasive grass. My second goal was to use models of disturbances to make projections about the ecology of the southeastern United States. In my third chapter, I simulated the effect of cogongrass invasions on a pine-oak stand. In my fourth chapter, I built a decision support tool for land managers to reduce tick-borne disease risk. My key findings were:

- Representing disturbances in terms of frequency and shape can accurately recreate landscape dynamics, and different ecoregion and mechanisms had signature disturbance shape and size distributions. This suggests that our methods could be coupled with dynamic vegetation models to represent the heterogeneity of disturbances.
- Iteratively reducing parameter uncertainty can reduce the output uncertainty in models. We used a workflow to reduce parameter uncertainty around cogongrass. We recommend starting with an uncertainty analysis based on model priors, and then cyclically integrating literature values, measurements, and statistical constraints, stopping when parameter uncertainty is sufficiently reduced. We found that integrating measurements reduced output uncertainty, but that

integrating both measurements and using statistical constraint increased output uncertainty, because model structural error began to dominate. This suggests that parameter uncertainty can be systematically reduced to the point when other forms of uncertainty dominate.

- Cogongrass had lower biomass and density under elevated temperatures compared to elevated CO_2 levels, and present-day conditions. Simulations where cogongrass was grown with pines and oaks became pine-dominant stands, but simulations with only pines and oaks became oak-dominant. Cogongrass facilitated a change in dominant tree despite extinction within the first 20 years of simulation. This suggests that cogongrass can affect the structural composition of a forest, and that pines can dominate southeastern stands without fire.
- Department of Defense land managers prioritize information about tick borne disease risk and tick populations. Our decision support tool lets land managers explore the interactions of fire, climate, vegetation, and tick borne disease risk. We found that tick populations were most sensitive to leaf litter and humidity.

Recommendations for Future Work

My first two chapters highlight the difficulty of balancing model parameters and model structure. Implementing contagious disturbances in dynamic vegetation models involves new model structures and parameters. Our theoretical scheme has the potential to capture heterogeneity in models (Fisher & Koven, 2020), but actual implementation may not be appropriate for all questions, and could introduce uncertainty, if information about disturbance size and shape is difficult to measure, or is variable (Famiglietti et al., 2021). While we found that disturbance shape and size were distinct in some contexts, more testing is necessary to determine how difficult estimating these parameters could be. For example, we found disturbances had distinct sizes and shapes across state-level landscapes, but many modeling problems work on smaller scales that may not have sufficient data to parameterize disturbance regimes. There are disturbance types that we would expect to have different sizes and shapes seasonally (ie insect disturbances, development, fire), in ways that may be difficult to measure without continuous monitoring. More validation against time series of remotely-sensed disturbances is necessary (Vogelmann et al., 2011).

Our workflow for parameter uncertainty encountered model structural error. We need better tools for deciding how and when to restructure models. Process-based models can be subject to “complexification”, where models become more intricate as more processes are implemented. Complexification can make comparing, parameterizing, and using models challenging (Fisher & Koven, 2020). Dynamic vegetation models are complex enough that traditional model selection metrics are logistically challenging, and basic model-evaluation questions like appropriate scoring metrics and benchmarks, are still being resolved (Fisher & Koven, 2020). Possible solutions to complexification include evaluating models based on their ability to confirm or refute specific hypotheses, evaluating models based on performance against a range of situations, and evaluating specific sub-processes within models (Collier et al., 2018; Fisher & Koven, 2020; Medlyn et al., 2015). umber

My second two chapters explored how vegetation in the southeast controls the system independently of fire. This is a useful finding because it distinguishes between the direct effect of fire, and possible indirect effects. This is a particularly relevant distinction for cogongrass, which has been hypothesized to be part of the fire-grass-cycle. D'Antonio hypothesized that grasses invade by altering fire regimes (D'Antonio & Vitousek, 1992). The "Fire-grass-cycle" hypothesis states that grasses expand their range into woodlands through four steps: 1) establishing in a natural forest-canopy gap, 2) changing the microclimate to favor flammability and ignitions, 3) when ignition occurs, burning at a higher intensity than native vegetation can withstand, causing mortality and new canopy gaps 4) expand into the new gap. This hypothesis is cited as an explanation for why forests, savannas, and grasslands can co-occur at similar latitudes and climates (Oliveras & Malhi, 2016).

There is compelling evidence that cogongrass could be part of the fire-grass cycle. Cogongrass has traits that could alter fire regimes, like intrinsic flammability, creating dry thatch layers, and growing in a monoculture (Brooks et al., 2004). Cogongrass establishes quicker in disturbed sites than native vegetation (Estrada et al., 2017). It burns longer and more intensely than native grasses (Dillon et al., 2021; Flory et al., 2022). Cogongrass is taller than native grasses, and has been observed acting as a fire ladder from the understory to the tree canopy (Lippincott, 2000). However, only one study examined cogongrass' effects on landscape-scale fire regime, a remote sensing study that attributed change in fire regimes to reports of invasive grasses, including Cogongrass (Fusco et al., 2019). Cogongrass was found to significantly affect fire frequency and fire occurrence in the Southeast compared to uninvaded sites, but this was based on correlations and cogongrass had a smaller effect than other anthropogenic factors like the distance to roads. It's unclear from this study if cogongrass actually changes fire regimes, or if cogongrass invades places with distinct fire regimes, because both effects are anthropogenically mediated. Given the Southeast's extensive fire-management history, anthropogenic control over fire regimes seems plausible.

Testing if Cogongrass is part of the fire-grass cycle would require testing if cogongrass changes existing fire regimes, and that those regimes change forest mortality. After my dissertation, it also involves testing if forest demographics change after cogongrass invasions because of fire, or because of facilitation. Cogongrass may have large structural effects on forests independent of its effect on disturbance regimes. Future work could clarify how closely cogongrass is tied to fire.

APPENDIX TO CHAPTER 1

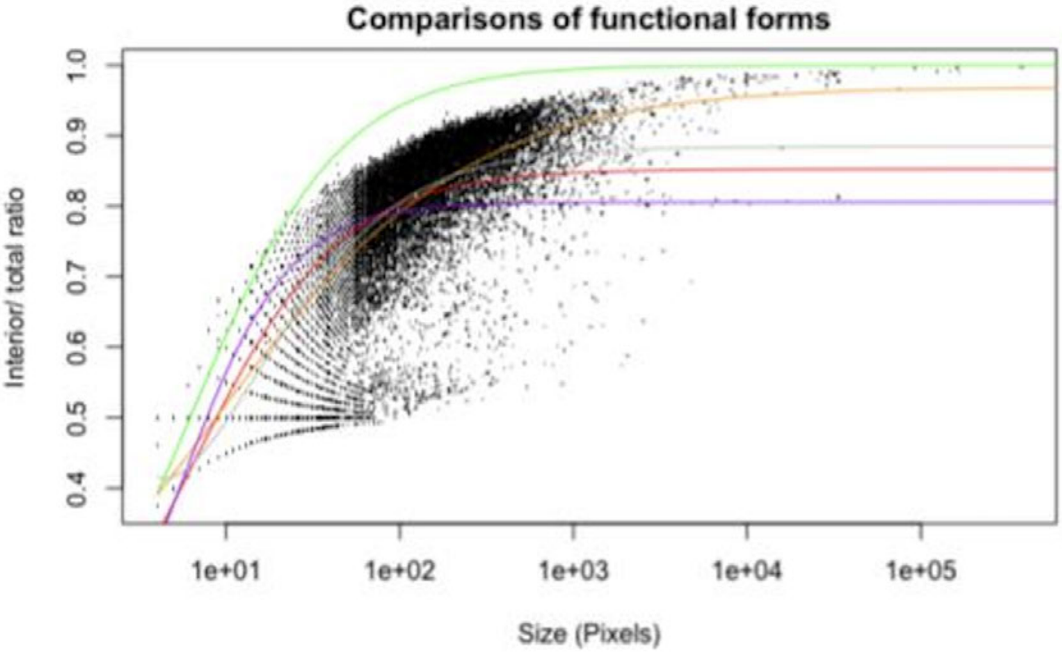
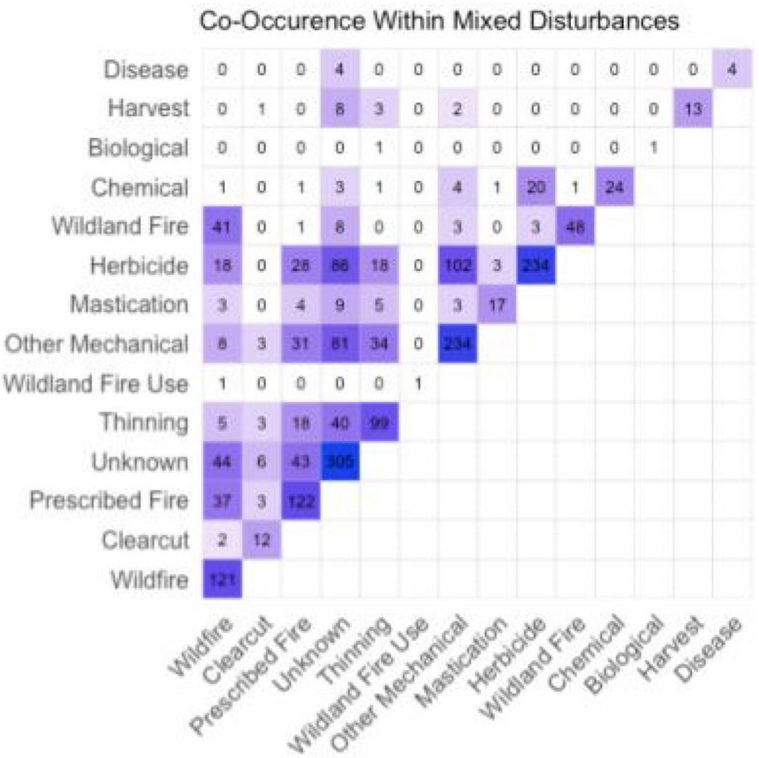


Figure S1.0.1: Comparisons of functional forms. Compared to all single-disturbance data larger than three pixels. For curve equations and fits, see Table S1.3.



	Wildfire	Clearcut	Prescribed Fire	Unknown	Thinning	Wildland Fire Use	Other Mechanical	Mastication	Herbicide	Wildland Fire	Chemical	Biological	Harvest	Disease
Disease	0	0	0	4	0	0	0	0	0	0	0	0	0	4
Harvest	0	1	0	8	3	0	2	0	0	0	0	0	13	
Biological	0	0	0	0	1	0	0	0	0	0	0	1		
Chemical	1	0	1	3	1	0	4	1	20	1	24			
Wildland Fire	41	0	1	8	0	0	3	0	3	48				
Herbicide	18	0	28	86	18	0	102	3	234					
Mastication	3	0	4	9	5	0	3	17						
Other Mechanical	8	3	31	81	34	0	234							
Wildland Fire Use	1	0	0	0	0	1								
Thinning	5	3	18	40	99									
Unknown	44	6	43	305										
Prescribed Fire	37	3	122											
Clearcut	2	12												
Wildfire	121													

Figure S1.0.2: Co-occurence of disturbance type within mixed disturbances.

Table S1.1: Summary Statistics of Disturbance types

	Percent Event Frequency	Percent Area	Number of Events
Unknown	0 728100113765643	0 20004122983	34560
Prescribed Fire	0 010175	0 0363565	483
Clearcut	0 000800	0 00059	38
Thinning	0 013125184	0 0107915249	623
Other Mechanical	0 07470610	0 030325679	3546

Herbicide	0 09807019	0 0930310	4655
Wildfire	0 0066363	0 06033	315
Mastication	0 0016222	0 0003213	77
Wildland Fire	0 00263	0 001288523	125
Chemical	0 0051826	0 00312636	246
Biological	8 42708465006531e-05	4 95050955096828e-05	4
Harvest	0 000463489655753592	0 000545727768843426	22
Disease	0 00012640	0 000198752705936803	6
Mixed	0 0122614	0 562501	582
Florida	0 428	0 207	20329
Southeastern USA Plains	0 182	0 0592	8618
Southeast Coastal Plains	0 247	0 147	11711
Oregon	0 572	0 793	27137
Western Cordilleras	0 418	0 757	19852
Marine West Coast Forest	0 153	0 0359	7285

Table S1.2: Pairwise comparisons of size density distributions statistics

Comparison	**P value**	**D statistic**
Clearcut x Wildland Fire	0.01743	0.28526
Clearcut x Wildfire	0.15749	0.19357

Clearcut x Prescribed	0.20314	0.18012
Clearcut x Thinning	0.00754	0.27912
Clearcut x Other mechanical	**0.00019**	**0.35089**
Clearcut x Unknown	**0.00025**	**0.34376**
Clearcut x Herbicide	**0.00002**	**0.38915**
Clearcut x Mastication	0.01197	0.31716
Clearcut x Harvest	0.07324	0.34450
Clearcut x Chemical	0.22988	0.18122
Clearcut x Mixed	**0.00009**	**0.37511**
Wildland Fire x Clearcut	0.01743	0.28526
Wildland Fire x Wildfire	0.01223	0.16876
Wildland Fire x Prescribed	**< 0.00001**	**0.38864**
Wildland Fire x Thinning	**< 0.00001**	**0.53880**
Wildland Fire x Other mechanical	0.25639	0.09218
Wildland Fire x Unknown	**< 0.00001**	**0.26273**
Wildland Fire x Herbicide	0.01244	0.14445
Wildland Fire x Mastication	0.01333	0.22930
Wildland Fire x Harvest	**0.00002**	**0.55673**
Wildland Fire x Chemical	0.00134	0.21002
Wildland Fire x Mixed	**< 0.00001**	**0.61245**
Wildfire x Clearcut	0.15749	0.19357
Wildfire x Wildland Fire	0.01223	0.16876
Wildfire x Prescribed	**< 0.00001**	**0.23837**
Wildfire x Thinning	**< 0.00001**	**0.39048**
Wildfire x Other mechanical	**< 0.00001**	**0.24830**
Wildfire x Unknown	**< 0.00001**	**0.15073**
Wildfire x Herbicide	**< 0.00001**	**0.30061**
Wildfire x Mastication	0.00121	0.24473

Wildfire x Harvest	**0.00071**	**0.43939**
Wildfire x Chemical	**0.00003**	**0.20186**
Wildfire x Mixed	**< 0.00001**	**0.47122**
Prescribed x Clearcut	0.20314	0.18012
Prescribed x Wildland Fire	**< 0.00001**	**0.38864**
Prescribed x Wildfire	**< 0.00001**	**0.23837**
Prescribed x Thinning	**< 0.00001**	**0.19531**
Prescribed x Other mechanical	**< 0.00001**	**0.44119**
Prescribed x Unknown	**< 0.00001**	**0.34588**
Prescribed x Herbicide	**< 0.00001**	**0.48387**
Prescribed x Mastication	**< 0.00001**	**0.39375**
Prescribed x Harvest	0.19780	0.23442
Prescribed x Chemical	**< 0.00001**	**0.23671**
Prescribed x Mixed	**< 0.00001**	**0.24544**
Thinning x Clearcut	0.00754	0.27912
Thinning x Wildland Fire	**< 0.00001**	**0.53880**
Thinning x Wildfire	**< 0.00001**	**0.39048**
Thinning x Prescribed	**< 0.00001**	**0.19531**
Thinning x Other mechanical	**< 0.00001**	**0.59121**
Thinning x Unknown	**< 0.00001**	**0.49625**
Thinning x Herbicide	**< 0.00001**	**0.62922**
Thinning x Mastication	**< 0.00001**	**0.52152**
Thinning x Harvest	0.12179	0.25660

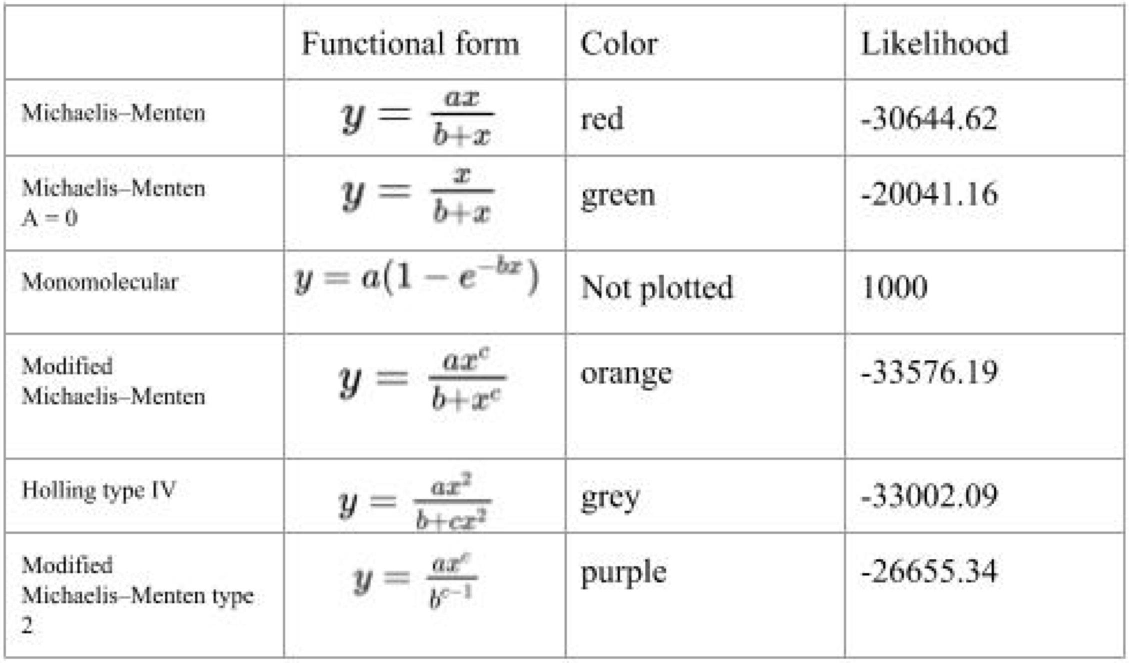
Thinning x Chemical	**< 0.00001**	**0.37551**
Thinning x Mixed	**< 0.00001**	**0.32425**
Other mechanical x Clearcut	**0.00019**	**0.35089**
Other mechanical x Wildland Fire	0.25639	0.09218
Other mechanical x Wildfire	**< 0.00001**	**0.24830**
Other mechanical x Prescribed	**< 0.00001**	**0.44119**
Other mechanical x Thinning	**< 0.00001**	**0.59121**
Other mechanical x Unknown	**< 0.00001**	**0.24823**
Other mechanical x Herbicide	**0.00002**	**0.05410**
Other mechanical x Mastication	**0.00010**	**0.25573**
Other mechanical x Harvest	**< 0.00001**	**0.63539**
Other mechanical x Chemical	**< 0.00001**	**0.23329**
Other mechanical x Mixed	**< 0.00001**	**0.67518**
Unknown x Clearcut	**0.00025**	**0.34376**
Unknown x Wildland Fire	**< 0.00001**	**0.26273**
Unknown x Wildfire	**< 0.00001**	**0.15073**
Unknown x Prescribed	**< 0.00001**	**0.34588**
Unknown x Thinning	**< 0.00001**	**0.49625**
Unknown x Other mechanical	**< 0.00001**	**0.24823**
Unknown x Herbicide	**< 0.00001**	**0.23206**
Unknown x Mastication	**< 0.00001**	**0.38511**

Unknown x Harvest	**< 0.00001**	**0.57247**
Unknown x Chemical	**< 0.00001**	**0.34878**
Unknown x Mixed	**< 0.00001**	**0.56315**
Herbicide x Clearcut	**0.00002**	**0.38915**
Herbicide x Wildland Fire	0.01244	0.14445
Herbicide x Wildfire	**< 0.00001**	**0.30061**
Herbicide x Prescribed	**< 0.00001**	**0.48387**
Herbicide x Thinning	**< 0.00001**	**0.62922**
Herbicide x Other mechanical	**0.00002**	**0.05410**
Herbicide x Unknown	**< 0.00001**	**0.23206**
Herbicide x Mastication	**< 0.00001**	**0.29271**
Herbicide x Harvest	**< 0.00001**	**0.68499**
Herbicide x Chemical	**< 0.00001**	**0.27288**
Herbicide x Mixed	**< 0.00001**	**0.71796**
Mastication x Clearcut	0.01197	0.31716
Mastication x Wildland Fire	0.01333	0.22930
Mastication x Wildfire	0.00121	0.24473
Mastication x Prescribed	**< 0.00001**	**0.39375**
Mastication x Thinning	**< 0.00001**	**0.52152**
Mastication x Other mechanical	**0.00010**	**0.25573**
Mastication x Unknown	**< 0.00001**	**0.38511**
Mastication x Herbicide	**< 0.00001**	**0.29271**
Mastication x Harvest	**0.00001**	**0.59091**
Mastication x Chemical	0.03765	0.18404

Mastication x Mixed	**< 0.00001**	**0.62574**
Harvest x Clearcut	0.07324	0.34450
Harvest x Wildland Fire	**0.00002**	**0.55673**
Harvest x Wildfire	**0.00071**	**0.43939**
Harvest x Prescribed	0.19780	0.23442
Harvest x Thinning	0.12179	0.25660
Harvest x Other mechanical	**< 0.00001**	**0.63539**
Harvest x Unknown	**< 0.00001**	**0.57247**
Harvest x Herbicide	**< 0.00001**	**0.68499**
Harvest x Mastication	**0.00001**	**0.59091**
Harvest x Chemical	0.00082	0.43939
Harvest x Mixed	0.10864	0.26211
Chemical x Clearcut	0.22988	0.18122
Chemical x Wildland Fire	0.00134	0.21002
Chemical x Wildfire	**0.00003**	**0.20186**
Chemical x Prescribed	**< 0.00001**	**0.23671**
Chemical x Thinning	**< 0.00001**	**0.37551**
Chemical x Other mechanical	**< 0.00001**	**0.23329**
Chemical x Unknown	**< 0.00001**	**0.34878**
Chemical x Herbicide	**< 0.00001**	**0.27288**
Chemical x Mastication	0.03765	0.18404
Chemical x Harvest	0.00082	0.43939
Chemical x Mixed	**< 0.00001**	**0.47025**
Mixed x Clearcut	**0.00009**	**0.37511**
Mixed x Wildland Fire	**< 0.00001**	**0.61245**
Mixed x Wildfire	**< 0.00001**	**0.47122**

Mixed x Prescribed	**< 0.00001**	**0.24544**
Mixed x Thinning	**< 0.00001**	**0.32425**
Mixed x Other mechanical	**< 0.00001**	**0.67518**
Mixed x Unknown	**< 0.00001**	**0.56315**
Mixed x Herbicide	**< 0.00001**	**0.71796**
Mixed x Mastication	**< 0.00001**	**0.62574**
Mixed x Harvest	0.10864	0.26211
Mixed x Chemical	**< 0.00001**	**0.47025**
Oregon x Florida	**< 0.00001**	**0.08044**
8.5 x 8.3	0.00649	0.02460
6.2 x 7.1	**< 0.00001**	**0.08656**

Table S1.3: Equations and Likelihoods of Functional Forms



	Functional form	Color	Likelihood
Michaelis–Menten	$y = \frac{ax}{b+x}$	red	-30644.62
Michaelis–Menten A = 0	$y = \frac{x}{b+x}$	green	-20041.16
Monomolecular	$y = a(1 - e^{-bx})$	Not plotted	1000
Modified Michaelis–Menten	$y = \frac{ax^c}{b+x^c}$	orange	-33576.19
Holling type IV	$y = \frac{ax^2}{b+cx^2}$	grey	-33002.09
Modified Michaelis–Menten type 2	$y = \frac{ax^c}{b^{c-1}}$	purple	-26655.34

Table S1.4: P values of model comparisons

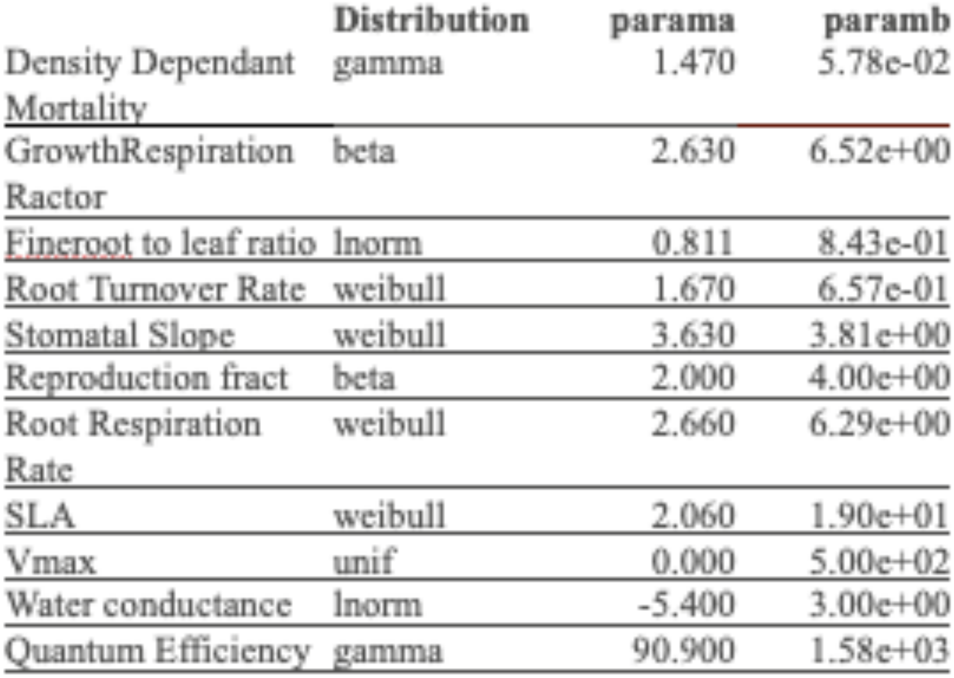
Null model to State Model	< 0.001
US State model to Ecoregion model	<0.001
Null Model to Disturbance model	<0.001
Florida to ecoregion	<0.001
Oregon to ecoregion	<0.001

Table S1.5: Parameter Values of Curves

	A	B	C	Sigma	
All data	0.9700	3.337	0.5858	0.0688	Null Model
Oregon	0.9873	3.377	0.5596	0.0784	US State Model
Florida	0.9432	3.2075	0.6272	0.0492	
Marine West Coast Forest	0.9654	3.5127	0.6442	0.0501	Ecoregion Model
Western Cordillera	0.9958	3.2727	0.5237	0.0836	
Southeastern USA Plains	0.9376	3.3096	0.6477	0.0475	
Mississippi Alluvial and Southeast Coastal Plains	0.9475	3.1364	0.6121	0.0503	
Wildfire	0.9836	2.6202	0.6165	0.0328	Disturbance Model
Clearcut	0.9851	2.1984	0.5576	0.0192	
Herbicide	0.732	4.011	0.889	-0.469	
other mechanical	1.0039	2.8596	0.4492	0.0918	
Prescribed Fire	0.9633	3.7391	0.7263	0.0324	
Unknown	0.9454	3.3184	0.6388	0.0484	
Thinning	0.9358	4.0150	0.8209	0.0253	

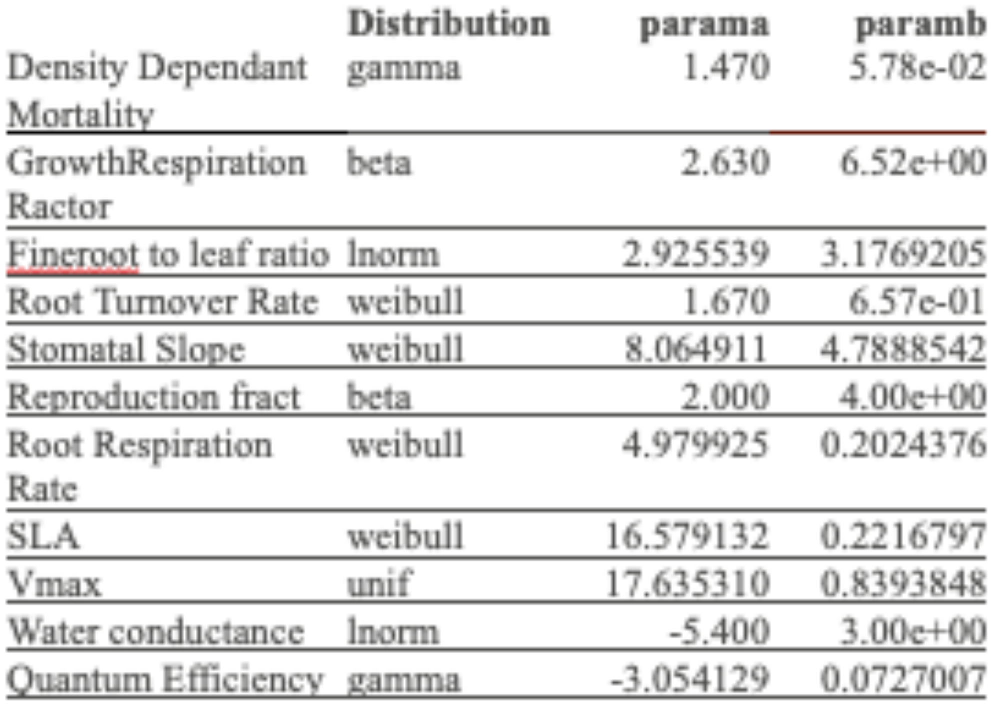
APPENDIX TO CHAPTER 2

Table S2.1**:** Prior Distribution Definitions from (LeBauer et al., 2013)



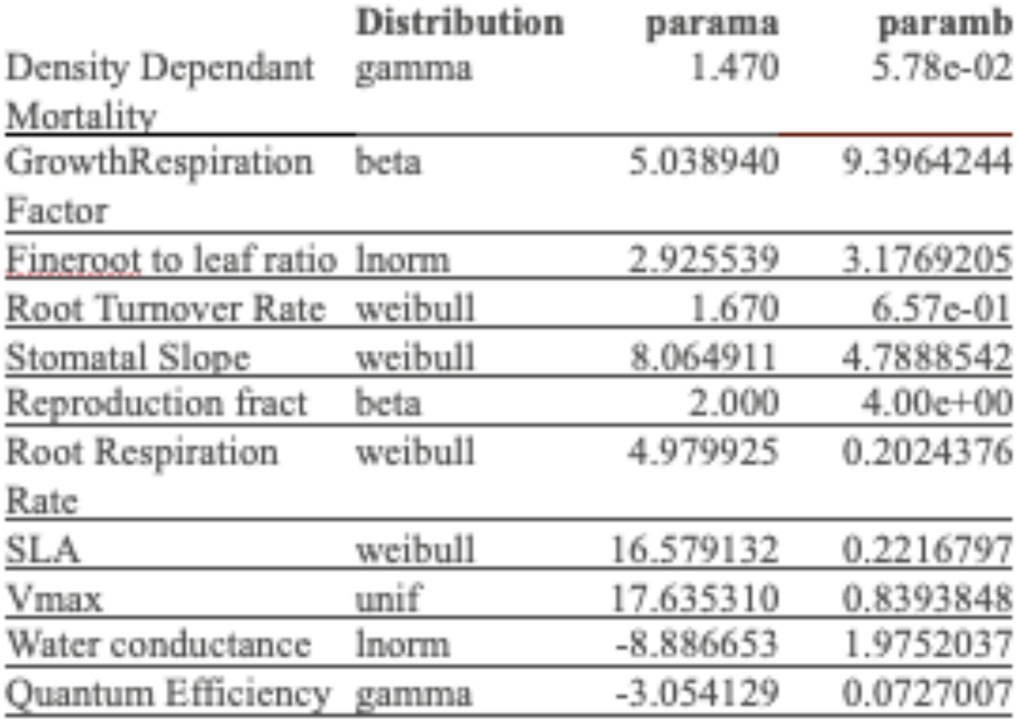
	Distribution	**parama**	**paramb**
Density Dependant Mortality	gamma	1.470	5.78e-02
GrowthRespiration Ractor	beta	2.630	6.52e+00
Fineroot to leaf ratio	lnorm	0.811	8.43e-01
Root Turnover Rate	weibull	1.670	6.57e-01
Stomatal Slope	weibull	3.630	3.81e+00
Reproduction fract	beta	2.000	4.00e+00
Root Respiration Rate	weibull	2.660	6.29e+00
SLA	weibull	2.060	1.90e+01
Vmax	unif	0.000	5.00e+02
Water conductance	lnorm	-5.400	3.00e+00
Quantum Efficiency	gamma	90.900	1.58e+03

Table S2.2**:** Distributions Definitions after Incorporating Field Data



	Distribution	parama	paramb
Density Dependant Mortality	gamma	1.470	5.78e-02
GrowthRespiration Ractor	beta	2.630	6.52e+00
Fineroot to leaf ratio	lnorm	2.925539	3.1769205
Root Turnover Rate	weibull	1.670	6.57e-01
Stomatal Slope	weibull	8.064911	4.7888542
Reproduction fract	beta	2.000	4.00e+00
Root Respiration Rate	weibull	4.979925	0.2024376
SLA	weibull	16.579132	0.2216797
Vmax	unif	17.635310	0.8393848
Water conductance	lnorm	-5.400	3.00e+00
Quantum Efficiency	gamma	-3.054129	0.0727007

Table S2.3: Distribution Definitions Field Data and Statistical Constraint



	Distribution	parama	paramb
Density Dependant Mortality	gamma	1.470	5.78e-02
GrowthRespiration Factor	beta	5.038940	9.3964244
Fineroot to leaf ratio	lnorm	2.925539	3.1769205
Root Turnover Rate	weibull	1.670	6.57e-01
Stomatal Slope	weibull	8.064911	4.7888542
Reproduction fract	beta	2.000	4.00e+00
Root Respiration Rate	weibull	4.979925	0.2024376
SLA	weibull	16.579132	0.2216797
Vmax	unif	17.635310	0.8393848
Water conductance	lnorm	-8.886653	1.9752037
Quantum Efficiency	gamma	-3.054129	0.0727007

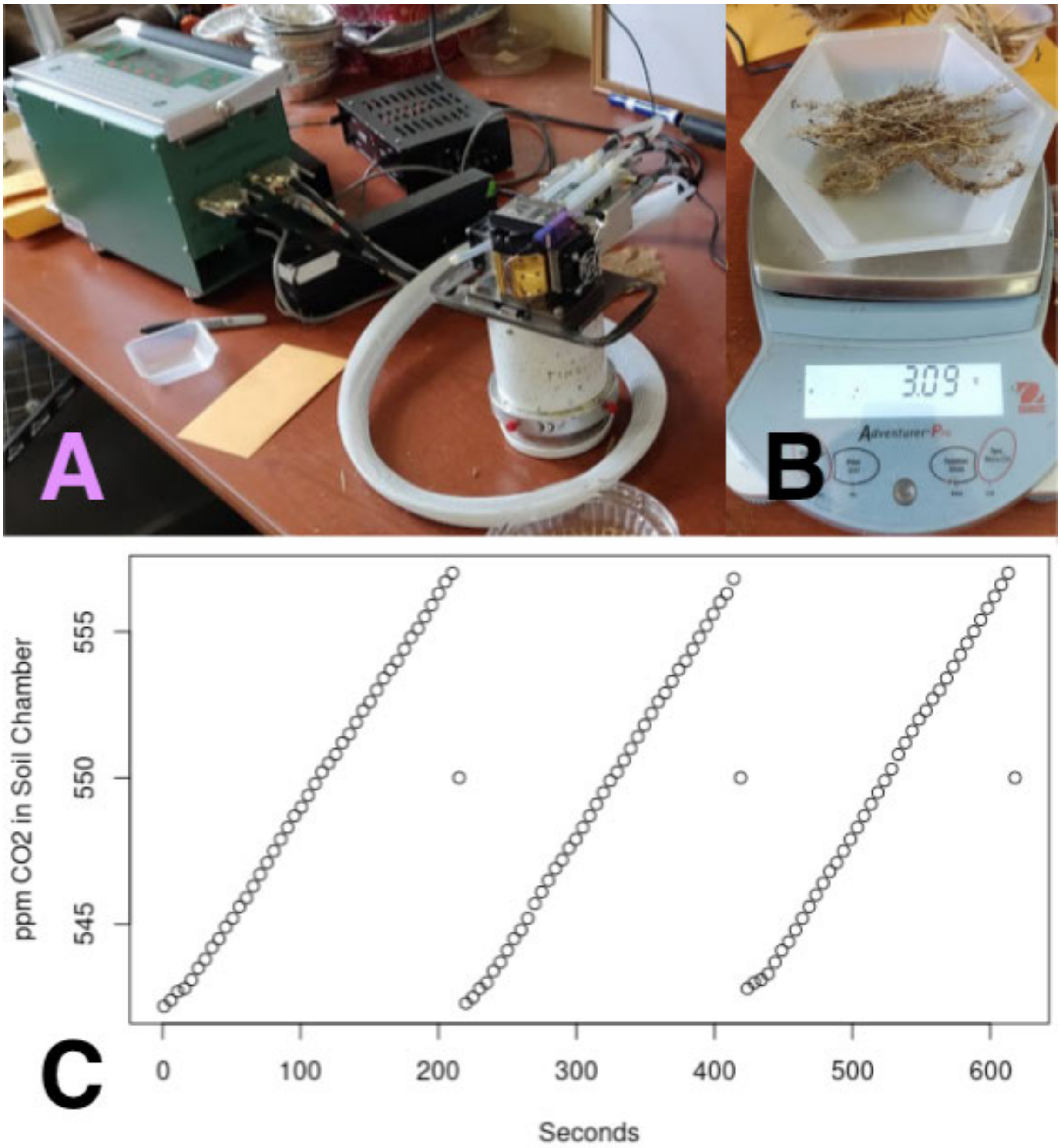


Figure S2.1: 2019 Field Season Closed-path Root Respiration measurement technique using LI-Cor 6400-09 soil chamber. Box A shows soil respiration chamber. Box B shows example fine roots being weighed. Box C shows the average CO_2 measurements through time. Box C corresponds to fine root measurement #15.

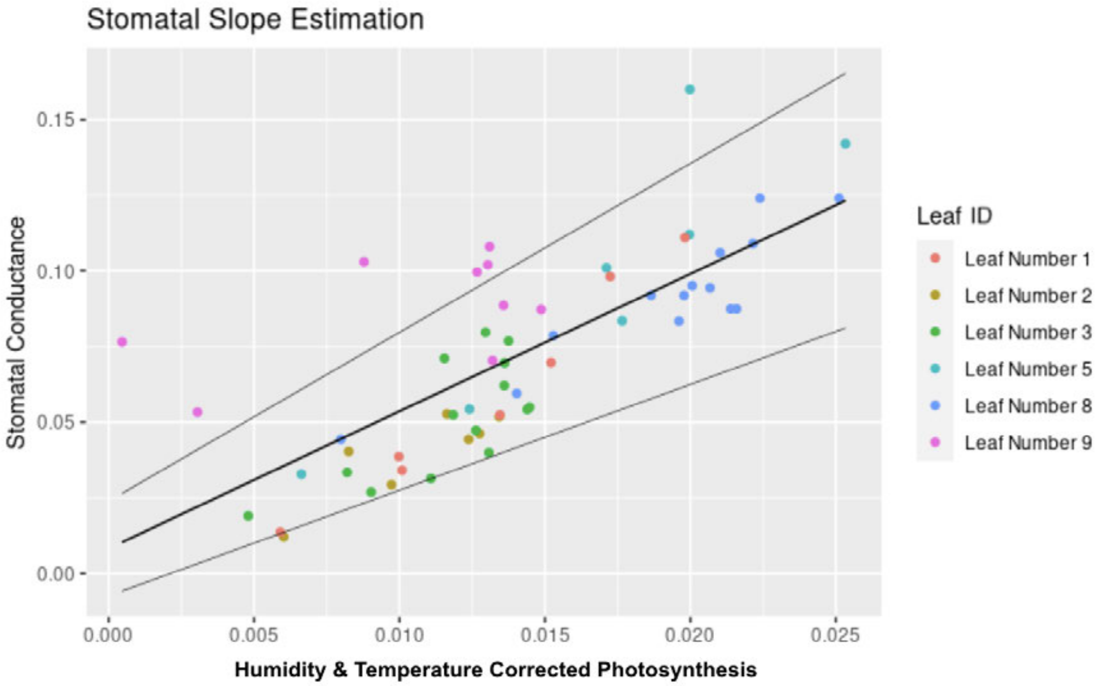


Figure S2.2: Estimate of stomatal slope from light curves. Each leaf had photosynthesis measured across progressive light changes. Different colored dots are distinct leaves. Dotted lines show 95% confidence interval.

Table S2.3: Parameter Distribution Mean Values Before and After Constraint.

Parameter	Prior Mean	Mean with Constraint
Fine Root Allocation	3.1235807	2.8388126
Growth Respiration	0.2924497	0.3509166
Quantum Efficiency	0.0572889	0.0471646

Root Respiration	5.5346419	4.9710924
Specific Leaf Area	16.6978538	16.5855974
Stomatal Slope	3.4000232	4.5366999
Vmax	248.9824621	17.6382072
Water Conductance	0.7003397	0.0007561

Table S2.5: Continuous Ranked Probability Score Modeled Biomass to Median Observation

	Priors	With Field Data	With Field Data + PF
Aboveground Biomass	0.0115	0.0187	0.0164
Belowground Biomass	0.0366	0.0205	0.0191
Aboveground/ Belowground	0.901	1.443	0.9148

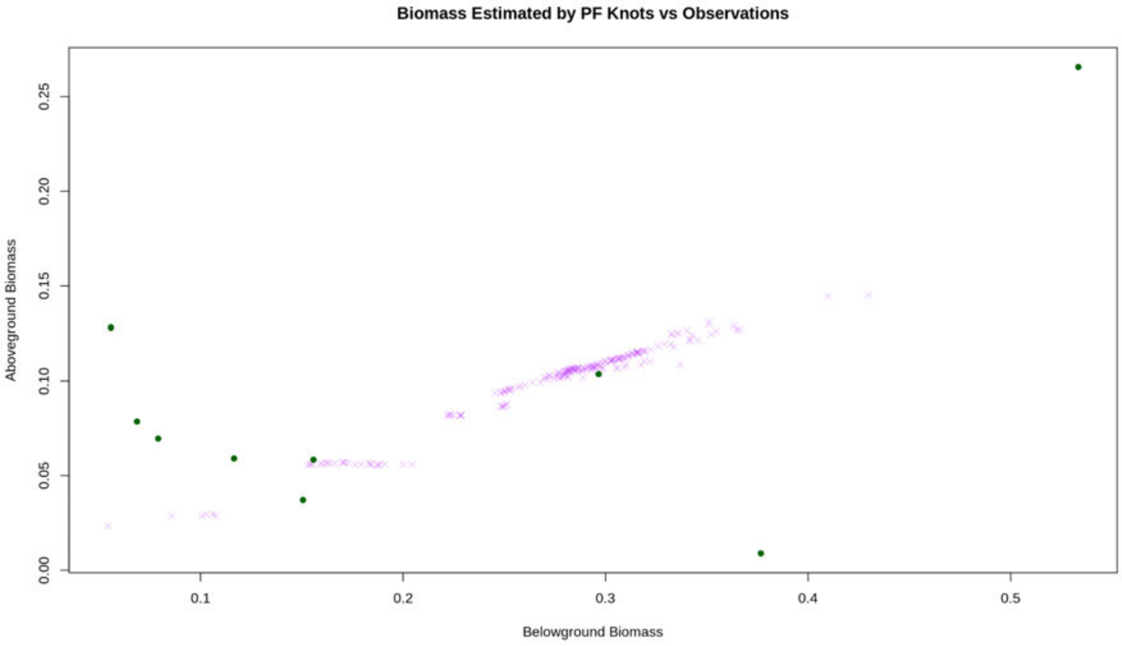


Figure S2.3: Observed above and belowground biomass compared to biomass estimated by the 200 knots used in the particle filter described in the Statistical Constraint section. Observations are dark green circles. Knot values are magenta crosses.

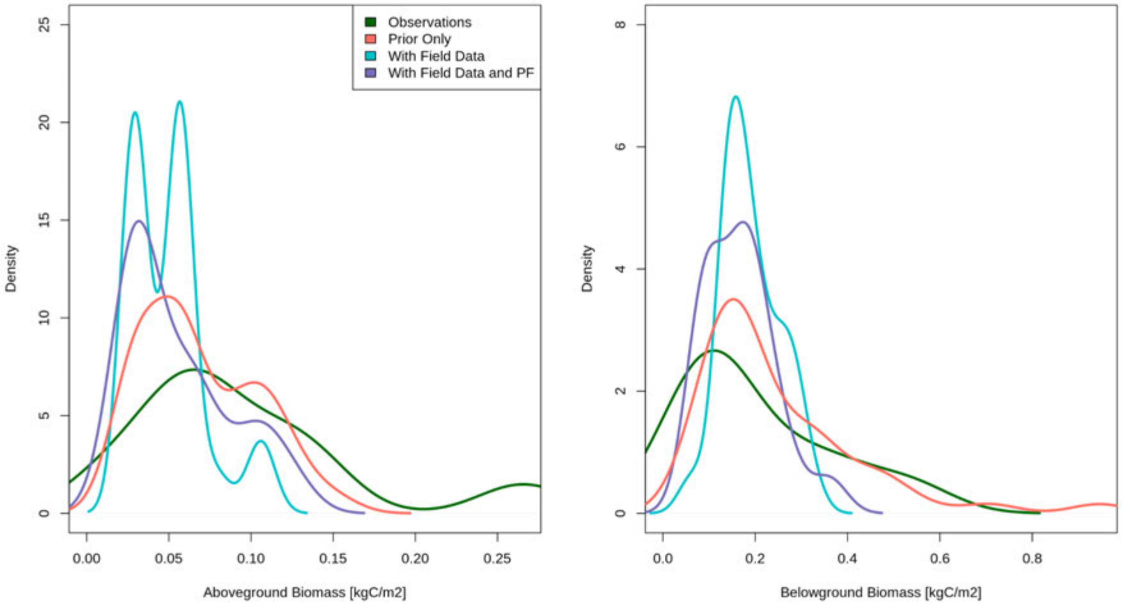


Figure S2.4: Density of observed above and belowground biomass compared to modeled above and belowground biomass. Modeled distributions come from 50-member ensembles with parameter distributions described in Tables S2.1-S2.3. Bivariate points in Figure S2.5.

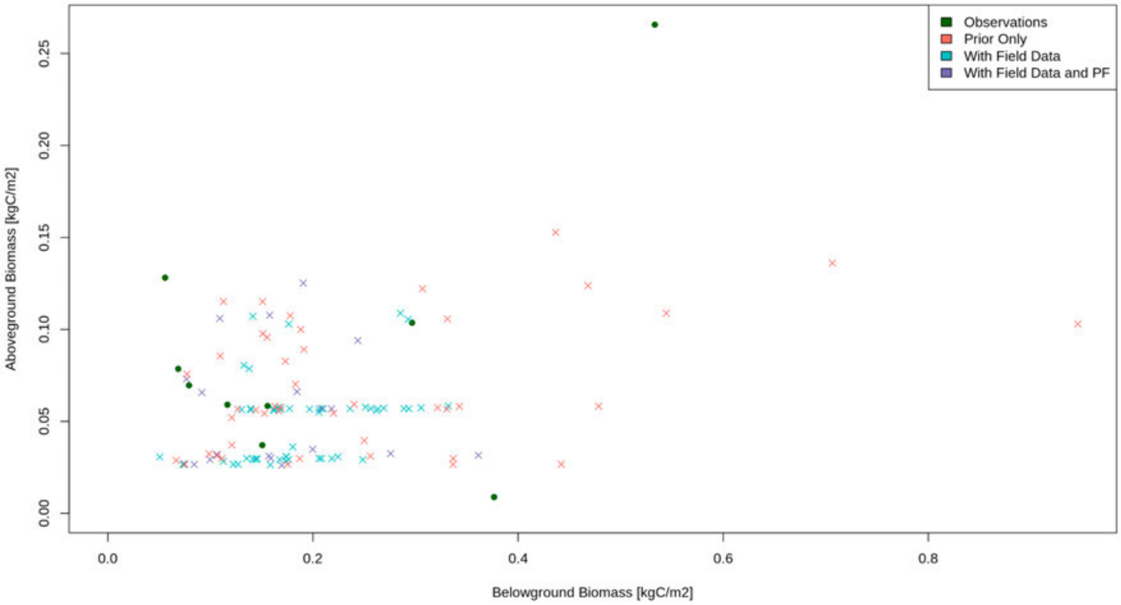


Figure S2.0.5: Observed above and belowground biomass compared to estimated above and belowground biomass using priors, field data constraint, and statistical constraint. Univariate distributions seen in Figure S2.4. Dark green circles are observations, crosses are model estimates.

APPENDIX TO CHAPTER 3

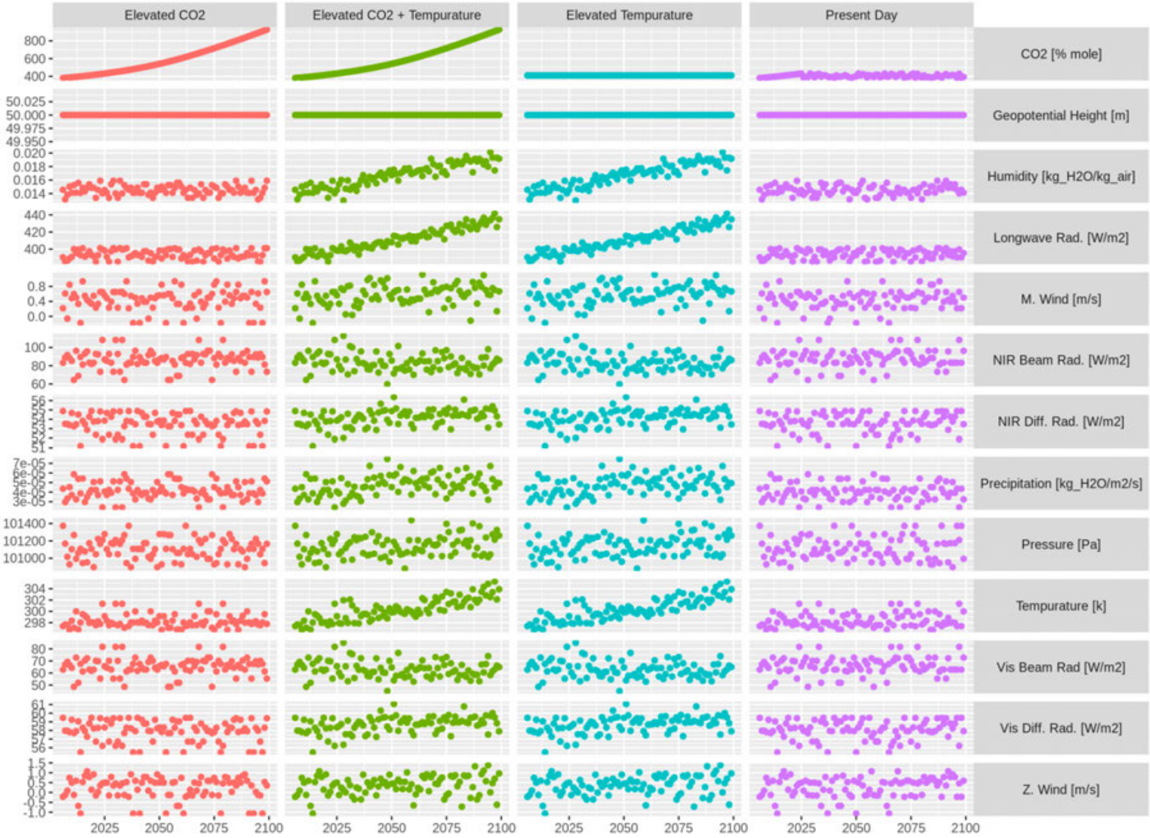


Figure S3.1: Average June climate variables from four climate treatments.

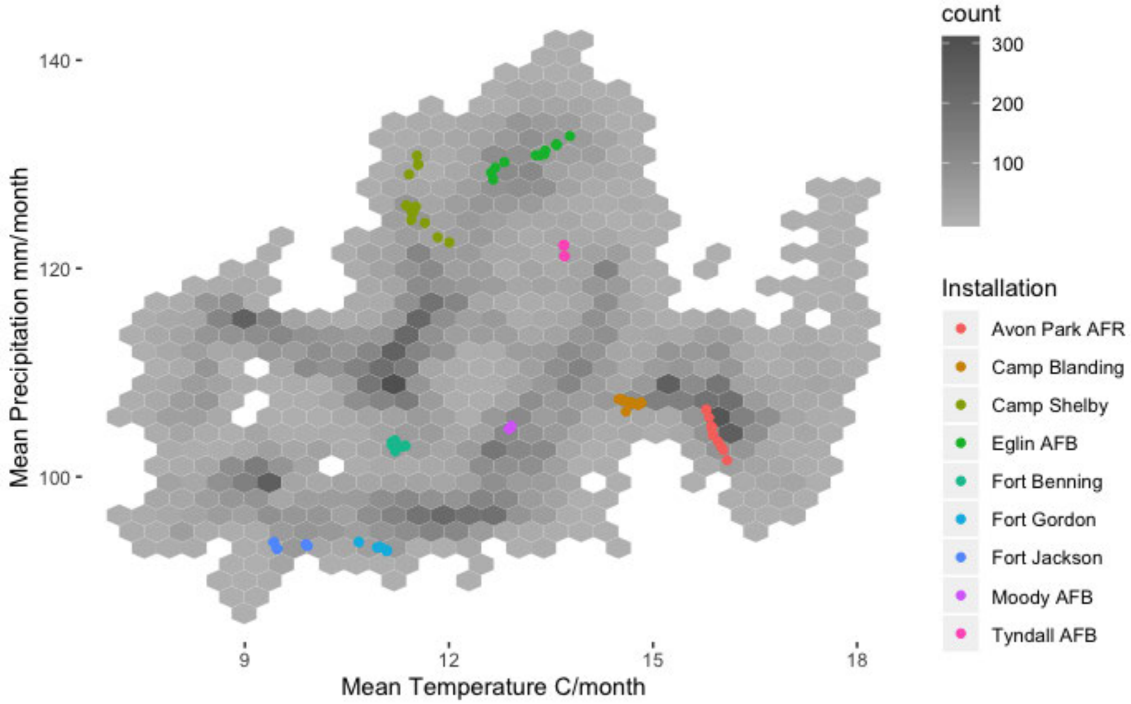


Figure S3.2: Where sites sampled fall in climate space. Precip and Temperature estimates are from Daymet (Thornton et al., 2016). Counts are the number of grid cells within the southeast ($1km^2$) with corresponding levels of temperature and precipitation. This data is plotted spatially in Figure 4.2 Sites were sampled as part of (RC-2636 Project Overview, n.d.)

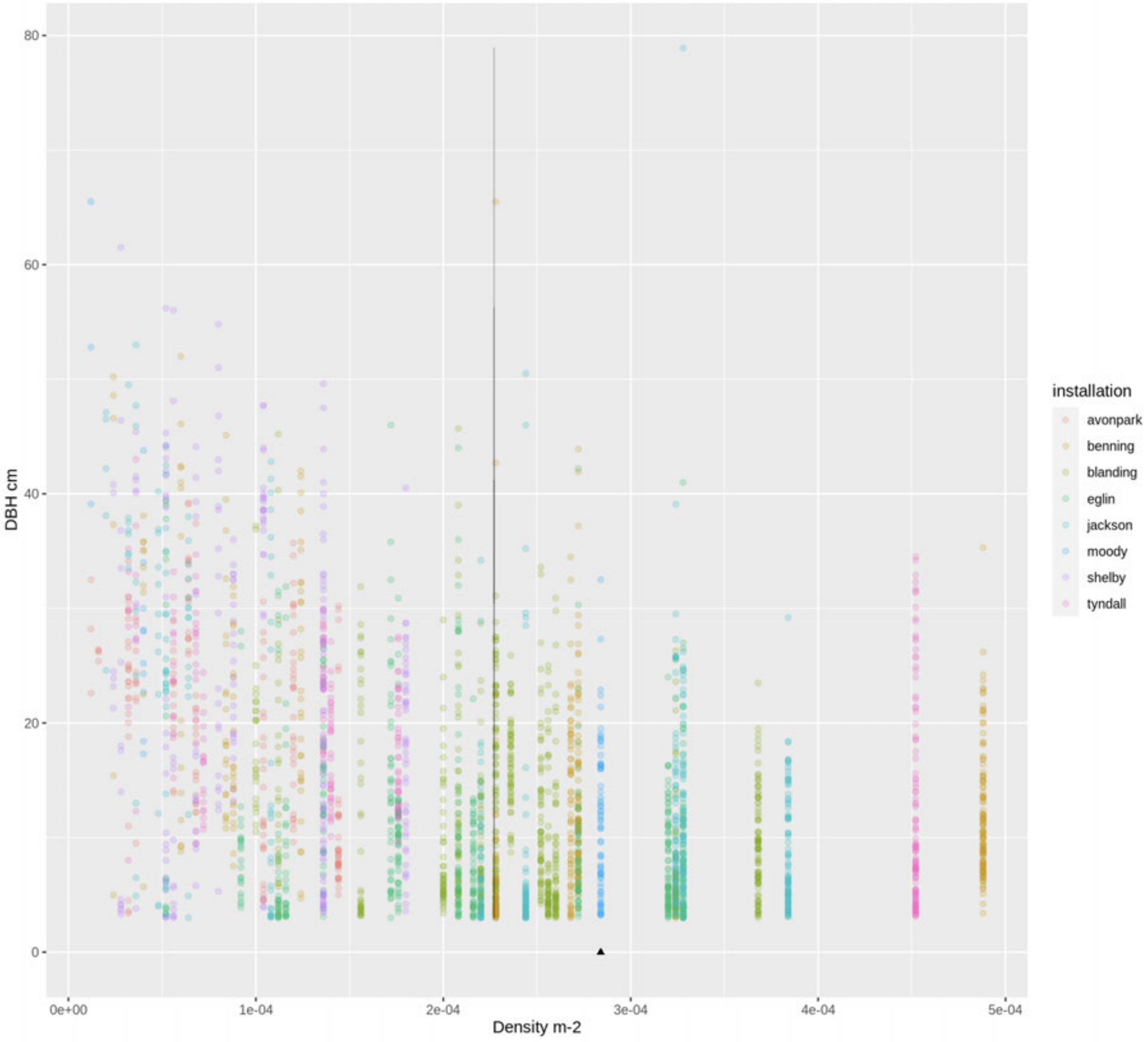


Figure S3.3: Plot-scale Density vs Tree DBH across all inventoried sites. Line indicates cross-sample mean. Triangle indicates the density of plot used for analyses. Points above the triangle are the trees used to initialize model runs.

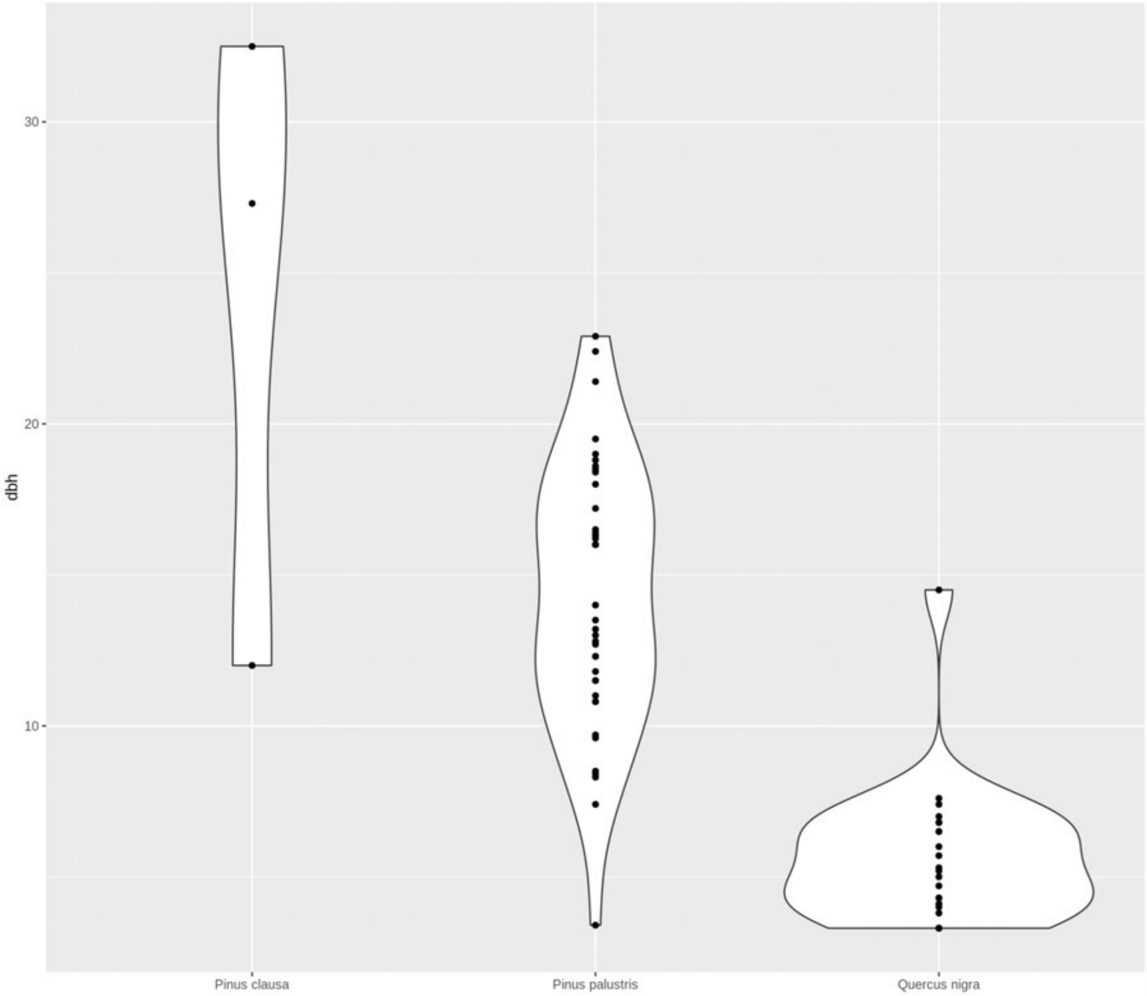


Figure S3.4: Species and DBH used to initialize ED2 for Trees, and Cogongrass + Trees competition treatments.

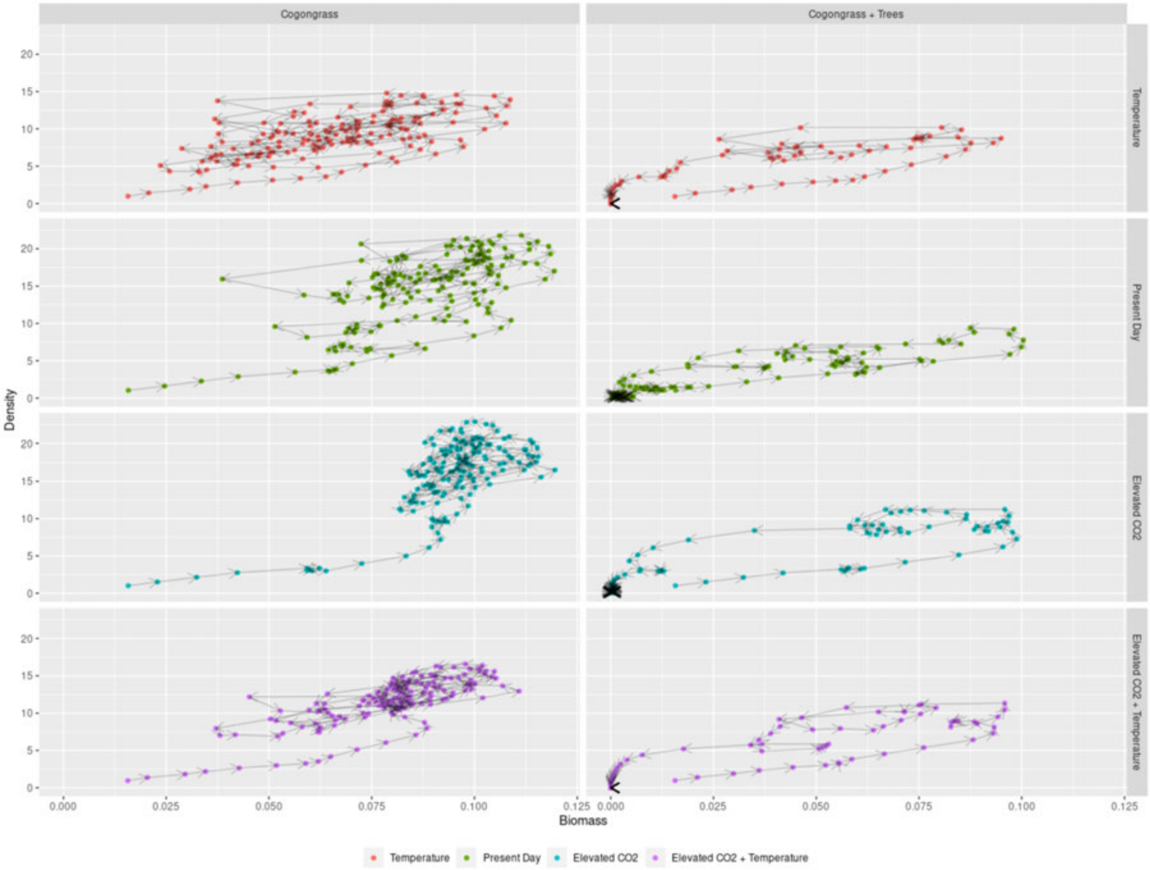


Figure S3.5**:** Density vs Biomass of Cogongrass. Arrows indicate movement through time, from 2085-2100.

APPENDIX TO CHAPTER 4

Hello and thank you for agreeing to meet with us!

My name is [Main interviewer], and this is [second interviewer], who will be taking notes.

We are both part of a research team that studied the effects of fire and invasive plant management on vegetation and tick populations on your installation [personal context- when did Whalen & Drew sample and who were they in contact with] .
One of the products of our contract is to design a "decision support tool". At this early design stage, by "decision support tool" we mean a tool that displays how land management decisions affect some aspect of your installation that we studied. For example, the effect of time since last burn on tick populations. We would like to know more about how you are making decisions and what you find valuable to make the final "decision support tool" as useful as possible.

Briefly, what is your role at the installation?

How does your installation make decisions around forested natural resources?

Do you use any decision support tools to make decisions now? Do you use any simulations or software to inform your decisions?

What goals does your installation have for its natural resources?

How do you prioritize goals?

How do you evaluate whether you've met your management goals?

What techniques do you use for management? Why?

How far into the future are you planning?

How often do troop training exercises conflict with natural resource management? Are areas that have been recently burned more likely to have troop training than areas that have a long history of no/minimal fires?

Our research has collected data on plant community composition, cogongrass invasion, climate projections, and tick populations and tick-borne pathogen prevalence at your installation. Are any of these topics relevant to your installation's management goals? If yes, what makes them relevant? If not, what research would be relevant to your goals?

If tick-borne disease risk could be incorporated into a decision support tool as an outcome of management, would that be useful and why?

If invasive species prevalence could be incorporated into a decision support tool as an outcome of management, would that be useful and why?

If climate projections could be incorporated into a decision support tool as an outcome of management, would that be useful and why?

What, if any, data do you collect for fire management, invasive species, or tick populations or tick-borne diseases?

What would be the most useful way of presenting our results? Have you had past collaborations we could emulate? What has worked well?

Hypothetically, if we had 10 or more years, and unlimited dedicated funding to build the decision support tool, and were building it just to cater to the needs of your installation, how would you advise us to design it?

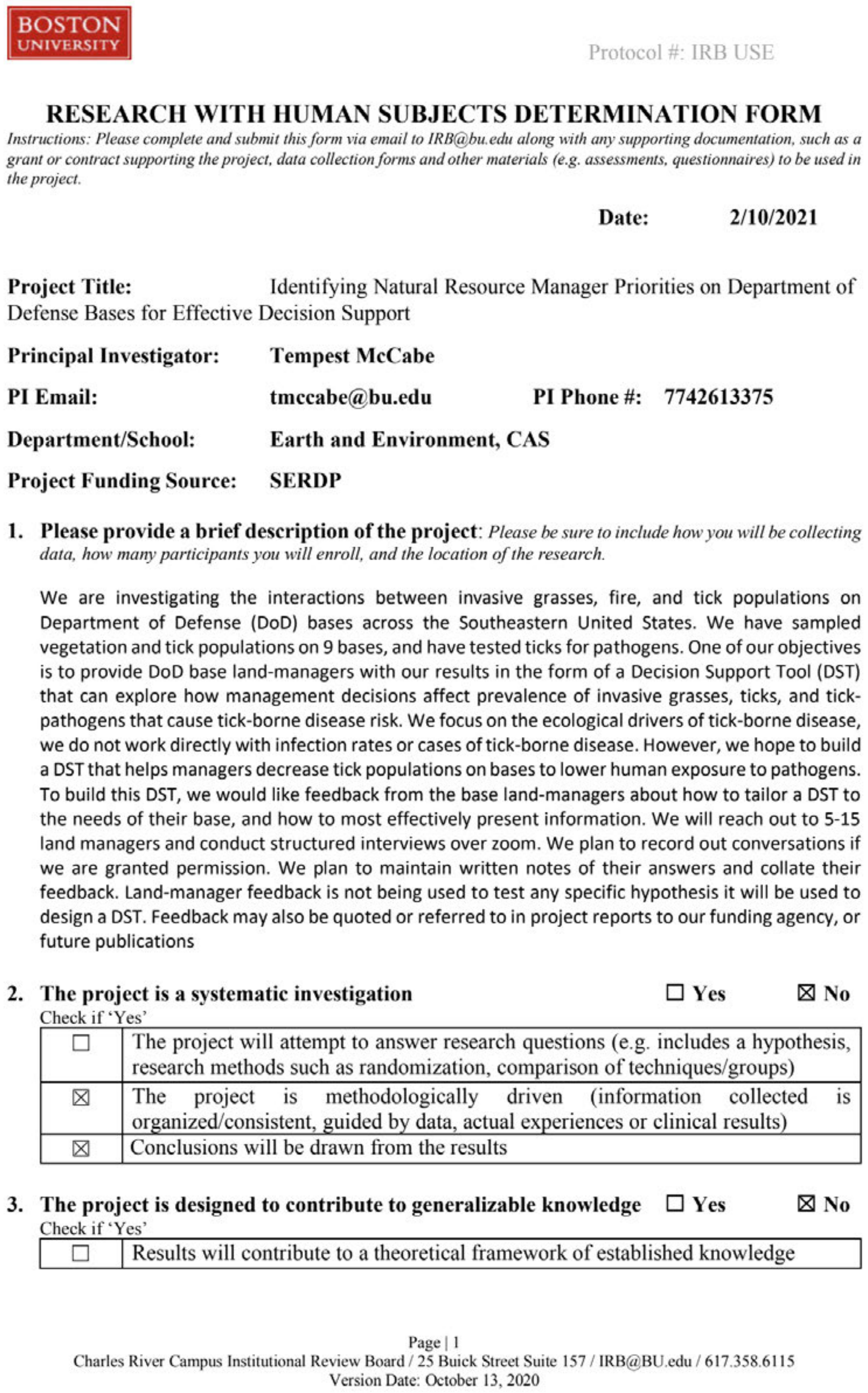
Do you have any questions for us?

Would you be willing to give us feedback on an early version of the decision support tool?

Do you have colleagues that you think we should reach out to?

Thank you again!

Figure S4.1: Structured Interview Script.



BOSTON UNIVERSITY

Protocol #: IRB USE

RESEARCH WITH HUMAN SUBJECTS DETERMINATION FORM

Instructions: Please complete and submit this form via email to IRB@bu.edu along with any supporting documentation, such as a grant or contract supporting the project, data collection forms and other materials (e.g. assessments, questionnaires) to be used in the project.

Date: **2/10/2021**

Project Title: Identifying Natural Resource Manager Priorities on Department of Defense Bases for Effective Decision Support

Principal Investigator: **Tempest McCabe**

PI Email: **tmccabe@bu.edu** **PI Phone #:** **7742613375**

Department/School: **Earth and Environment, CAS**

Project Funding Source: **SERDP**

1. **Please provide a brief description of the project**: *Please be sure to include how you will be collecting data, how many participants you will enroll, and the location of the research.*

   We are investigating the interactions between invasive grasses, fire, and tick populations on Department of Defense (DoD) bases across the Southeastern United States. We have sampled vegetation and tick populations on 9 bases, and have tested ticks for pathogens. One of our objectives is to provide DoD base land-managers with our results in the form of a Decision Support Tool (DST) that can explore how management decisions affect prevalence of invasive grasses, ticks, and tick-pathogens that cause tick-borne disease risk. We focus on the ecological drivers of tick-borne disease, we do not work directly with infection rates or cases of tick-borne disease. However, we hope to build a DST that helps managers decrease tick populations on bases to lower human exposure to pathogens. To build this DST, we would like feedback from the base land-managers about how to tailor a DST to the needs of their base, and how to most effectively present information. We will reach out to 5-15 land managers and conduct structured interviews over zoom. We plan to record out conversations if we are granted permission. We plan to maintain written notes of their answers and collate their feedback. Land-manager feedback is not being used to test any specific hypothesis it will be used to design a DST. Feedback may also be quoted or referred to in project reports to our funding agency, or future publications

2. **The project is a systematic investigation** ☐ **Yes** ☒ **No**

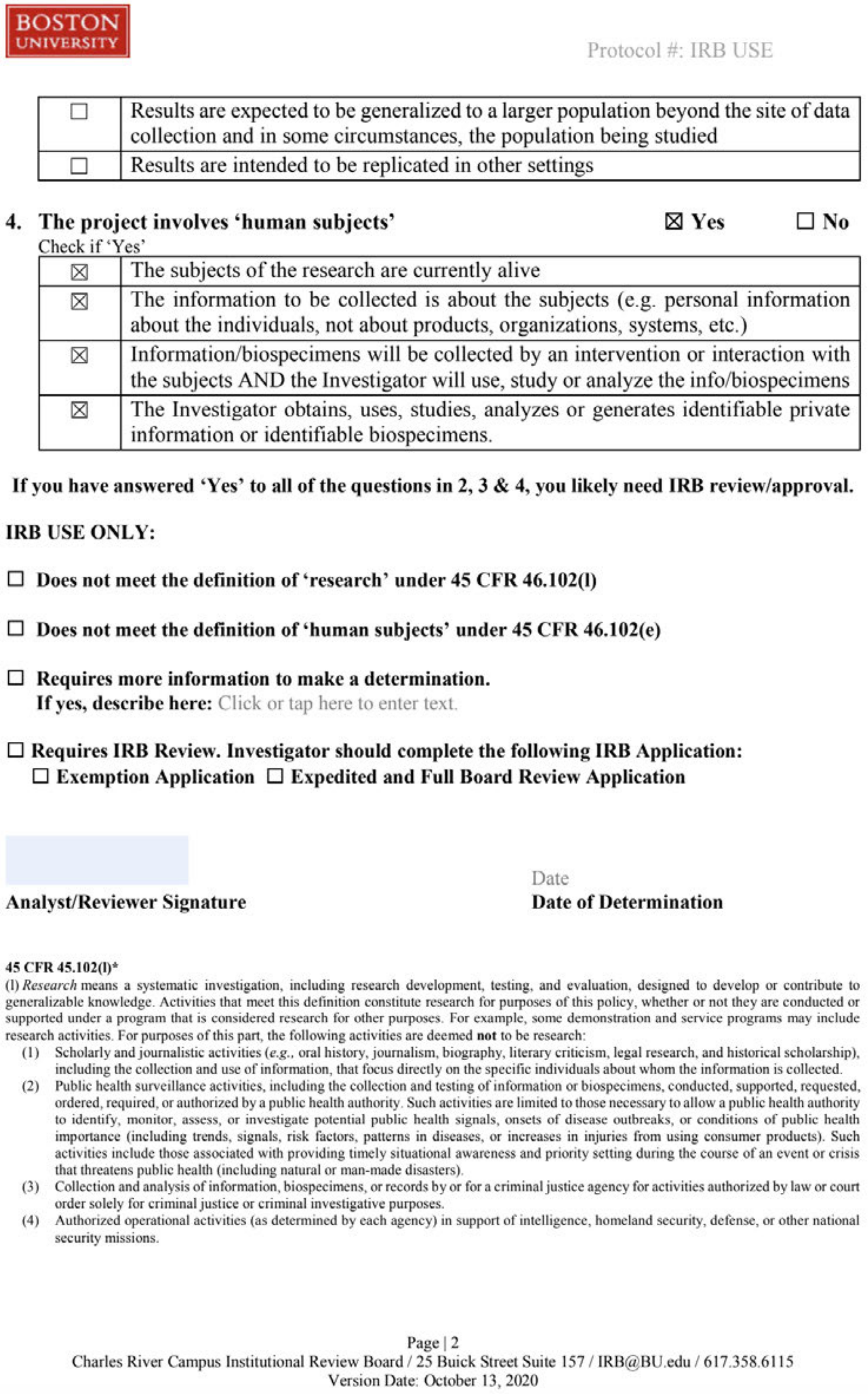
   Check if 'Yes'

☐	The project will attempt to answer research questions (e.g. includes a hypothesis, research methods such as randomization, comparison of techniques/groups)
☒	The project is methodologically driven (information collected is organized/consistent, guided by data, actual experiences or clinical results)
☒	Conclusions will be drawn from the results

3. **The project is designed to contribute to generalizable knowledge** ☐ **Yes** ☒ **No**

   Check if 'Yes'

☐	Results will contribute to a theoretical framework of established knowledge



BOSTON UNIVERSITY

Protocol #: IRB USE

☐	Results are expected to be generalized to a larger population beyond the site of data collection and in some circumstances, the population being studied
☐	Results are intended to be replicated in other settings

4. The project involves 'human subjects' ☒ **Yes** ☐ **No**

Check if 'Yes'

☒	The subjects of the research are currently alive
☒	The information to be collected is about the subjects (e.g. personal information about the individuals, not about products, organizations, systems, etc.)
☒	Information/biospecimens will be collected by an intervention or interaction with the subjects AND the Investigator will use, study or analyze the info/biospecimens
☒	The Investigator obtains, uses, studies, analyzes or generates identifiable private information or identifiable biospecimens.

If you have answered 'Yes' to all of the questions in 2, 3 & 4, you likely need IRB review/approval.

IRB USE ONLY:

☐ **Does not meet the definition of 'research' under 45 CFR 46.102(l)**

☐ **Does not meet the definition of 'human subjects' under 45 CFR 46.102(e)**

☐ **Requires more information to make a determination.**
If yes, describe here: Click or tap here to enter text.

☐ **Requires IRB Review. Investigator should complete the following IRB Application:**
☐ **Exemption Application** ☐ **Expedited and Full Board Review Application**

Analyst/Reviewer Signature

Date
Date of Determination

45 CFR 45.102(l)*

(l) *Research* means a systematic investigation, including research development, testing, and evaluation, designed to develop or contribute to generalizable knowledge. Activities that meet this definition constitute research for purposes of this policy, whether or not they are conducted or supported under a program that is considered research for other purposes. For example, some demonstration and service programs may include research activities. For purposes of this part, the following activities are deemed **not** to be research:

(1) Scholarly and journalistic activities (*e.g.*, oral history, journalism, biography, literary criticism, legal research, and historical scholarship), including the collection and use of information, that focus directly on the specific individuals about whom the information is collected.

(2) Public health surveillance activities, including the collection and testing of information or biospecimens, conducted, supported, requested, ordered, required, or authorized by a public health authority. Such activities are limited to those necessary to allow a public health authority to identify, monitor, assess, or investigate potential public health signals, onsets of disease outbreaks, or conditions of public health importance (including trends, signals, risk factors, patterns in diseases, or increases in injuries from using consumer products). Such activities include those associated with providing timely situational awareness and priority setting during the course of an event or crisis that threatens public health (including natural or man-made disasters).

(3) Collection and analysis of information, biospecimens, or records by or for a criminal justice agency for activities authorized by law or court order solely for criminal justice or criminal investigative purposes.

(4) Authorized operational activities (as determined by each agency) in support of intelligence, homeland security, defense, or other national security missions.

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Figure S4.2: Research With Human Subjects Determination Form.

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