CONSERVATION AND RESTORATION OF MARITIME LIVE OAK FORESTS: HERBIVORY, INVASIVE SPECIES, AND MODELING MANAGEMENT STRATEGIES

by

DESSA LEIGH BENSON

(Under the Direction of Elizabeth G. King)

ABSTRACT

Rapid and ongoing environmental change and additional anthropogenic stress pose a threat to many forest ecosystems. Environmental stresses including changes in disturbance regimes, altered land use, and introduced species can directly affect native tree and plant abundance and alter natural ecological functions and processes. Small forests face additional vulnerability to these environmental stresses due to their size and isolation or lack of connectivity to other forest ecosystems. As there are a myriad of situations in which to conserve, restore, and manage forest ecosystems at small spatial scales of 50 ha or less, it is imperative that forest land managers and owners, restoration practitioners, and environmental consultants and stewards realize what management tools and restoration efforts are available and understand their ecological consequences.

To address some small forest management concerns and restoration challenges, my dissertation research uses a range of methods to better understand small forest ecology and identify management consequences of different tools and restoration efforts. I will first evaluate forest dynamics models that are available and appropriate for small forest use and can help answer questions small forest managers have about their forests. Then, I will demonstrate how demographic modeling and decision-making frameworks can help guide forest managers to make management decisions about tree population dynamics, using maritime live oak (*Quercus virginiana*) (MLO) forests on Jekyll Island and other barrier islands along the Georgia, U.S. coast as a case study. I will then continue to explore MLO forest ecology within Jekyll Island by evaluating the effects of deer on native plant and tree seedling abundance and note whether deer are facilitating a camphor (*Cinnamomum camphora*) invasion using an experiment with deer exclosures on one of the island's small forests. Finally, I will use multivariate analyses to understand how abiotic and biotic environmental conditions such as soil moisture and adult tree composition affect native plant communities on Jekyll Island.

INDEX WORDS: Small forests, Forest ecology, Forest management,
Forest dynamics modeling, Maritime forests, Live oak, Herbivory,
Invasive species, Multivariate analysis

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and forward-thinking environment amongst stewards, managers, professionals, and other stakeholders.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Rapid and ongoing environmental change and additional anthropogenic stress pose a threat to many forest ecosystems. Environmental stresses including a change in fire regime and altered land use can directly affect native tree and plant abundance and alter natural ecological processes including hydrological flow and soil structure. Stresses such as introduced herbivore, parasitic, or invasive species can also indirectly influence native plant composition and ecosystem functions by changing interspecific plant competition dynamics. Small forests face additional vulnerability to these environmental stresses due to their size and isolation or lack of connectivity to other forest ecosystems (Decocq et al., 2016; Valdés et al., 2020). Small forests, especially those less than 1km^2 in size, have greater edge effects, which can lessen resilience to disturbances and stochastic events (Turner & Corlett, 1996) like storms and hurricanes. Tree mortality has been shown to increase closer to edges due to a change in microclimate, and there is less of a buffer from human activity like resulting smoke from fire and water diversion from channeling compared to larger forests (Decocq et al., 2016). When small forests are isolated, they may be less likely to recover after a disturbance (Godefroid & Koedam, 2003).

Small forest ecology is unique and not as well understood compared to larger or "more natural" and undisturbed counterparts (Agrawal et al., 2007; Morrison, 2017), which is one of the various challenges of managing and conserving small forests. A common ecological concern is the fate of the tree and plant community itself, especially when many native communities within small forests are facing a suite of environmental stresses. Without management action, environmental stresses like altered land use and invasive plant species can have undesired effects on the future condition of small forests including loss of valued tree or plant species and biodiversity (Shifley et al., 2014).

1. Modeling small forest change

Forest dynamics models have become increasingly valuable tools for simulating and projecting change in forest attributes through time based on current conditions or knowledge about forest structure and behavior (Pretzsch et al., 2015; Shifley et al., 2017). There are many forest dynamics models available, each developed to predict certain forest attributes at a specified spatial resolution. Among them, models with outputs relating to forest composition and structure, ecosystem functions, and landscape-level changes can potentially inform many common small forest management concerns. Yet, some small forest management concerns, such as faunal diversity, visitor accessibility, or stream health, may not be directly informed from using forest dynamics models, unless coupled with additional ecological knowledge to predict these conditions from modeled forest attributes (Fontes et al., 2011).

Despite the broad utility of forest dynamics models, some may not be appropriate for small forests or the particular forest attributes of interest in a given management context. Each model entails assumptions and simplifications. The model's representation of ecological dynamics and outputs must align with the complexity and level of detail required to inform specific management concerns, in a number of important ways (Battaglia & Sands, 1998; Bellehumeur et al., 1997; Monserud, 2003; Porté & Bartelink, 2002). First, models that simulate dynamics at large spatial scales may not help address particular small forest management concerns such as local species turnover during succession or regeneration and competition in single treefall gaps (Fontes et al., 2011; Shifley et al., 2017; Twery, 2004). Second, models developed for single tree species or specific forest types may not be informative for managers of multi-use, mixed small forests, who are often concerned with multi-species community structure and dynamics that contribute to the forest's desired ecosystem services (Forrester, 2014; Pretzsch et al., 2015). Third, because of the smaller spatial scale, it is more critical to understand localized ecological interactions that depend on the explicit spatial relations among trees, often at the level of individual trees (Shugart et al., 2018). Fourth, managers are often striving to anticipate the consequences of environmental change or novel ecological conditions; models that simulate forest change based on underlying processes rather than past empirical observations will be better able to predict novel dynamics and outcomes (Fontes et al., 2011; Larocque et al., 2016). Lastly, however, models that simulate underlying processes may require detailed physiological data to parameterize, which are rarely available for non-commercial tree species and may be technically difficult or impossible for small forest managers to obtain themselves (Fontes et al., 2011). Managers or model users may opt to use simpler models to avoid the extensive input information or complex calculations (Härkönen et al., 2010; Porté & Bartelink, 2002; Pretzsch et al., 2015). Choosing a model is therefore dependent on aligning the specific information needs for a given small forest management context with the data requirements and relevance of model outputs. Based on the reasoning above, these five issues of alignment between model characteristics and the particular concerns of small forest managers can serve as a useful set of criteria for evaluating the suitability of forest dynamics models to inform small forest management.

The purpose of the review reported in Chapter 2 is to evaluate different existing forest dynamics models—including models of individual tree species, communities, succession, and ecosystem processes—to assess their applicability to address common small forest management concerns. To do so, we arranged the five identified issues—(1) spatial resolution, (2) species the model can simulate, (3) spatial structure, (4) approach for modeling ecological processes, and (5) mechanistic detail—as a tiered hierarchy of criteria that can be queried based on model characteristics. We then applied the tiered criteria to evaluate 54 existing forest dynamics models to address the central question of which available models are the most suitable for addressing the concerns of small forest managers. The review is intended to provide small forest managers with a convenient guide to facilitate the selection and adoption of appropriate models to inform their management efforts.

2. Environmental stresses and small forest management on the Georgia Coast

Maritime live oak (*Quercus virginiana*; MLO) forests on barrier islands along the southeastern Atlantic coast from North Carolina to Florida are highly regarded for their multiple natural and cultural heritage values (Evans & Keen, 2013; Horsley, 2020; Jones et al., 2013). MLO forests play a central role in supporting biodiversity and the ecological health of islands and are globally rare but one of the least studied coastal ecosystems (Jones et al., 2013; Shiflett et al., 2013; Smith et al., 2015). In recent decades, these MLO forests are also facing various environmental stresses including climate change, land development, invasive plant species, and altered wildlife abundances (Helm et al., 1991). Storm damage, intense fire, and beach erosion are an increasingly observed cause of mature tree mortality on barrier islands (Conner et al., 2005; Helm et al., 1991), and now managers on Jekyll Island and other barrier islands along the Georgia coast have seen little evidence of live oak seedlings or saplings. With low live oak recruitment, these environmental stresses could create undesired long-term effects on tree community structure, function, and resilience.

Jekyll Island is a state park that conserves about 65% of the island as natural areas while also supporting tourism amenities and a residential community. Jekyll Island offers opportunities for the public to enjoy the unique heritage of barrier island maritime live oak (MLO) forests in Georgia. It contains roughly 400ha of MLO forests (Jekyll Island Authority, 2020), which are undergoing several environmental stresses that could be affecting live oak regeneration. First, on Jekyll Island, and in many forests throughout North America, white-tailed deer (*Odocoileus virginianus*) pose a critical constraint on tree seedling establishment and survival to maturity (Aronson & Handel, 2011; Blossey et al., 2017; Rooney & Waller, 2003; Slater & Anderson, 2014; Thyroff et al., 2019). Jekyll Island Authority (JIA), a self-supporting state agency that is responsible for management and stewardship of Jekyll Island, is especially concerned how the deer could affect the future of its maritime live oak forests (Jekyll Island Authority, 2020). Herbivores like deer can affect plant communities directly through biomass loss and plant mortality (Averill et al., 2018) but can also indirectly influence interspecific plant competition through selective herbivory. A second concern Jekyll Island managers have is invasive plant species, especially camphor (*Cinnamomum camphora*), an Asian evergreen tree that was introduced for horticulture but has now invaded a few natural areas on the island. Fast-growing and with prolific seed production, camphor may out-compete native plant species and its establishment raises concerns about native plant biodiversity (Schenk, 2009). A third concern is hurricane and storm damage resulting in adult live oak crown damage and biomass loss (Conner et al., 2005; Helm et al., 1991). However, disturbances that damage the canopy also create light gap conditions that promote live oak regeneration, but it is uncertain whether regeneration can successfully compete to reach the overstory. A fourth concern on Jekyll Island is the ecological consequence of long-term fire exclusion, which has led to a thick shrub layer of saw palmetto (*Seneroa repens*) and a heavy accumulation of litter and duff. Fire is a keystone process that maintains forest biodiversity by creating fluctuations in resource availability and preventing competitive exclusion (Kerns & Day, 2017). Therefore, fire exclusion creates an additional stress for tree species and the herbaceous layer that rely on periodic reduction in litter and shrub cover to regenerate and reach above the shrub layer. This suite of ecological concerns is why Jekyll Island and its MLO forests are an excellent context for exploring how small forest ecology research can benefit restoration and conservation success.

To address some of these management and restoration challenges on Jekyll Island, my dissertation research used a range of methods to begin understanding small forest ecology and management consequences of different tools restoration efforts. Chapters 3, 4, and 5 explore different ways that small forest managers can address their ecological problems.

In Chapter 3, we collaborated with JIA and other coastal stewards to use structured decision-making (SDM), an organized framework (Gregory et al., 2012), to find potential MLO management actions to solve the live oak regeneration problem. This chapter first explores how our team has used SDM to define management objectives and identify management alternatives that meet those objectives. Because stakeholders agreed that planting live oaks would best meet their management needs, we compiled different types of knowledge to build a demographic model and decision support tool that projects likely outcomes, costs, and associated uncertainties with alternative tree-planting strategies and the degree to which they would meet different management objectives.

In Chapter 4, we sought to explore whether deer herbivory is affecting native understory vegetation cover, abundance of native hardwood tree seedlings, and camphor seedling abundance and growth. We established 22 6m x 6m plots in a 40ha forest on Jekyll Island with heavy camphor proliferation, of which 11 were fenced to exclude deer and 11 were not. Within each plot for two years, we measured total understory vegetation cover, cover by species, and abundance of hardwood tree seedlings. We also tagged and measured two cohorts of camphor seedlings. In this chapter, I examined the relationship between herbivory effects on camphor versus native species and discuss the implications for efforts to control camphor invasion and support native tree recruitment and native plant establishment.

Finally, understanding how local environmental conditions influence native plant abundance, composition, and biodiversity can provide valuable contextual information for ecological restoration and invasive species control (Hess et al., 2019; Holmes & Webster, 2011; Ozinga et al., 2004). Chapter 5 thus explored how abiotic and biotic environmental conditions including soil moisture and temperature, elevation, leaf litter depth, adult tree composition, and light availability influence native understory plant composition. I used multivariate analyses on data collected from Chapter 4 to observe variations in species richness, total understory vegetation cover, species cover, and cover by growth form across a heterogeneous landscape. Because JIA plans to exclude deer and eradicate camphor populations, I also assessed how deer exclosures affect native plant composition through these analyses.

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CHAPTER 2

FOREST DYNAMICS MODELS FOR CONSERVATION, RESTORATION, AND MANAGEMENT OF SMALL FORESTS[1]

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[1] Benson, D.L.; King, E.G.; O'Brien, J.J. Forest Dynamics Models for Conservation, Restoration, and Management of Small Forests. *Forests* **2022**, *13*, 515. https//doi.org/10.3390/f13040515. Reprinted here with permission of the publisher under the open access Creative Commons CC By 4.0 License.

Abstract

Globally, there are myriad situations in which people aim to conserve, restore, or manage forest ecosystems at small spatial scales of 50 ha or less. To inform management, forest dynamics models provide an increasingly diverse and valuable portfolio of tools for projecting forest change under different management and environmental conditions. Yet, many models may not be appropriate or feasible to use in small forest management because of their design for larger-scale applications, the information needed to initialize models, or discrepancies between model outputs and information relevant for small forest management objectives. This review explores the suitability of 54 existing forest dynamics models to inform the management of small forests. We evaluated the characteristics of each model using five criteria with implications for small forest management: spatial resolution, number of species the model can simulate, inclusion of spatial structure, modeling approach, and mechanistic detail. While numerous models can be suitable under certain conditions, the review criteria led us to conclude that two models offered the broadest versatility and usability for small forest contexts, SORTIE and FORMIND. This review can help orient and guide small forest managers who wish to add modeling to their forest management efforts.

Keywords: simulation models; mixed-species models; spatially explicit models; empirical models; process-based models; mechanistic models

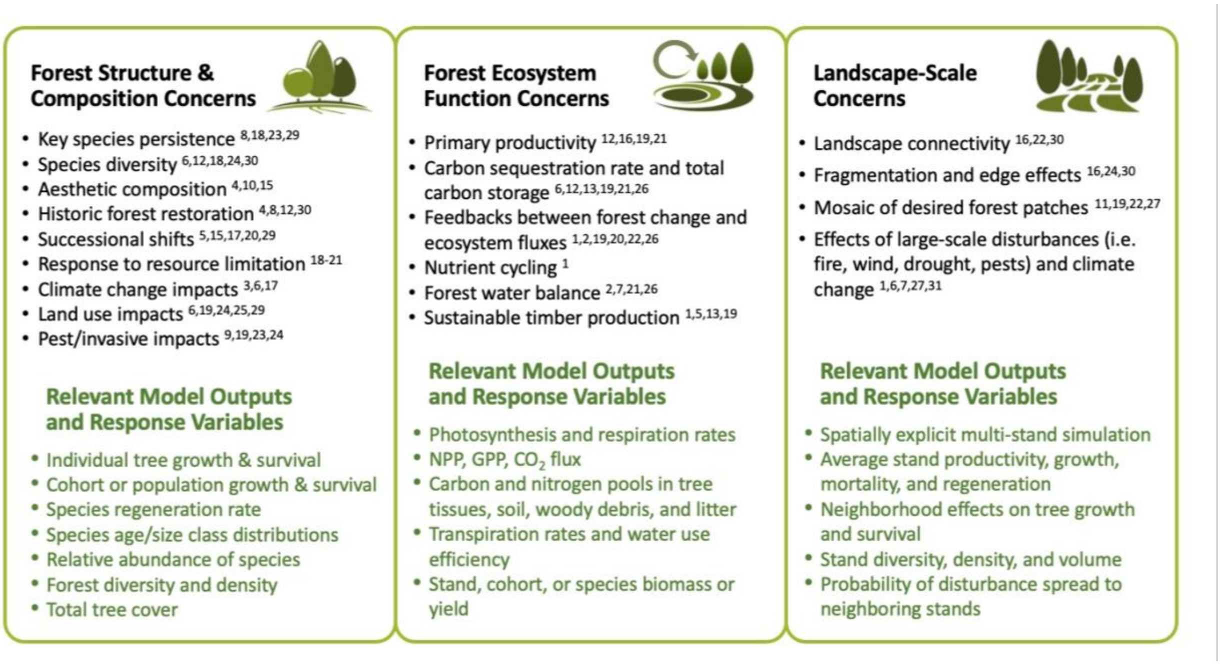
1. Introduction

Trends of increasing forest fragmentation (Grantham et al., 2020; Taubert et al., 2018), parcellation (Weiss et al., 2019), devolution of forest stewardship (Hajjar et al., 2021), and forest cover gains in fragmented landscapes (Decocq et al., 2016) are seen around the world—all of which can result in more forest fragments and parcels being managed at smaller scales (Mayer, 2019). In the United States, for instance, forest land area has remained relatively stable for several decades (Alig et al., 2010; Georgia Forestry Commission, 2019; Oswalt & Smith, 2014), but the mean size of individual forest parcels has steadily decreased due to continued parcellation, land conversion, and fragmentation (Caputo et al., 2020). Forests that exist or are managed as parcels less than 50 ha in size have thus increased in number (*Forest? Woodland? - The Importance of Small Acreages in Stewardship*, 2019; *Small Woodlot Improvement Guide*, n.d.) and make up about 95% of the nation's privately owned forests (Mehmood & Zhang, 2001). In addition to private properties, small forests are also found as green spaces in urban and residential areas, in nature reserves and state parks, and as woodlands or woodlots in other fragmented landscapes.

While fragmentation and parcellation are significant threats to the ecological integrity of forested landscapes (Grantham et al., 2020), people are increasingly recognizing the value of small forests for the host of ecosystem services and benefits they offer (Bengston, 1994; Endreny, 2018; Felipe-Lucia et al., 2018; Khanal & Straka, 2021; Nowak et al., 2010; Valdés et al., 2020). In both urban and agricultural landscapes, small forests provide ecosystem functions including nutrient cycling, soil stabilization, water purification, flood control, and carbon sequestration. Small forests can also offer an array of recreational or economic opportunities including walking trails and timber production. Some contain rare species, communities, and ecosystems or are prized for the biological or cultural heritage they represent. Many small, forested lands are managed to preserve historical landmarks and educate its visitors. In urban areas, forested greenspaces can significantly improve individual and community well-being and public health by providing desired aesthetics, reducing noise and heat, improving air quality, or offsetting carbon dioxide emissions (Khanal & Straka, 2021; Nowak et al., 2010). Furthermore, while fragmentation is generally detrimental to service provision, the persistence of small forests within a fragmented landscape can still promote landscape biodiversity by providing habitat connectivity for pollinators, birds, and other wildlife (Proesmans, 2019).

In addition to the aims of maintaining or enhancing these benefits, many small forest managers must also face concerns about the future of the small areas they manage. Environmental changes and anthropogenic stressors such as climate change, altered land use, pests and invasive species, and limiting resources can directly alter forest tree density, composition, and structure (Endreny, 2018; Felipe-Lucia et al., 2018; Shifley et al., 2014). Natural disturbances (or lack thereof) including storms, drought, and fire can result in undesired effects on forest health and function (Nowak et al., 2010; Seidl et al., 2011; Shifley et al., 2014). In addition, managing forest composition or structure for multiple uses often requires complex coordination with governmental agencies, forest users, and other stakeholders to meet management objectives and optimize benefits. This is especially evident in urban greenspaces and parks as forest managers balance recreational use and aesthetic value with forest ecological integrity and habitat quality (Khanal & Straka, 2021; Nowak et al., 2010; Wear & Greis, 2013). As one forest parcel can influence the potential of another, coordination with managers and stakeholders of adjacent lands may also be necessary (Bengston, 1994; Nowak et al., 2010; Valdés et al., 2020; Wear & Greis, 2013).

The types and extent of benefits that small forests provide depend on the attributes of the structure and composition, ecosystem functioning, and landscape-level context of forest parcels (Felipe-Lucia et al., 2018). Understanding how these attributes of forests will change through time as a result of internal community dynamics, succession, feedbacks with ecological processes, management interventions, disturbance, and other environmental factors, is vital for restoring, sustaining, and enhancing desired ecological services and benefits (Porté & Bartelink, 2002; Shifley et al., 2014, 2017). For instance, altered surface hydrology and invasive plants can result in population declines of valued tree or plant species, or reduced resilience to natural disturbances (Shifley et al., 2014). As a consequence, the management concerns of small forest stewards tend to focus on how forest structure/composition, ecosystem function, and landscape-scale attributes will change under the influence of different drivers, and how different management alternatives can direct that change (Forrester, 2014; Pretzsch et al., 2015). Forest dynamics models have become increasingly valuable tools for simulating and projecting change in forest attributes through time based on current conditions or knowledge about forest structure and behavior (Pretzsch et al., 2015; Shifley et al., 2017). There are many forest dynamics models available, each developed to predict certain forest attributes at a specified spatial resolution. Among them, models with outputs relating to forest composition and structure, ecosystem functions, and landscape-level changes can potentially inform many common small forest management concerns (Figure 2.1). Yet, some small forest management concerns, such as faunal diversity, visitor accessibility, or stream health, may not be directly informed from using forest dynamics models, unless coupled with additional ecological knowledge to predict these conditions from modeled forest attributes (Fontes et al., 2011).



Forest Structure & Composition Concerns

- Key species persistence [8,18,23,29]
- Species diversity [6,12,18,24,30]
- Aesthetic composition [4,10,15]
- Historic forest restoration [4,8,12,30]
- Successional shifts [5,15,17,20,29]
- Response to resource limitation [18-21]
- Climate change impacts [3,6,17]
- Land use impacts [6,19,24,25,29]
- Pest/invasive impacts [9,19,23,24]

Relevant Model Outputs and Response Variables

- Individual tree growth & survival
- Cohort or population growth & survival
- Species regeneration rate
- Species age/size class distributions
- Relative abundance of species
- Forest diversity and density
- Total tree cover

Forest Ecosystem Function Concerns

- Primary productivity [12,16,19,21]
- Carbon sequestration rate and total carbon storage [6,12,13,19,21,26]
- Feedbacks between forest change and ecosystem fluxes [1,2,19,20,22,26]
- Nutrient cycling [1]
- Forest water balance [2,7,21,26]
- Sustainable timber production [1,5,13,19]

Relevant Model Outputs and Response Variables

- Photosynthesis and respiration rates
- NPP, GPP, CO_2 flux
- Carbon and nitrogen pools in tree tissues, soil, woody debris, and litter
- Transpiration rates and water use efficiency
- Stand, cohort, or species biomass or yield

Landscape-Scale Concerns

- Landscape connectivity [16,22,30]
- Fragmentation and edge effects [16,24,30]
- Mosaic of desired forest patches [11,19,22,27]
- Effects of large-scale disturbances (i.e. fire, wind, drought, pests) and climate change [1,6,7,27,31]

Relevant Model Outputs and Response Variables

- Spatially explicit multi-stand simulation
- Average stand productivity, growth, mortality, and regeneration
- Neighborhood effects on tree growth and survival
- Stand diversity, density, and volume
- Probability of disturbance spread to neighboring stands

Figure 2.1. Small forest management concerns that can be informed by forest dynamics models, and the types of forest dynamics model outputs and response variables that can help address them. They are grouped in columns as issues related to forest structure and composition, ecosystem function, and landscape-scale patterns and processes. Management concerns with closed bullets may be relevant for many types of small forests, including urban forests, parks, isolated forest fragments, and small parcels with contiguous forested landscapes. Open bullets, which relate to timber production and larger forested matrices, are generally not relevant for urban forests. Superscripted citations provide examples from the literature: **1**- Battaglia et al., 2004 ; **2**- Deckmyn et al., 2008 ; **3**- Decocq et al., 2016 ; **4**- Felipe-Lucia et al., 2018 ; **5**- Fischer et al., 2010 ; **6**- Fischer et al., 2016 ; **7**- Gielen et al., 2010 ; **8-** Godefroid & Koedam, 2003 ; **9** - Fontes et al., 2011 ; **10**- Khanal & Straka, 2021 ; **11**- Landsberg, 2003 ; **12**- Mäkelä et al., 2012 ; **13**- Miehle et al., 2009 ; **14**- Monserud, 2003 ; **15**- Nowak et al., 2010 ; **16**- Peng, 2000 ; **17**- Perot et al., 2010 ; **18**- Porté & Bartelink, 2002 ; **19**- Pretzsch et al., 2008 ; **20**- Robinson & Ek, 2000 ; **21**- Sampson et al., 2006 ; **22**- Scheller & Mladenoff, 2007 ; **23**- Seidl et al., 2011 ; **24**- Shifley et al., 2014 ; **25**- Shifley et al., 2017 ; **26**- Siqueira et al., 2006 ; **27**- Snell et al., 2017 ; **28**- Taylor et al., 2009 ; **29**- Thurnher et al., 2017 ; **30**- Valdés et al., 2020 ; **31**- Wang et al., 2013

Despite the broad utility of forest dynamics models, some may not be appropriate for small forests or the particular forest attributes of interest in a given management context. Each model entails assumptions and simplifications. The model's representation of ecological dynamics and outputs must align with the complexity and level of detail required to inform specific management concerns, in a number of important ways (Battaglia & Sands, 1998; Bellehumeur et al., 1997; Monserud, 2003; Porté & Bartelink, 2002). First, models that simulate dynamics at large spatial scales may not help address particular small forest management concerns such as local species turnover during succession or regeneration and competition in single treefall gaps (Fontes et al., 2011; Shifley et al., 2017; Twery, 2004). Second, models developed for single tree species or specific forest types may not be informative for managers of multi-use, mixed small forests, who are often concerned with multi-species community structure and dynamics that contribute to the forest's desired ecosystem services (Forrester, 2014; Pretzsch et al., 2015). Third, because of the smaller spatial scale, it is more critical to understand localized ecological interactions that depend on the explicit spatial relations among trees, often at the level of individual trees (Shugart et al., 2018). Fourth, managers are often striving to anticipate the consequences of environmental change or novel ecological conditions; models that simulate forest change based on underlying processes rather than past empirical observations will be better able to predict novel dynamics and outcomes (Fontes et al., 2011; Larocque et al., 2016). Lastly, however, models that simulate underlying processes may require detailed physiological data to parameterize, which are rarely available for non-commercial tree species and may be technically difficult or impossible for small forest managers to obtain themselves (Fontes et al., 2011). Managers or model users may opt to use simpler models to avoid the extensive input information or complex calculations (Härkönen et al., 2010; Porté & Bartelink, 2002; Pretzsch et al., 2015). Choosing a model is therefore dependent on aligning the specific information needs for a given small forest management context with the data requirements and relevance of model outputs.

Based on the reasoning above, these five issues of alignment between model characteristics and the particular concerns of small forest managers can serve as a useful set of criteria for evaluating the suitability of forest dynamics models to inform small forest management. The purpose of this review is to evaluate different existing forest dynamics models—including models of individual tree species, communities, succession, and ecosystem processes—to assess their applicability to address common small forest management concerns. To do so, we arranged the five identified issues—(1) spatial resolution, (2) species the model can simulate, (3) spatial structure, (4) approach for modeling ecological processes, and (5) mechanistic detail—as a tiered hierarchy of criteria that can be queried based on model characteristics (Figure 2.2). The following section provides a detailed explanation of each criterion, describing the different model characteristics affecting their suitability for modeling small forests. We then applied the tiered criteria to evaluate 54 existing forest dynamics models to address the central question of which available models are the most suitable for addressing the concerns of small forest managers. The Results section describes how the evaluation narrowed the pool of suitable models at each step. Ultimately, two models, SORTIE and FORMIND, were found to have the strongest and broadest suitability characteristics.

This review aims to provide small forest managers with a convenient guide to facilitate the selection and adoption of appropriate models to inform their management efforts. To that end, the Discussion section has three subsections. The first distills the key findings of the model suitability evaluation for small forests, and why SORTIE and FORMIND were most favorable, given the criteria, constraints, and tradeoffs. The second subsection discusses additional considerations that managers and modelers may face when applying a model specifically in a new context—including technical feasibility aspects, software accessibility, and the reliability and usefulness of outputs—and how those issues can be navigated when using SORTIE and FORMIND in particular. The discussion concludes with some practical recommendations for getting a new modeling endeavor successfully underway.

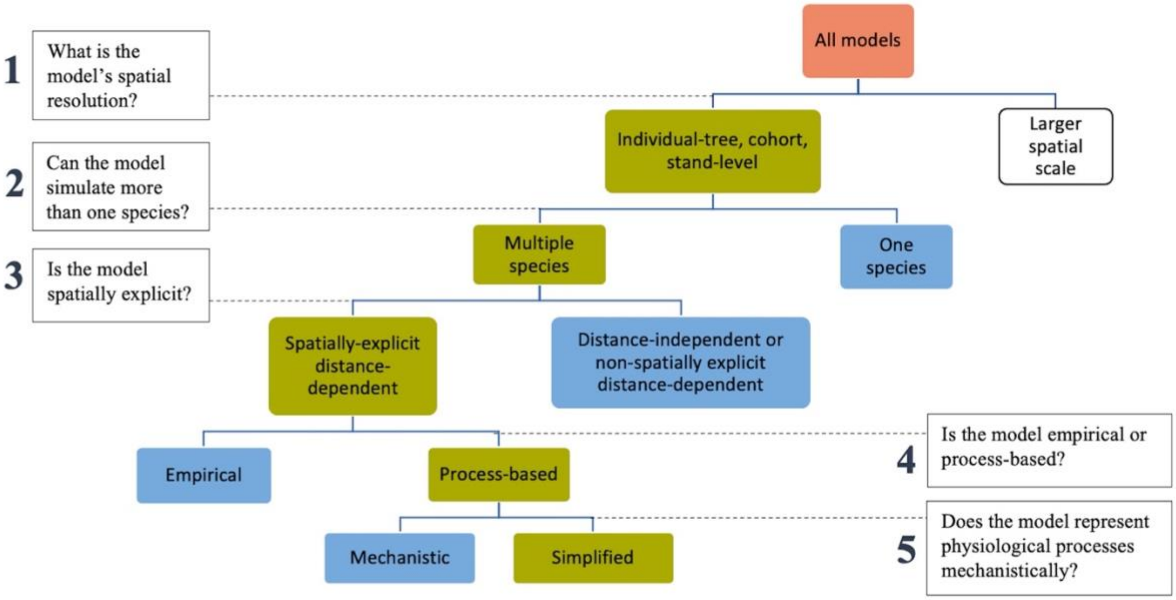


Figure 2.2. Tiered series of evaluation criteria used to assess the suitability of 54 forest dynamics models for informing small forest management concerns. Characteristics that are more relevant and appropriate for small forests are in green. Characteristics with weaker relevance, or narrow applicability to specific management concerns, are in blue. Characteristics that will not help inform small forest management are in white.

2. Five Criteria for Assessing Model Suitability for Small Forests

The suitability criteria focus on attributes of models that have been previously used to classify forest dynamics models. We adopted and modified a common typology following (Porté & Bartelink, 2002; Pretzsch et al., 2015; Robinson & Ek, 2000) and other published works (Landsberg, 2003; Larocque et al., 2016; Mäkelä et al., 2000; Monserud, 2003; Peng, 2000) to define differences among model attributes that are specifically relevant for small forests. Similar to other existing typologies, we organized the suitability factors hierarchically, allowing us to conduct our subsequent evaluation of models by applying the tiered set of five criteria for small forest suitability, illustrated in Figure 2: (1) What is the model's spatial resolution, (2) how many species can the model simulate, (3) is the model spatially explicit, (4) is the model's approach empirical or process based, and (5) does the model represent physiological processes mechanistically?

2.1 What Is the Model's Spatial Resolution?

Forest dynamics models can be classified by their spatial resolution, defined as the smallest spatial unit at which the model evaluates forest dynamics or reports outcomes. Spatial resolution determines the types of forest attributes the model can simulate or project, and thus the types of management issues the model can inform (Porté & Bartelink, 2002; Taylor et al., 2009). Forest dynamics models are broadly categorized into four spatial resolutions: individual-tree, cohort or size-class, stand, and landscape (Pretzsch et al., 2015; Robinson & Ek, 2000). Individual-tree models consider each tree as a unit, and they help explore how individual trees compete with one another for sunlight, nutrients, and other resources. Cohort models simulate aggregates of trees as separate groups, which can be defined by species, functional types, diameter or height size classes, or ecological layers (Robinson & Ek, 2000). Typically, cohort models apply one representative set of characteristics to all trees within a group (Köhler & Huth, 1998; Shugart et al., 2018). Separating groups by specific characteristics can help study the variation and relative performance between species, cohorts of the same species, and other size classes (Blanco et al., 2015).

Most stand and landscape models, on the other hand, have less resolution and treat large forest patches as a single unit, within which species age and composition are assumed to be uniform (Taylor et al., 2009). Stand models represent one or more forest patches that typically correspond to management units (Taylor et al., 2009) and can be applied to study mosaics of forest patches with different compositions. When stand models represent the interactions of a stand and neighboring patches, they can help understand how litter decomposition, water cycling, and other environmental processes in one patch can influence an adjacent patch (Porté & Bartelink, 2002). Stand models can therefore provide useful outputs for issues relating to ecosystem function as well as landscape-level management issues (Figure 2.1). Landscape-scale models, also called forest landscape simulation models (FLSMs), can simulate similar processes that drive change but at a much larger spatial resolution (Scheller & Mladenoff, 2007). Landscape models tend to focus on carbon and water balance over large, homogeneously represented areas, and thus better address broader-scale management concerns such as regional or global effects of climate change (Scheller & Mladenoff, 2007; Shifley et al., 2017). Forest landscape models such as LANDIS PRO and LANDCLIM typically lack species differentiation or size differentiation that finer-resolution models have (Schumacher et al., 2004; Wang et al., 2013). Although some forest landscape models may simulate succession at a stand or larger scale, they are unable to simulate interspecific competition or heterogeneity in tree growth and survival at an individual or plot level (Schumacher et al., 2004).

Individual-tree, cohort, and stand models are likely to be more useful when simulating small forest dynamics (Taylor et al., 2009) compared to landscape models because their smaller scale resolution can inform many common issues concerning forest structure and com-position, including the persistence of specific tree species, rates and trajectories of succession, and fine-scale responses to environmental change (Figure 2.1). When choosing a suitable spatial scale for a model, managers should consider whether the required parameterizing data are available or feasible to obtain, and also whether the resolution of outputs will provide enough detail to answer management questions (Taylor et al., 2009). The subsequent evaluation criteria consider these decision points further.

2.2 Can the Model Simulate More than One Species?

This tier distinguishes forest dynamics models by how many species and what types of species they can simulate. Single-species models treat the entire forest as one species, using a single set of species-specific parameters, such as average growth rate or adult height, to simulate forest dynamics (Pretzsch et al., 2015; Shugart et al., 2018). Most single-species models were developed to estimate timber production in monoculture forestry of commercially important native or exotic tree species, so their outputs are typically yield estimates such as total biomass or productivity (Pretzsch et al., 2015; Shifley et al., 2017). Other single-species models were designed for natural forests that contain only one species or one dominant species (Larocque et al., 2013). Single-species models have been applied to multi-species forests by simulating each species' dynamics separately as a monoculture without considering tree–tree interactions and combining these simulation outputs proportionally to species abundance in the forest (Pretzsch et al., 2015; Shifley et al., 2017). On the other hand, there are a growing number of multi-species models with species-mixing capabilities, which use different sets of growth, mortality, and resource allocation parameters for more than one tree species. Multi-species models may also account for interspecific interactions, either abstractly using competition indices or more explicitly by modeling the processes or mechanisms through which trees interact (Pretzsch et al., 2015).

Choosing between single- or multi-species models depends on management needs and the forest under observation. Single-species models can be more beneficial when managing total tree cover for timber production, carbon storage, or aesthetic value (Figure 2.1) (Battaglia et al., 2004; Hauhs et al., 1995; Kramer et al., 2010). When addressing these concerns, treating a multi-species forest as a monoculture may not necessarily compromise the usefulness of model outputs if managers are seeking aggregate stand-level predictions (Battaglia et al., 2004). However, increased interest in the dynamics of mixed-species, multi-use forests has made multi-species models a vital tool for forest management. Most tree species differ in how they photosynthesize, grow, and allocate resources (Pretzsch et al., 2015), which will influence the relative abundances of individual trees, species, and cohorts over time (Porté & Bartelink, 2002). Thus, multi-species models can better inform many small forest management concerns because they can simulate changes in forest composition and structure, patch and landscape heterogeneity, and species-specific environmental responses (Figure 2.1).

Some single-species and multi-species models were primarily developed for a particular species, site, or region to serve specific needs (Larocque et al., 2013; Pretzsch et al., 2015; Shifley et al., 2017) and modifying them to apply to other species and regions may be difficult or impossible for small forest managers in different contexts. For example, the individual-tree, single-species model FOREGEM uses a set of allometric rules or equations derived from species- and site-specific parameters to simulate the forest response to environmental change (Kramer et al., 2010). To parameterize the model for a different species or site, the model user must have knowledge of physiological parameters and phenotypically plastic traits, including the timing of bud burst, pollen dispersal distance, or relation between stomatal conductance and water stress, which may not be known for non-commercial tree species (Kramer et al., 2008;

Kramer et al., 2010; Pretzsch et al., 2015; Shugart et al., 2018) On the other hand, the individual-tree, multi-species model FORMIND can be more readily adapted to different contexts because it classifies species into functional groups and then uses physiological parameters and allometric equations that generally represent each functional group (Fischer et al., 2016). When choosing between single- and multi-species models, small forest managers should consider not only the specific management concerns, but also the inputs necessary to run the model and the type of trees it was designed to simulate in order to select the simplest model that can generate relevant outputs. Multi-species models are likely to satisfy these considerations for a broader range of small forest management concerns.

2.3 Is the Model Spatially Explicit?

Individual-tree, cohort, and stand models differ in terms of whether and how they represent the spatial location or distribution of trees. Most distance-independent models are stand models that do not specify the locations of individual trees, cohorts, or species. Instead, they often treat the entire stand as one unit, implicitly assuming that all individual trees within the stand have the same growing space (Figure 2.3A). These models abstractly infer intra- and interspecific competition using stand-level variables of density or basal area (Goreaud et al., 1997; Houllier et al., 1991).

Distance-dependent models do not assume all trees within a stand have the same growing space. Instead, they implicitly or explicitly describe tree–tree competition by incorporating intra- and interspecific interactions into model functions (Pretzsch et al., 2015). Distance-dependent models can be further classified as either spatially explicit or non-spatially explicit, with the classification depending on the spatial resolution of model inputs and outputs. Most non-spatially explicit models are stand or cohort models that use a statistical approach when representing spatial distributions by assuming a random or clustered distribution of individual trees or species within a stand or grid cell (Goreaud et al., 1997; Larocque et al., 2016; Porté & Bartelink, 2002) (Figure 2.3B). They use competition indices or multipliers within the model's algorithms to estimate individual-tree, species-specific, or stand growth and mortality at the stand level as a function of assumed distance to neighbors. Stand structure is therefore a feedback loop between species-specific competition indices and multipliers, tree growth and mortality, and stand growth (Pretzsch et al., 2015), and outputs mostly represent stand-level attributes. Spatially explicit models, on the other hand, are often individual based. They can generate tree locations either by simulating them within a forest patch or plot based on distance or distribution statistics (Figure 2.3C), or they can use full stem maps of (x, y) coordinates to recreate an observed distribution of individual trees across a stand (Figure 2.3D) (Larocque et al., 2016). In gap models, forest patches spatially represent the influence zone of a large, mature tree, and tree species and size classes compete for resources within that patch. Spatially explicit models describe horizontal spatial structure at a higher resolution and provide individual-tree or cohort and size class information as model outputs, whereas non-spatially explicit model outputs provide stand-level attributes (Goreaud et al., 1997; Larocque et al., 2016; Shugart et al., 2018; Zhang et al., 2018).

Both distance-independent and -dependent models can help guide small forest management planning. Most distance-independent models and non-spatially explicit, distance-dependent models provide stand outputs such as total stand growth, biomass yield, and density (Deckmyn et al., 2008; Forrester & Tang, 2016; Kimmins et al., 1999), which can prove useful when managing timber production or estimating carbon and nutrient pools and fluxes (Figure 2.1). However, many small forest management concerns require acknowledgement of within-stand spatial heterogeneity to predict the relevant attributes of future forest composition and structure (Goreaud et al., 1997; Porté & Bartelink, 2002). Although distance-dependent models typically have higher data input requirements to represent variable tree spacings, they can better predict how individual trees' interactions with one another can influence forest change and are thus more broadly useful for informing small forest management concerns (Miehle et al., 2009; Pretzsch et al., 2015). For example, the initial design of the stand-level, distance-independent model FOREST-DNDC requires biomass per unit area but no spatial information inputs, and assumes monospecific characteristics at the grid level, including survival rate and mean tree height (Miehle et al., 2009). In contrast, the distance-dependent cohort model CABALA can incorporate the effects of within-stand tree spatial distributions in biophysical processes and outcomes of management actions because it requires tree spacing information within and between grid cells (Battaglia et al., 2004). In a study comparing *Eucalyptus* forest growth estimates from different models, FOREST-DNDC overestimated forest growth because of its spatial simplification of competition and growth processes while CABALA provided the most accurate predictions (Miehle et al., 2009). Thus, FOREST-DNDC is often used to simulate stand-level information such as photosynthesis, respiration, and carbon and nitrogen pools and fluxes when there is little concern about local tree competition and resources to parameterize and calibrate are limited.

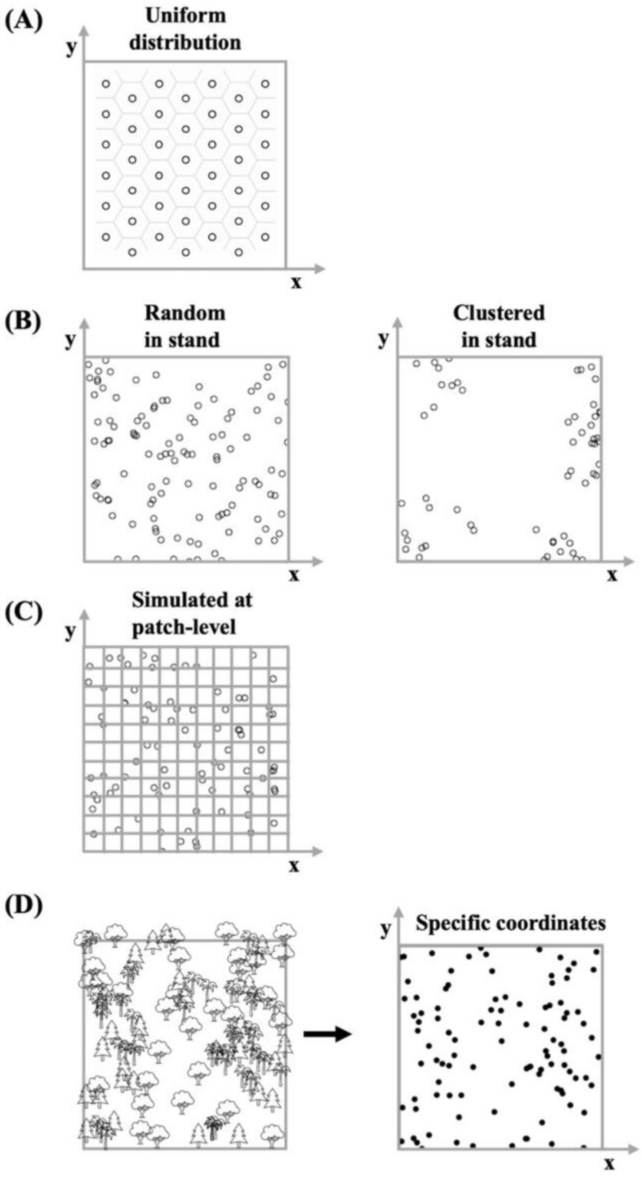


Figure 2.3. Representation, or implied representation, of tree distributions in different model types. Distance-independent models do not specify locations in space; they implicitly assume all trees have equal space, which would imply an equidistant lattice if represented spatially (A). Distance-dependent, non-spatially explicit models assume different statistical distributions of distances between individual trees across a stand. Examples of distributions, realized spatially for illustrative purposes, include random and clustered (B). In distance-dependent spatially explicit models, the locations of individual trees are typically simulated within a forest gap (represented by grid cells) (C) or are mapped as (x, y) coordinates within a stand (D) (Goreaud et al., 1997).

Distance-dependent models can be useful when studying smaller, mixed-species forests because they contain the spatial relationships required to simulate how trees of different species interact with one another and the local environment (Perot et al., 2010), which is especially beneficial to small forest managers concerned with species assembly, succession, invasion, or responses to limiting resources (Figure 2.1). Simulating a mixed-species forest without considering more specific tree, species, or cohort distributions can lead to unrealistic predictions about small forest dynamics, such as how light competition influences the age structure and species composition of a forest (Goreaud et al., 1997; Pretzsch et al., 2015). The CABALA example demonstrates how accounting for spatial distribution of individual trees or species can result in more reliable model projections in a single-species forest. For multi-species forests, incorporating distance dependence becomes even more valuable to account for the effects of spatial pattern on both intra- and interspecific interactions. Spatially explicit models are particularly well suited for simulating the localized effects of intra- and interspecific interactions.

2.4 Is the Modeling Approach Empirical or Process Based?

Two modeling approaches, empirical and process based, differ in the way that biological processes or physical mechanisms are incorporated into the model and how they influence tree growth (Fontes et al., 2011; Peng, 2000; Pretzsch et al., 2015). Empirical models typically use correlations between repeated measurements of tree species, age, diameter, and height and observed environmental parameters from forest inventories to derive allometric equations and growth functions (Shifley et al., 2017). The models then simulate forest dynamics by applying those relationships deterministically or probabilistically (Taylor et al., 2009; Twery, 2004). Process-based models, on the other hand, simulate forest dynamics via the biological and physical principles and processes and that govern tree growth and forest development, with varying degrees of mechanistic detail (discussed in Tier 5) (Korzukhin et al., 1996; Larocque et al., 2016; Larocque et al., 2016). Both modeling approaches have their advantages and disadvantages for addressing different management concerns related to small forest growth, succession, and responses to environmental change. Each approach is also constrained by data availability—empirical models by the availability of inventory data relevant to the species and conditions to be modeled, and process-based models by the detailed environmental and physiological data needed to parameterize them.

Projecting tree and forest growth may be valuable to small forest managers concerned with timber production, carbon sequestration, or rates of recovery from disturbance. Empirical models can provide simple and accurate projections of forest growth, but only if the species and conditions used to derive allometric relationships are well matched to the scenario being modeled (Taylor et al., 2009; Thürig et al., 2005). However, data needed to describe allometric growth relationships for non-commercial, multi-species forests are generally rare and highly site specific. In contrast, process-based models predict tree growth by simulating the underlying physiological processes, which allows these models to predict forest growth under a range of conditions for which there may be no empirical growth data. This advantage comes at a cost in terms of model complexity and data needs, however. For instance, in order to project change in tree biomass, many models simulate the process of photosynthesis mechanistically, which requires the accurate parameterization of several physical variables such as radiation, rainfall, vapor pressure deficit, and soil type, as well as species-specific physiological traits (Fontes et al., 2011).

Empirical and process-based models have the potential to inform small forest managers' concerns regarding compositional change over time, such as the persistence of certain tree species, shifts toward or away from desired forest composition, or the restoration of historic forest communities. Historically, empirical models were developed primarily to project single-species timber production after harvest, but their outputs and more recent multi-species variants can also inform site-specific questions about the succession and trajectories of forest composition change (Shifley et al., 2017). To achieve this, empirical models often predict stand-level community change by linking successional stages through probabilistic or deterministic state-and-transition pathways. However, establishing the patterns and rates of shifts in species composition requires extensive prior observational data of stand-level changes in relative species abundance over time or tree-level transition probabilities (Taylor et al., 2009). Competition for light is a dominant driver of forest composition change. Empirical models represent this process phenomenologically, usually through gross correlations between neighborhood or stand density and species-specific growth (Taylor et al., 2009), which limits realism and resolution. Process-based models offer advantages for modeling community change, especially for representing light availability as a driver, because growth is modeled via the process of photosynthesis, which is driven by light availability (Porté & Bartelink, 2002). Process-based models at gap and individual tree levels calculate light availability as a dynamic function of the surrounding tree canopy structure when simulating tree growth, mortality, and recruitment to project forest compositional change (Larocque et al., 2016). To achieve this, however, these models introduce additional complexities and data requirements (Fontes et al., 2011; Twery, 2004) regarding canopy structure and light attenuation, species-specific photosynthesis–light response curves, and additional physiological parameters in more mechanistic models.

For many small forest management concerns, incorporating responses to environmental change is vital because many small forests experience continuous change due to their size and proximity to humans, and novel suites of environmental factors will create different future states of a forest (Peng, 2000). Empirical models are generally limited in their ability to simulate responses to a changing environment. Because empirical models use fixed relationships fitted to direct forest observations, they are often referred to as "static" (Robinson & Ek, 2000; Shifley et al., 2017; Taylor et al., 2009). Accurate projections are limited to the suite and range of environmental conditions that were measured during inventories used to build the model (Pretzsch et al., 2015; Thürig et al., 2005), and these models often offer no reliable way to account for disturbances or the effects of climate change (Fontes et al., 2011; Korzukhin et al., 1996; Taylor et al., 2009) which are common small forest management concerns (Figure 2.1).

Most process-based models can account for responses to environmental change dynamically because they contain one or more sub-models or behaviors that interact with one another to simulate the effects of environmental conditions on photosynthesis and thus tree growth from basic physical and physiological principles (Monserud, 2003; Pretzsch et al., 2015). The most commonly modeled environmental processes that influence photosynthesis are climate, soil and site conditions, including soil texture and nitrogen content, and water balance (Fontes et al., 2011; Pretzsch et al., 2015). However, including these additional processes greatly increases computational complexity and demand for accurate atmospheric, soil, and hydrological parameter values. Because inaccurate parameter estimates can be compounded when coupling processes and scaling up, these models are more often used to study underlying processes in research, rather than to make reliable projections for informing management (Taylor et al., 2009). Process-based models are better suited for understanding forest ecosystems and simulating different management or climate scenarios than providing absolute predictions of future forest composition and structure (Adams et al., 2013; Larocque et al., 2016; Pretzsch et al., 2008). Other seasonal or episodic changes of relevance to small forest managers, such as altered storm, fire, and pest disturbance regimes, are not as easily represented or parameterized in model structures (Fontes et al., 2011; Pretzsch et al., 2015).

Empirical and process-based models represent two ends of a modeling approach spectrum (Adams et al., 2013). So-called hybrid models couple together various components of empirical and process-based approaches to take advantage of both physiological and empirical data to span scales from leaf-level metabolism to forest-level change (Peng, 2000; Taylor et al., 2009). In practice, most individual-tree and gap process-based models must rely on at least some empirical tree-level data in order to scale up physiological processes, even if not fully coupled to an empirical model (Korzukhin et al., 1996). In choosing a modeling approach, small forest managers should ask what input and output details are necessary to answer their management question or concern. If a manager has sufficient inventory data that span the environmental conditions of interest, an empirical model may sufficiently and accurately provide the desired projections of forest change (Taylor et al., 2009). Otherwise, process-based models can simulate many relevant dynamics, including projections that account for environmental change and light competition, but they require at least some physiological information for the species to be modeled. If a forest manager wishes to pursue forest dynamics modeling but lacks both appropriate empirical allometric data and physiological parameters, the latter can usually be obtained or estimated from existing forests, whereas allometric relationships require time-series inventory data collected over many years. Thus, from a pragmatic stance, the data limitations of process-based models may be more easily overcome than limitations for empirical models.

2.5 Does the Model Represent Physiological Processes Mechanistically?

Although all process-based models simulate forest dynamics via the underlying biological and physical processes that govern tree growth and forest development, some employ more mechanistic representations of these processes than others. As models vary in their degrees of mechanism and abstraction, so do different scholars' terminologies and criteria for categories (Blanco et al., 2015; Fontes et al., 2011; Larocque et al., 2016; Pretzsch et al., 2015). Herein, we distinguish between mechanistic and simplified process-based models, as this has relevant implications regarding model complexity and usability for small forest managers. So-called mechanistic process-based models explicitly simulate tree growth as a function of species-specific physiology, morphology, and/or architecture using established equations (Larocque et al., 2013; Letort et al., 2008). These physiological equations, with those for photosynthesis and respiration being the most common (Larocque et al., 2016; Larocque et al., 2016), entail numerous input parameters at the tree organ or (sub-)cellular level such as stomatal density, photosynthetic photon flux density on a leaf, and potential electron transport rate (Larocque et al., 2016; Larocque et al., 2016; Letort et al., 2008; Porté & Bartelink, 2002).

Process-based models that require less mechanistic information and feature simpler parameterization protocols are often called simplified process-based models because they use simpler metabolic relationships to represent more detailed biochemical and bio-physical mechanisms (Larocque et al., 2016; Shugart et al., 2018). These models still simulate the processes that are the underlying causes of tree growth, competition, and mortality, but do so via coarser relationships between tree or species allometry and organ-specific photosynthesis and respiration rates (Larocque et al., 2016). For instance, the cohort-model FORMIX simulates tree growth using a carbon balance approach that calculates carbon assimilation from photosynthesis–light response curves and canopy allometric relationships. This is an example of a simplified process-based models because it incorporates the underlying causes of tree growth but does not calculate photosynthesis and respiration at a mechanistic level. In addition to the core behaviors of growth and mortality as simplified functions of light availability and photosynthesis, some simplified process-based models allow model users to include additional degrees of mechanistic and environmental detail. For example, the individual-tree models SORTIE and FORMIND provide optional sub-models to simulate processes that directly affect growth dynamics, including precipitation, harvest and disturbance, and dispersal functions (Canham, 2017).

In principle, both physiological and simplified process-based models can help address small forest management questions regarding changes in forest structure and composition through time. Their outputs can project the age or size class distributions of individual species and relative abundances of different species or functional groups (Figure 2.1). Because mechanistic process-based models often include more physiological, phenotypical, and genetic information as inputs and model parameters (Fontes et al., 2011; Grote & Pretzsch, 2002) and describe eco-physiological feedbacks at a (sub-) cellular level, they can increase our understanding of forest and tree function (Grote & Pretzsch, 2002; Letort et al., 2008). However, generally speaking, as a model's mechanistic detail increases, so does the difficulty of measuring, estimating, and validating the detailed, species- and size-class specific biophysical parameters and abstract coefficients their equations require (Monserud, 2003). This can render them nearly impossible to use for small forest managers studying non-commercial trees for which these parameters are unknown. In addition, few attempts have been made to create or calibrate physiological process-based models beyond the study systems for which they were developed, so the pool of models that can be feasibly adopted to project forest structure and composition in a new context is limited (Fontes et al., 2011).

Simplified process-based models have much greater potential feasibility for small forests. Their simplified representation carbon assimilation and allocation still simulate forest growth processes dynamically, yet they require more easily obtainable data and are computationally less complex (Larocque et al., 2016; Larocque et al., 2016; Poorter et al., 2013). Simplified process-based models provide information to help small forest managers answer questions about individual tree growth, forest structure, and species composition at appropriately local scales (Figure 2.1), while decreasing uncertainty in model parameters relative to mechanistic models.

3. Methods

To compile a set of models to evaluate, we first used Google Scholar and Web of Science to gather publications that developed or used forest dynamics models. We used search terms “forest” and “model” with other terms, including “dynamics”, “growth”, “allometric”, “simulation”, “stand”, “gap”, and “tree”. For each publication, we identified the name of the model used, its general purpose (i.e., modeling timber production, change in forest composition, etc.), and the specific management question asked. The search identified several review papers, from which we tabulated the set of models covered in the review. Among the publications we gathered, one review by Pretzsch and others (Pretzsch et al., 2015) covered a sufficiently complete, representational, and recent set of 54 foundational models, which were compiled from other literature searches and reviews (Burkhart & Tomé, 2012; Fontes et al., 2011; Pretzsch et al., 2015). This set included a wide range of models that varied in how they represent forest function, structure, and environmental processes. Furthermore, Pretzsch and others (Pretzsch et al., 2015) summarized several common model attributes that were relevant to our criteria of applicability to small forests, including spatial resolution, species-mixing potential, spatial structure, modeling approach, and mechanistic complexity. In this study, we re-assessed the 54 models reviewed in Pretzsch et al. (Pretzsch et al., 2015) specifically to evaluate their suitability for small forests according to our tiered series of evaluation criteria. At each tier, we evaluated whether each model had characteristics that are suitable for small forests, as described in Section 2. Those models that were deemed most likely to be useful for informing small forest management were forwarded for evaluation at the subsequent tier level.

4. Results

The tiered small forest evaluation criteria (Figure 2.2) consider five model characteristics: (1) spatial resolution, (2) number of species the model can simulate, (3) whether spatial structure is incorporated, (4) modeling approach used, and (5) mechanistic detail. At each tier, we considered each of the 54 reviewed model's attributes in light of their suitability to address the potential management concerns that small forest managers may have. Below we describe the outcomes of the model attributes evaluations.

4.1 Tier 1: What Is the Model's Spatial Resolution?

All 54 models that we evaluated simulate forest dynamics at an individual, cohort, or stand level. In effect, this first tier suitability criterion was applied in our initial selection of models to review. Small forest managers do frequently have landscape-scale concerns, such as habitat connectivity and the broader-scale spread of invasive species or pests. However, landscape-scale forest dynamics models on their own may not be the most appropriate tools to evaluate these effects. These concerns would be more readily addressed by incorporating outputs of stand-scale or finer simulations into geospatial analyses of the matrix surrounding the focal small forest (Pretzsch et al., 2008). Additionally, forest dynamics models can be coupled with regional hydrological models to capture important feedbacks between forest change and water availability (Ameztegui, Cabon, et al., 2017), which is another salient concern for many small forest managers.

4.2 Tier 2: Can the Model Simulate for More than One Species?

Of the 54 models evaluated, 38 can simulate more than one species. Some of the multi-species models were developed for specific species. For instance, COMMIX was designed to study two species, *Fagus sylvatica* (European beech) and *Pseudotsuga menziesii* (Douglas fir) (Bartelink, 2000). FINNFOR evaluates three different species native to Finland: *Picea abies* (Norway spruce), *Pinus sylvestris* (Scots pine), and *Betula pendula* (Silver birch) (Fontes et al., 2011). These models would likely require extensive re-parameterization to simulate other tree species. Therefore, small forest managers may find these models less convenient when studying forests that contain species other than those. Other multi-species models, including SORTIE, FORMIND, FORMIX, and 3-PG, are more flexible and can generally be applied to various species and forest types (Blanco et al., 2015; Landsberg, 2003; Pretzsch et al., 2015; Shugart et al., 2018).

4.3 Tier 3: Is the Model Spatially Explicit?

For each of the 38 multi-species models identified in Tier 2, we assessed whether they were distance dependent, and if so, whether they were spatially explicit and at what resolution. We found that 10 models can incorporate horizontal spatial structure at an individual-tree or patch level and provide individual-tree, cohort, and size-class information as model outputs (Table 2.1). FORMIX is a distance-dependent but non-spatially explicit size-class or cohort model, and the other nine models are spatially explicit individual-tree models.

Table 2.1. Model characteristics of the 10 reviewed distance-dependent, multi-species models that simulate tree coordinates of more than one tree species at an individual-tree or patch level. Characteristics include spatial resolution, species capacity, (horizontal) spatial explicitness of distance-dependence, modeling approach, and whether the model represents physiological processes mechanistically. Spatial explicitness and mechanistic details were determined by other reviews: (Blanco et al., 2015; Fontes et al., 2011; Larocque et al., 2016; Pretzsch et al., 2008; Pretzsch et al., 2015).

Model Name	Spatial Resolution (Pretzsch et al., 2015)	Potential # of Species (Pretzsch et al., 2015)	Spatial Explicitness	Approach (Empirical, Process-Based, or Hybrid) (Pretzsch et al., 2015)	Use of Physiological Mechanisms to Simulate Processes
BALANCE	Individual	5	Explicit, individual-tree coordinates (Rötzer et al., 2010)	Process-based	Yes (Rötzer et al., 2010)
BWIN PRO, TreeGrOSS	Individual	Several	Explicit, individual-tree coordinates (Albrecht et al., 2011; Yousefpour & Hanewinkel, 2009)	Empirical	No (Nagel, 2003)
COMMIX	Individual	2	Explicit, individual-tree coordinates (Bartelink, 2000)	Process-based	Yes (Bartelink, 2000)
EFIMOD	Individual	3	Explicit, individual-tree coordinates (Packalen et al., 2013)	Hybrid	Yes
FORMIND	Individual	Several	Explicit, individual-tree coordinates (Fischer et al., 2016; Helmholtz Centre for Environmental Research, 2021)	Process based	Not required
FORMIX	Cohort	5 groups	Explicit, statistical distribution at patch or plot level	Process based	Not required
MAESTRO/ MAESPA	Individual	Several	Explicit, individual-tree coordinates (Charbonnier et al., 2013; Duursma & Medlyn, 2012)	Process based	Yes (Charbonnier et al., 2013; Duursma & Medlyn, 2012)
MOSES	Individual	4	Explicit, individual-tree coordinates (Thurnher et al., 2017)	Empirical	No (Mikac et al., 2013; Thurnher et al., 2017)
SILVA	Individual	5	Explicit, individual-tree coordinates	Hybrid	Not required

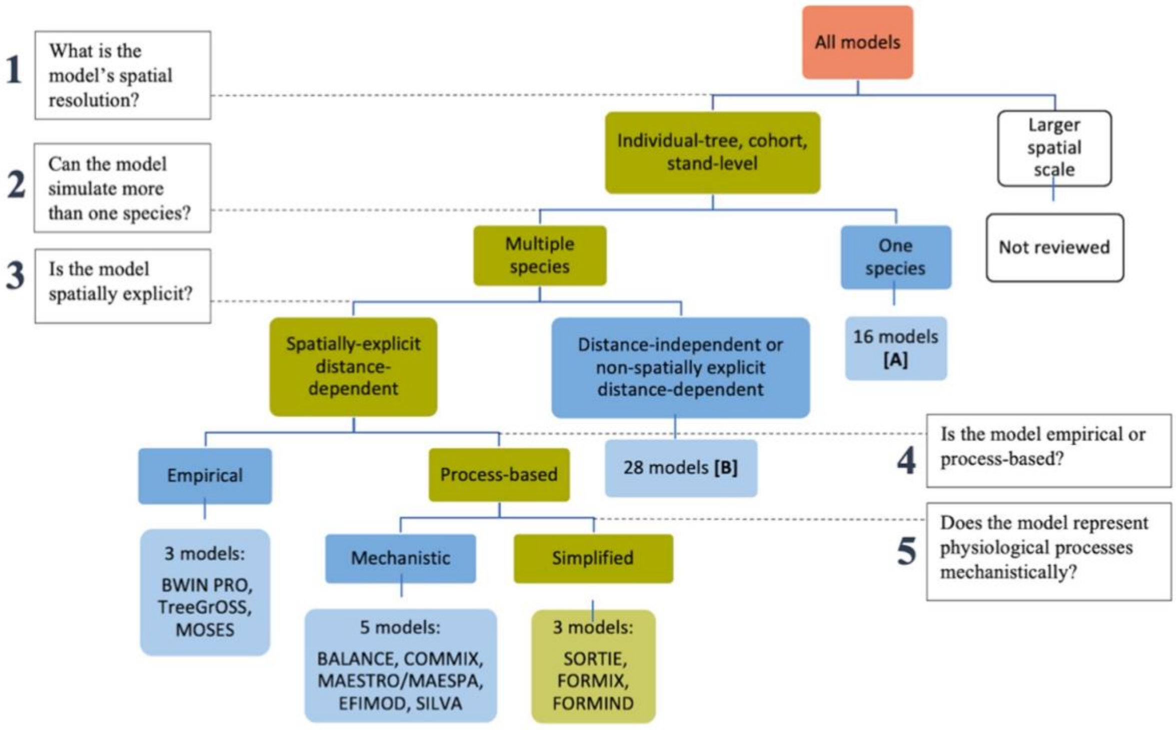
SORTIE/BC	Individual	Several	Explicit, individual-tree coordinates (Canham, 2017)	Process based	Not required (Canham, 2017)

4.4 Tier 4: Is the Modeling Approach Empirical or Process-Based?

We evaluated each of the 10 distance-dependent, spatially explicit models according to their modeling approach (Table 2.1). Empirical models include BWIN PRO/TreeGroSS and MOSES. Hybrid models EFIMOD and SILVA contain both empirical and process-based components. The remaining six models use a process-based approach. Although empirical models such as BWIN PRO/TreeGroSS and MOSES and the hybrid models with empirical components can accurately predict forest structure and composition, they lack a dynamic approach to account for changing environments. Because models with process-based components vary in their degrees of mechanistic detail, they pose different tradeoffs between biological realism and data requirements. In Tier 5, we explore the implications of these differences for the eight process-based and hybrid models.

4.5 Tier 5: Does the Model Represent Physiological Processes Mechanistically?

The evaluation at Tier 5 identified three simplified process-based models, SORTIE, FORMIX, and FORMIND, and three fully mechanistic process-based models, COMMIX, BALANCE, and MAESTRO/MAESPA. Two hybrid physiological models, EFIMOD and SILVA, statistically simulate tree growth based on empirically fitted physiological parameters for sub-organ- and organ-level mechanisms in the most basic model versions (Pretzsch et al., 2015). The Tier 5 attributes of these models, and other model characteristics from previous tiers, are summarized in Table 2.1. Figure 2.4 summarizes the tier-by-tier evaluation of all models.



[A] Single-species models: AMORPHYS (PIPESTEM), BIOME-BGC, CABALA, CASTANEA, DF.HGS, EMILIION, FORGEM, FORGRO(-SWIF), G-DAY, LIGNUM, PIPEQUAL, SIMWAL, TRAGIC, TREE-BGC, TRIPLEX, YIELD-SAFE **[B] Distance-independent (non-spatial) models:** 3-PG, 4C, ANAFORE, CO2FIX V.2, FINNFOR, FORCLIM, FORCYTE, FORCYTE 11, FORECAST, FOREST v5.1, FOREST-BGC, FORSKA, FORSPACE, FORUG, FULCAM, FVS, GOTILWA+, HYBRID, MGM, N.N., N.N., N.N., PICUSv1.3, PNET(-CN,-DAY), TREEDYN3, TREEMIG. **Non-spatially explicit, distance-dependent models:** SECRETS, WoodPaM

Figure 2.4. Tiered series of evaluation criteria used to assess the suitability of 54 forest dynamics models for informing small forest management concerns. Characteristics that are more relevant and appropriate for small forests are in green. Characteristics with weaker relevance, or narrow applicability to specific management concerns, are in blue. Characteristics that will not help inform small forest management are in white. Models that best met small forest evaluation criteria include SORTIE, FORMIX, and FOR-MIND.

As simplified, process-based, multi-species models, SORTIE, FORMIX, and FORMIND have the broadest potential application to small forest management out of the models we evaluated. FORMIND and FORMIX are highly cited models (Blanco et al., 2015; Larocque et al., 2016) and have primarily been used by the research team that developed them to evaluate forest change in species-rich tropical regions (Helmholtz Centre for Environmental Research, 2021). They have similar model structures and algorithms (Blanco et al., 2015). However, FORMIX is cohort based and not fully spatially explicit at an individual-tree resolution, while FORMIND is an individual-tree, spatially explicit model. The most recent versions of FORMIX (i.e., FORMIX3 and FORMIX3-Q) contain improved equations that more accurately describe tree productivity (Blanco et al., 2015; Huth et al., 1997; Kammesheidt et al., 2001; Tietjen & Huth, 2006), but FORMIND has the capacity to address finer-scale interspecific interactions that influence forest structure and composition issues of concern to small forest managers as well as more adaptable equations that have been calibrated for various forest types. Like FORMIND, SORTIE is also an individual-tree, spatially explicit model, and it has evolved (the most recent version being called SORTIE-ND) to become more adaptable across ecosystems and can help inform small forest management for different regions. Because of their spatially explicit simulations and potential portability to other systems, SORTIE and FORMIND are thus deemed the most suitable, flexible, and potentially applicable models for informing small forest management goals and concerns, particularly in new modeling contexts. In the discussion, we explore additional practical aspects and offer guiding recommendations for new implementations of SORTIE or FORMIND in small forests.

5. Discussion

5.1 Key Findings from the Model Suitability Evaluation

The five-tiered suitability criteria assess different aspects of model scale, structure, and approach, from which we inferred their potential suitability of 54 forest dynamics models for informing several common small forest management issues. Tiers 1 and 3 focus on spatial resolution; we concluded that models that simulate forests at the stand level or finer resolution are most suitable, with spatially explicit models affording more nuanced treatments of environmental effects and interspecific interactions. Tier 2 evaluates model design in terms of number of tree species represented; except in the contexts of small forests dominated by a single well-studied species, models with the capacity to represent multiple species can inform a broader the range of small forest management concerns. Tier 4 examines empirical versus process-based models; we found that both have their own forms of data availability limitations, yet process-based models offer the advantage of simulating dynamic environmental effects and growth dynamics beyond those measured empirically in the past. Lastly, Tier 5 assesses the level of mechanistic detail in process-based models, and we posited that because of the difficulty of parameterizing highly mechanistic models, simplified process-based models are likely to be much more feasible for small forest management applications. Of the three simplified models identified in this final tier, we concluded that SORTIE and FORMIND have advantageous combinations of spatially explicit individual-tree simulations and flexible model designs to address a range of potential processes that influence small forest dynamics (Table 2.2).

Table 2.2. Summary of advantageous attributes of SORTIE and FORMIND, in terms of criteria for (**A**) suitability for small forests and for (**B**) application in new contexts.

Suitability Criteria	**SORTIE and FORMIND Attributes**	**Advantages**
A. Suitability for small forest management concerns		
1. Spatial resolution	Individual tree	Aligns with small spatial scale concerns and localized processes
2. Number of species	Multiple	Broadest applicability across diversity of small forest contexts
3. Spatial explicitness	Explicit	Captures effects of heterogeneous environments and local interactions
4. Empirical or process-based	Process based	Better suited for modeling dynamic and novel environments
5. Mechanistic or simplified processes	Simplified	Reduces technical complexity and need for hard-to-measure physiological parameters
B. Suitability for application in new contexts		

1.	Data needs and availability	Tree size attributes plus establishment, mortality, light-growth rates	Requires multiple data sources, but less demanding for site-specific and physiological data than other models
2.	Model portability	Simplified, process-based multi-species simulations	Facilitates transfer to new systems without detailed physiological parameterization
3.	Range of application conditions	Numerous optional modules	Modules can be added to address different applied management scenarios and questions
4.	Software availability	Freely available, well-documented	User-friendliness lowers obstacles for use in new contexts and by new or novice modelers
5.	Model robustness	Highly parameterizable	Tailoring parameters improves robustness but assumptions and uncertainties should be explored with sensitivity analyses

5.2 Considerations for Implementing Models in New Contexts

The tiered criteria fruitfully address a range of factors particularly relevant to management concerns in small forests, as well as some factors relevant to new contexts, by which we mean forest units, conditions, and/or management contexts that have not been modeled previously. Because this review is intended to orient and inform forest managers who are not yet using forest dynamics models, the pragmatic feasibility of implementing a model in new contexts is an especially important topic, as emphasized in other forest model reviews (Monserud & Robinson, 2002; Robinson & Monserud, 2003). We highlight five key issues for model suitability in new contexts, which were previously identified (but categorized slightly differently) by Monserud and Robinson (Monserud & Robinson, 2002). The tiered criteria already provide a lens for considering three key pragmatic issues: (1) input data needs and availability, (2) model portability, and (3) range and extendibility of application conditions. Two other key issues have not been addressed explicitly thus far and warrant further evaluation: (4) technical accessibility of modeling software, and (5) the reliability, or robustness, of model outputs.

Input data needs are determined by model structure and design, but input data *availability* is determined by the extent of research and monitoring efforts applicable to the new forest context (Robinson & Monserud, 2003). In each tier, we discussed both data needs and likelihood of adequate data availability. The latter was a key factor in determining model suitability in Tiers 4 and 5, where we concluded that data availability for both empirical models (Pretzsch et al., 2015; Thürig et al., 2005) and mechanistic models (Fontes et al., 2011) is expected to be prohibitively low for most novel small forest applications, leading to our recommendation for simplified process-based models. At their basic model structures, SORTIE and FORMIND require relatively easily obtainable information about size attributes of different life history stages such as height, diameter, and crown characteristics (Figures 2.5 and 2.6) (Canham, 2017; Helmholtz Centre for Environmental Research, 2021). However, some physiological and environmental knowledge—notably, species-specific establishment, mortality rates, and growth responses to varying light conditions—is required (Larocque et al., 2016). Because the models are process based, these characteristics do not need to be site specific, but they should be species specific (Larocque et al., 2016). If estimates are unavailable, parameterization and calibration will prove difficult, and the usefulness of model outputs will be limited.

Model portability, or the ease at which a model can be calibrated for an intended use, is largely determined by model design (Blanco et al., 2015; Robinson & Monserud, 2003). Portability to both small forests and new forest contexts was addressed in Tiers 2, 4, and 5. These evaluations found that single-species and empirical model designs require prior information about species- and site-specific growth rates, and most models of those types were developed for specific forest types (Pretzsch et al., 2015). These factors limit their portability to other forests with different species and environmental conditions. In the Tier 5 evaluation, we concluded that simplified process-based models are more portable to new contexts than heavily mechanistic models because they can simulate growth under novel conditions based on relatively simple light-growth relationships (Blanco et al., 2015). In particular, SORTIE and FORMIND have a history of sequential applications to new contexts and also have modules that can expand the range of forest processes that models can represent, which strengthens their portability and expandability (Canham, 2017; Helmholtz Centre for Environmental Research, 2021; Schumacher et al., 2004; Shugart et al., 2018).

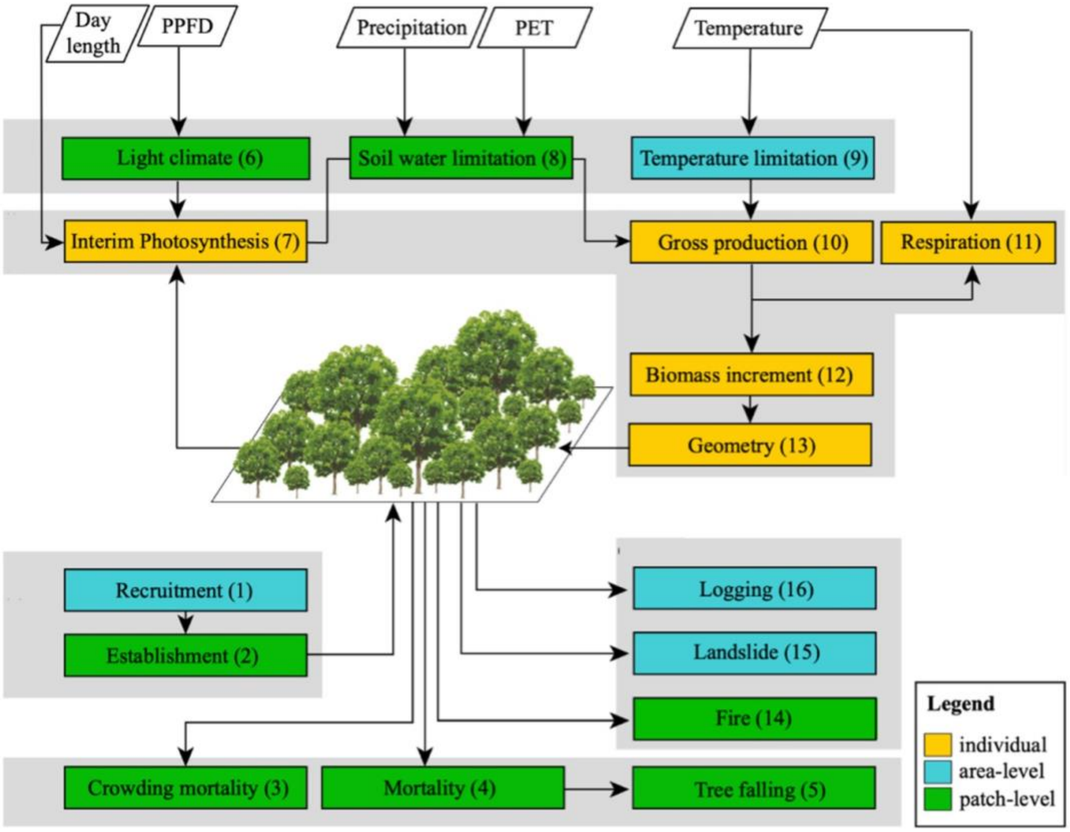


Figure 2.5. Schematic of the FORMIND model. Main processes are in white, and parallelograms indicate climatic parameters, some of which are required to run the model (abbreviations: PET—

potential evapotranspiration; PPFD—photoactive photon flux density). Yellow, blue, and green boxes show physiological, demographic, and optional extensions including logging, harvesting, and fire at different spatial scales. Numbers in parentheses indicate scheduled flow of individual processes within the model, and grey frames underlying boxes group them according to their processes and chapters associated with the FORMIND handbook. Reprinted from (Helmholtz Centre for Environmental Research, 2021) with the author's permission and under Creative Commons license.

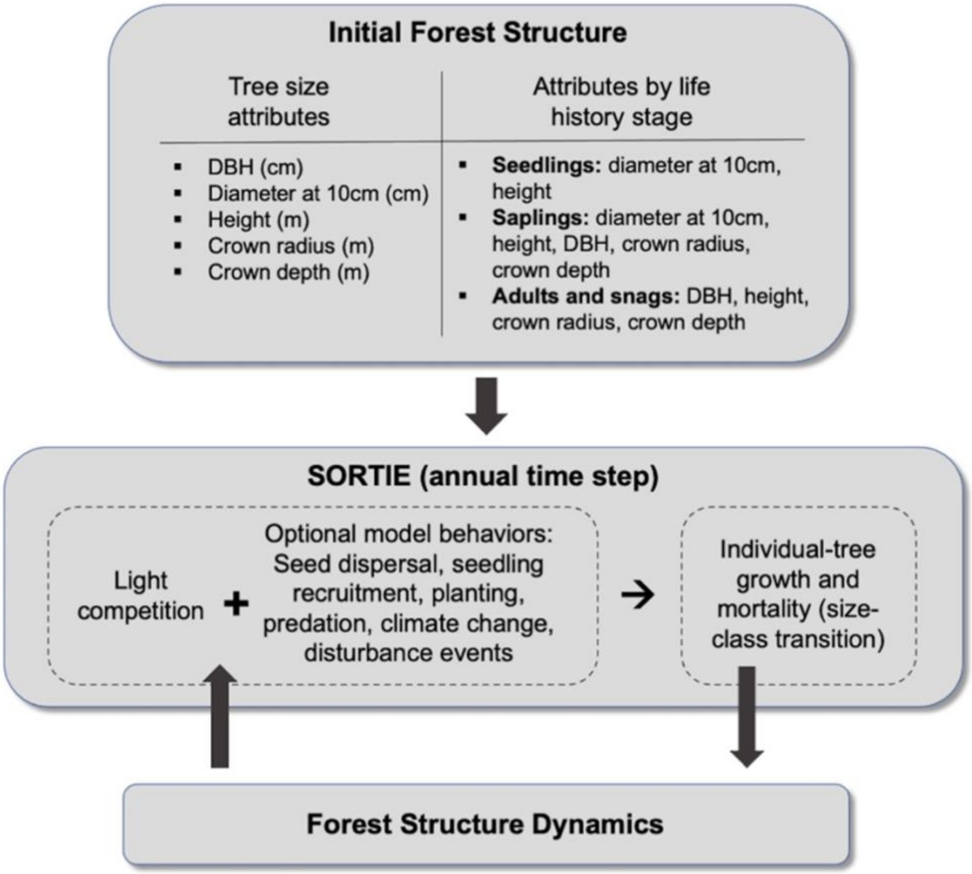


Figure 2.6. Basic schematic of the SORTIE model. Initialization requirements include tree size attributes of four different size classes or life history stages (i.e., seedlings, saplings, adults, and snags). In each annual timestep, neighborhood density and light–growth relationships drives individual-tree growth and mortality. SORTIE is pre-loaded with growth parameters for eight North American tree species, and users can upload values for additional species. Optional sub-models can be coupled at each timestep to account for other factors that influence forest community change. After SORTIE annually projects individual-tree growth and mortality, the resulting forest structure determines light that is available for the next annual time-step. Information source: (Canham, 2017).

Application conditions refer to a model's ability to simulate management-relevant factors such as environmental change, disturbance, and management actions when projecting future forest conditions, and *extendibility* refers to the ease of adding more sub-models or behaviors (Robinson & Monserud, 2003). Application conditions were key considerations when assessing models' suitability for small forest issues (Figure 2.1) in Tiers 3, 4, and 5. The arguments in Tier 4 and 5, regarding the advantages of process-based models to simulate novel environmental conditions, also relate to new forest contexts. Because process-based models simulate environmental effects via underlying processes instead of via previously observed growth responses, they are more suitable than empirical models for informing a wider range of application conditions in new contexts as well. While mechanistic process-based models also generate useful outputs for many application conditions, the data needs and availability for parameterizing such application conditions in new forest contexts presents a larger obstacle, as discussed in Tier 5.

Although both SORTIE and FORMIX were originally designed for specific application conditions, they contain adaptable equations that are calibrated for various forest types across the world (Blanco et al., 2015; Canham, 2017; Evans & Moustakas, 2016; Helmholtz Centre for Environmental Research, 2021; Shugart et al., 2018), and they can simulate the effects of a variety of management scenarios through optional model behaviors and sub-models (Figures 2.4 and 2.5) (Canham, 2017; Ditzer et al., 2000; Huth et al., 1997). These options extend both the portfolio of useful model outputs as well as the applications conditions that the models can simulate. For example, SORTIE and FORMIND have been used to study logging and harvesting (Bose et al., 2015; Canham et al., 2013; Kammesheidt et al., 2001); climate change scenarios (Bugmann et al., 2019; Canham & Murphy, 2017); and insect, pathogen, and herbivore intensity

(Dantas de Paula et al., 2018; Forsyth et al., 2015) in tropical, temperate, and boreal forests. Many forest management studies have also incorporated other environmental processes like water balance, nitrogen deposition, and natural disturbances into the model process (Ameztegui, Paquette, et al., 2017; Canham, 2017; Kunstler et al., 2013). FORMIND is one of the few forest dynamics models that has a sub-model called ForFire (Figure 2.5) that can simulate the impact of fire events (Fischer, 2021; Knapp et al., 2018; Ribeiro et al., 2021). However, many of the optional functions within FORMIND and SORTIE that are relevant to new management contexts cannot be parameterized without additional data collection (Evans & Moustakas, 2016).

Technical availability of modeling software, an issue we have not yet addressed in this review, includes both source code availability and adequate documentation to guide its use (Robinson & Monserud, 2003). This is critical to the feasibility of implementing a forest dynamics model for a new context. SORTIE and FORMIND are widely used internationally and have free source code that is available online (Blanco et al., 2015; Canham, 2017; Helmholtz Centre for Environmental Research, 2021; Shugart et al., 2018). Thus, they meet the essential criterion of technical availability. However, the utility of SORTIE and FORMIND to small forest management is still heavily influenced by the number of parameters that can be estimated within the source code. Simply supplying these models with only DBH or other more easily obtainable data leaves little room for calibrating many of the allometric equations required to provide accurate model predictions (Evans & Moustakas, 2016). Without existing forest inventory data, a substantial data collection effort may be required to get reliable model outputs.

Therefore, the last issue, which is a perennial concern in all modeling work, is *model robustness*—the model's ability to provide accurate and reliable estimates (Blanco et al., 2015; Monserud & Robinson, 2002; Robinson & Monserud, 2003). Model robustness does not depend on model complexity but on the variability and un-certainty of model inputs and parameters (Blanco et al., 2015). This is a limitation in any modeling context, but parameter uncertainty is likely to be particularly high for small forests due to the lack of well-studied analogs. Uncertainty or inaccuracy in parameter estimates do not all have proportional effects on the robustness of model outputs. Rather, model outputs tend to be more sensitive to uncertainties in some parameters, and more robust to others. Thus, it is important to evaluate the reliability of functional relationships within the model structure and model outputs through sensitivity analyses. Sensitivity analyses systematically alter model inputs and parameters through multiple simulations to identify those that contribute the most to model fluctuations outputs (Larocque et al., 2016; Vanclay & Skovsgaard, 1997). This technique offers small forest managers a way to identify model limitations and also recognize highly influential ecological information that can be prioritized during parameterization and calibration (Larocque et al., 2016; Vanclay & Skovsgaard, 1997). For instance, it often recommended to focus on light competition variables when applying a simplified process-based model (Evans & Moustakas, 2016). For SORTIE and FORMIND, the most basic light competition variables include tree crown geometry and estimates of size-dependent growth rates (Ameztegui, Cabon, et al., 2017; Canham, 2017). These variables can be derived for a large number of tree species, and studies have generally found the models' community-level predictions to be rather robust to uncertainties in those parameters. However, if forest community change is driven by factors other than light competition, and relevant available sub-models are other major drivers not incorporated, SORTIE and FORMIND and other simplified process-based models can generate unrealistic or inaccurate estimates (Evans & Moustakas, 2016). Model calibration, validation, and sensitivity analyses are thus particularly important if quantitative model estimates are used as the basis for making management decisions (Blanco et al., 2015; Vanclay & Skovsgaard, 1997). When model robustness is limited due to the novelty of a new context, an alternative use of model outputs for forest management is more qualitative evaluations of management alternatives, and to explore the relative influence of different factors that can affect the trajectory of forest change. Sensitivity analyses of both SORTIE and FORMIND have helped researchers make both quantitative and qualitative inferences from model outputs, as appropriate given parameter uncertainties (Coates et al., 2003). Thus, SORTIE and FOR-MIND do not offer immunity to this challenge of model robustness or the previously discussed issues that arise when implementing a model in a new context, but since they were designed for wide adoption and user friendliness, they offer options, advantageous attributes, and documented implementation examples that can help minimize obstacles (Table 2.2B).

5.3 Recommendations

Choosing a model ultimately depends on alignment between management concerns, the information needed to answer that question, and the generation of robust outputs to inform management (Porté & Bartelink, 2002). SORTIE and FORMIND are accessible, relevant, and relatively user-friendly tools that can address a wide range of small forest management concerns, as summarized in Table 2.2. They are often seen as alternatives to one another (Evans & Moustakas, 2016) because they both have similar input parameters, requiring at minimum initial stand structure, tree geometries, and species-specific tree growth rates (Figures 2.4 and 2.5) (Canham, 2017; Evans & Moustakas, 2016; Helmholtz Centre for Environmental Research, 2021). SORTIE has been more frequently applied in temperate forests, and FORMIND in tropical forests, but they are not constrained to those contexts. Rather, selection should be guided by alignment between the salient management concerns, the likely ecological importance of available sub-model options, and the usefulness of available simulation outputs. When resources and information are limited, we recommend starting with the simplest forms of the model and structuring management questions to compare management actions and alternatives instead of depending solely on quantitative model estimates. Combining different sources of information and collaborating with modelers, research organizations, ecological forestry consultants, academic institutions, and other partners and scientists of different disciplines can also help fulfill model requirements and data needs, facilitate implementation, and build capacity and management effectiveness through multi-directional knowledge sharing (Evans & Moustakas, 2016; Larocque et al., 2016; Pretzsch et al., 2008; Thurnher et al., 2017).

Collaborating with decision-support experts can also help small forest managers relate model outputs to particular management actions. Model outputs can feed a decision-support tool, framework, or system to help landowners, small forest managers, and stewards transfer scientific knowledge to practical forest management actions to meet their objectives (Packalen et al., 2013). For example, a SORTIE model was built to incorporate climatic and management prescription data, creating an array of future forest projections that served as a decision-support tool to evaluate how different forest management actions and climate change scenarios may affect ecosystem services (Cristal et al., 2019). Other decision tools are not specific to any forest dynamics model and can incorporate model outputs describing future forest structure and composition. As decision-support tools that require information about forest structure and composition are becoming more popular for forest management (Abelson et al., 2021; Beier et al., 2008; Cristal et al., 2019; Packalen et al., 2013; Thrippleton et al., 2020), they are a potential resource for many small forest managers to couple with forest dynamics modeling when addressing forest benefits and concerns.

6. Conclusions

Although forest dynamics models have become increasingly vital when answering management questions, their appropriateness for simulating the dynamics of management concern in smaller forested areas had not been systematically explored. In this literature review, we evaluated the suitability of 54 existing forest dynamics models to small forest management using five criteria. All models had some drawbacks. However, two, SORTIE and FORMIND, offered the most suitable balance of scale appropriateness, forest type flexibility, structural definition, management relevance, model dynamism and simplicity, plus portability, robustness, and pragmatic usability for application in new, small forest contexts. Establishing a robust implementation of either of these models in a new, small forest context, including those of varying agricultural and urban influences, is likely to proceed incrementally as model calibration improves and environmental factors are incorporated. While full model validation may be an unrealistic near-term goal in most small forest contexts, sensitivity analyses provide useful, accessible techniques for gaining insights regarding achievable conditions and the potential impact of management actions. Each of these models have their advantages and can therefore be applied to different management scenarios (Robinson & Ek, 2000) whether preserving key tree species, conserving a particular forest structure and composition, restoring historical tree communities, or managing a forest for multi-use.

These findings will hopefully inform small forest managers about the suite of available forest dynamic models available to them and which models to use for specific research questions and help them make sound management decisions. As more and more forests globally exist and are managed at smaller spatial scales, guidance through modeling is also becoming increasingly relevant, feasible and accessible through models like SORTIE and FORMIND.

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CHAPTER 3

DEVELOPING A DECISION SUPPORT TOOL FOR MANAGEMENT ALTERNATIVES TO RESTORE AND CONSERVE MARITIME LIVE OAK FORESTS[2]

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[2] Benson, D.L.; Moore, C.T.; King, E.G.; Nibbelink, N.P.; Morris, H.R. To be submitted to *Forestry Ecology and Management.*

Abstract

Maritime Live Oak (*Quercus virginiana*; MLO) forests along the Georgia (U.S.A.) coast are highly regarded for their multiple natural and cultural heritage values. In recent decades, MLO forests have shown evidence of limited live oak recruitment, which may result in undesired long-term effects on tree community structure, function, and resilience. Many MLO forest stewards and other stakeholders share a common interest in conserving forests by planting live oaks to augment existing populations. But there is uncertainty regarding potential restoration strategies because knowledge about MLO ecosystem dynamics is limited and fragmented among stakeholders. We used structured decision making to collaboratively develop a decision support tool for live oak tree-planting strategies. First, we held workshops with MLO forest stewards to identify: the managers' long-term objectives and shorter-term success indicators; spatial and temporal scales of likely management actions; a set of potential management options; and data, legal, and resource constraints. Then we constructed transition matrix models using empirical data and expert knowledge to estimate parameters for juvenile tree growth and survival rates associated with alternative tree-planting strategies. The decision support tool incorporated the transition models and associated cost estimates of management alternatives in order to project likely outcomes, costs, associated uncertainties, and the degree to which alternatives would meet different management objectives. This process ensured that we capitalized on diverse understandings and perspectives and that the decision support tool would be directly relevant to stewards' values, objectives, and information needs.

1. Introduction

1.1 Problem: Maritime live oak forests—conservation, management, and knowledge gaps

Maritime live oak (*Quercus virginiana*; MLO) forests on barrier islands along the southeastern Atlantic coast from North Carolina to Florida are highly regarded for their multiple natural and cultural heritage values (Evans & Keen, 2013; Horsley, 2020; Jones et al., 2013). MLO forests play a central role in supporting biodiversity and the ecological health of islands and are globally rare but one of the least studied coastal ecosystems (Jones et al., 2013; Shiflett et al., 2013; Smith et al., 2015). As a result of the southeastern coast's varying geology, hydrology, ecological diversity, and human history, its MLO forests are complex, dynamic, and variable. In recent decades, these MLO forests are also facing various environmental stresses including climate change, land development, invasive plant species, and altered wildlife abundances (Helm et al., 1991). Storm damage, intense fire, and beach erosion are an increasingly observed cause of mature tree mortality on barrier islands (Conner et al., 2005; Helm et al., 1991), and now managers on Jekyll Island and other barrier islands along the Georgia coast have seen little evidence of live oak seedlings or saplings. With low live oak recruitment, these environmental stresses could create undesired long-term effects on tree community structure, function, and resilience.

Jekyll Island is a state park that conserves about 65% of the island as natural areas while also supporting tourism amenities and a residential community. Jekyll Island offers opportunities for the public to enjoy the unique heritage of barrier island MLO forests in Georgia. It contains roughly 400ha of maritime live oak forests (Jekyll Island Authority, 2020), which are undergoing several environmental stresses that could be affecting live oak regeneration. First, on Jekyll

Island, and in many forests throughout North America, white-tailed deer (*Odocoileus virginianus*) pose a critical constraint on tree seedling establishment and survival to maturity (Aronson & Handel, 2011; Thyroff et al., 2019a). Jekyll Island Authority (JIA), a self-supporting state agency that is responsible for management and stewardship of Jekyll Island, is especially concerned how the deer could affect the future of its maritime live oak forests (Jekyll Island Authority, 2020). Herbivores like deer can affect plant communities directly through biomass loss and plant mortality (Averill et al., 2018) but can also indirectly influence interspecific plant competition through selective herbivory. A second concern Jekyll Island managers have is invasive plant species, especially camphor (*Cinnamomum camphora*), an Asian evergreen tree that was introduced for horticulture but has now invaded a few natural areas on the island. Fast-growing and with prolific seed production, camphor may out-compete native plant species and its establishment raises concerns about native plant biodiversity (Schenk, 2009). A third concern is hurricane and storm damage resulting in adult live oak crown damage and biomass loss (Conner et al., 2005; Helm et al., 1991). However, disturbances that damage the canopy also create light gap conditions that promote live oak regeneration, but it is uncertain whether regeneration can successfully compete to reach the overstory. A fourth concern on Jekyll Island is the ecological consequence of long-term fire exclusion, which has led to a thick shrub layer of saw palmetto (*Seneroa repens*) and a heavy accumulation of litter and duff. Fire is a keystone process that maintains forest biodiversity by creating fluctuations in resource availability and preventing competitive exclusion (Kerns & Day, 2017). Therefore, fire exclusion creates an additional stress for tree species and the herbaceous layer that rely on periodic reduction in litter and shrub cover to regenerate and reach above the shrub layer.

For the project presented in this chapter, a team of researchers, decision-scientists, and graduate students including myself have addressed these suites of concerns about live oak regeneration and the future of MLO forests using structured decision making (SDM), an organized framework that can help stakeholders solve an environmental problem by finding management alternatives that best meet their ultimate goals or fundamental objectives. We have collaborated with JIA and other island managers and coastal stewards along the Georgia coast through SDM to integrate knowledge and find potential MLO management actions to evaluate the low live oak regeneration problem. This chapter first explores how our team used SDM to define management objectives and identify management alternatives to help pursue those objectives. Because stakeholders agreed that planting live oaks would best meet their management needs, we have then compiled different types of knowledge to build a demographic model and decision support tool that projects likely outcomes, costs, and associated uncertainties under alternative tree-planting strategies and the degree to which each alternative would meet different management objectives.

1.2 Approach: Structured decision making with coastal land managers and stewards

SDM is an organized decision making framework that uses a series of steps to incorporate uncertainties, risk analyses, and decision-theory to help solve complex ecological and environmental problems (Gregory et al., 2012). SDM has proven effective in promoting sound environmental management, particularly when faced with conflicting management objectives (Gregory & Keeney, 2002). Although this project was inspired by ecological concerns on Jekyll Island, our team agreed that collaborating with other island managers and coastal stewards would best identify knowledge gaps and research priorities. Therefore, this framework is ideal to addressing potentially alternative management styles and goals.

Figure 3.1 demonstrates the general SDM process (Gregory et al., 2012). (1) The first step is to identify and clearly define a management problem within a decision context such as poor habitat quality or low endangered species population density. (2) Then, stakeholders identify fundamental objectives or ultimate goals that reflect individual stakeholder needs, which often represent various ecological, social, and economic values (Brown & Ferguson, 2019; Kozak & Piazza, 2015; Robinson et al., 2016b). There is also often an objective hierarchy that defines means objectives or sub-objectives, which further clarifies how to achieve the fundamental objective, and measurable attributes or performance measures, which are specific measurements to realize how a management alternative meets an objective (Gregory et al., 2012). After defining management objectives, (3) the third step is to identify management alternatives that can help meet those objectives. This information also usually reflects stakeholder preferences and avoidances but does need to include practical management actions that decision-makers could consider (Gregory et al., 2012). Next, (4) scientists use a variation or combination of empirical and statistical models, population simulation models, expert or stakeholder elicitation techniques, or other performance or analysis tools to evaluate consequences of each management action or alternative (Robinson et al., 2016a). Consequences predict the outcomes or measurable attributes of each management alternative on each of the objectives (Robinson et al., 2016a). Next, after (5) evaluating trade-offs and exploring optimizations between actions and management objectives, (6) stakeholders collectively decide on a management strategy. Typically, steps (1) Problem, (2) Objectives, (3) Alternatives, and (6) Decide and Take Action reflect stakeholder aims and values while steps (4) Consequences and (5) Trade-Offs and Optimization use ecological knowledge like scientific research and monitoring (Moore & Runge, 2012).

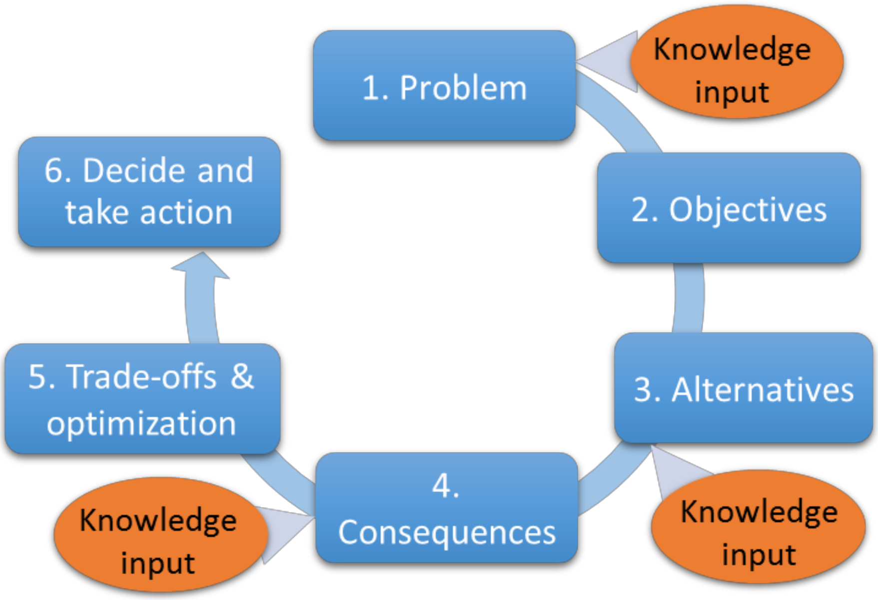


Figure 3.1. Structured decision making is a six-step process designed to help stakeholders solve a problem while balancing different management objectives. SDM requires different types of knowledge like empirical ecological information, expert opinion, and stakeholder values to run. Knowledge can be incorporated at various points during the SDM process, a couple of which are shown in orange. Adapted from Gregory et al. (2012).

1.3 Application of SDM to MLO forest restoration under uncertainty

Because of its stepwise structure and organization, SDM can be applied to nearly any system, including those found in engineering, economics, and natural resource management (Guntenspergen, 2014). The studies using SDM for forest or plant community management have mostly been interested in preserving endangered and threatened animal populations, improving habitat quality for fish and wildlife, prioritizing policies and values when managing larger forest ecosystems (Ogden & Innes, 2009; Zakaria, 2020). However, there is little evidence in the literature of using SDM to direct actions at individual plant or tree populations, especially for conservation and restoration purposes (Guerrero et al., 2017). Therefore, one key component of this chapter will be to combine different sources of information and addressing uncertainty within the information that is gathered.

Ultimately, the type of knowledge used is entirely dependent on the decision context and what constitutes as the best available information (Gregory et al., 2012). Although there is some ecological field research conducted on live oak seedlings that observe the effects of deer herbivory, light availability, and competing vegetation on seedling growth and survival (Thyroff et al., 2019a; Thyroff et al., 2019b), there is not enough information to inform tools for evaluation as each of these studies have observed live oak growth and survival for a limited number of years, which may underestimate the time it takes for live oak seedlings to reach the canopy. Furthermore, there are some knowledge gaps in how different management alternatives like planting live oaks at later life stages or how extensive watering can affect live oak seedling performance. Therefore, we have synthesized and combined available empirical data with elicited information from stakeholders through workshops and interviews using a participatory process and methods of knowledge co-production.

Most steps within the SDM framework require different types of information but they can also integrate other forms of knowledge. Local managers' and other stakeholders' direct experience and expertise are increasingly recognized as valuable sources of knowledge (Kuhnert et al., 2010; Reed, 2008), although not always well documented or available. Knowledge co-production has therefore been used within the decision-making process to incorporate various types of stakeholder and expert knowledge regarding the ecological problem. In knowledge co-production, scientists, decision-makers, and other stakeholders share and combine knowledge to inform environmental decision-making (Djenontin & Meadow, 2018). Pieces of knowledge are usually directly incorporated into qualitative and quantitative statements as management objectives or alternatives, parameter values for modeling and other analysis tools when assessing consequences, or direct decision-making (Czembor & Vesk, 2009). Many studies have used a combination of knowledge sources to fill knowledge gaps within the SDM framework, especially during steps (4) Consequences and (5) Trade-Offs and (Brown & Ferguson, 2019; Liu et al., 2012; Moore & Runge, 2012; Ogden & Innes, 2009).

This chapter is a technical report on how our team has worked within the structured decision making approach to evaluate the live oak regeneration problem when facing limited knowledge about live oak life history and community-dynamics of MLO forest ecology. We will explain our approach organized around the SDM steps, ultimately describing how our designed decision support tool can help meet different fundamental objectives. The decision support tool will be run with different management scenarios selected by stakeholders to help them make decisions about their MLO forests.

2 Methods

2.1 Steps 1 and 2: Identifying the problem and objectives

Our first workshop was held in March 2018. We invited seventeen stakeholders to obtain three goals: discuss the problem of live oak regeneration, elicit and synthesize knowledge regarding live oak regeneration, and begin defining fundamental objectives for the SDM framework. We first asked our participants to write lists of ecological factors they thought would influence live oak regeneration. We compiled their lists and found that the participants had identified 18 factors, and the five most common factors included mammal herbivory, water availability, herbaceous plant competition, light availability, and fire (Table 3.1). We then asked each manager to define their fundamental objectives relating to MLO forest management. The key management objectives for four main barrier islands are shown in Table 3.2. Ossabaw and

St. Catherines Island managers stated that they favored a more passive approach to live oak management, allowing forest processes to occur naturally and evolve. Jekyll Island and Sapelo managers were more concerned with maintaining specific conditions in their MLO forests and favored active management to ensure success. These stakeholders were highly interested in identifying management alternatives and site prioritization for restoration through live oak planting.

Table 3.1. Top factors influencing live oak regeneration, ranked by the percentage of participants that cited them during the first workshop.

Influence Factor	% of Participants Citing
Mammal herbivory	100
Water availability	100
Herbaceous (understory) plant competition	88
Light/canopy gaps	75
Fire	75
Soil Conditions	63
Acorn production and viability	63
Salt stress	56
Management & human impacts	50
Climate	44
Past land use	38
Litter conditions	31
Genetics	31
Weather/storms	31
Acorn predation	25
Pests/disease	19
Acorn dispersal	13
Forest composition	6

Table 3.2. Key management objectives of four barrier islands. Those interested in passive versus active management through restoration are noted below.

Key Management Objectives of Four Barrier Islands			
Ossabaw	**St. Catherines**	**Sapelo**	**Jekyll**
Maintain and allow landscape to exist as it would naturally occur	Allow forests to evolve with minimal intervention	Maintain and enhance existing maritime live oak forests	Maintain maritime live oak forest composition
		Identify and prioritize sites for maritime live oak restoration	Manage fire risk

Passive management **Active management through restoration**

2.2 Steps 2 (continued) and 3: Refining objectives and identifying management alternatives

Our second workshop was held in April 2019. We included the eight participants from Jekyll and Sapelo who were interested in active restoration through the planting of young live oaks to address the live oak regeneration problem. These stakeholders were highly concerned about the lack of live oak seedlings and saplings in their forests and wanted to find a specific solution to ensure live oak juveniles successful grew into the canopy to replace other mature live oak trees. Our main goal for this workshop was to build on the first workshop by refining fundamental objectives for MLO restoration and identifying management alternatives for planting live oaks to help meet those objectives.

We first asked our participants to individually list their desired future MLO forest condition (i.e., long-term goal or fundamental and means objectives) and their desired MLO condition within 10 years (i.e., short-term goal or means objective). We then held an open discussion about what our participants would define as *fundamental* objectives to optimize within the SDM framework. Ultimately, participants identified two main fundamental objectives: cost-effectiveness and high live oak juvenile survival after planting.

We then held a brainstorming session about what management alternatives or practical management actions would ensure some juvenile trees would ascend to the canopy. We asked questions such as the density of planted juveniles, site location, what accompanying treatments might enhance survival, and whether treatments were too costly to be practical. As we considered what factors might significantly influence the success of planted seedlings, we reviewed our list of 18 factors that influence live oak regeneration from our first knowledge co-production workshop (Table 3.1). Although many conditions affect juvenile live oak growth and survival, they are not all feasible to control as a management action. For instance, Jekyll Island has suppressed fire from many of their forests for decades, and any burning treatment would require additional permitting and safety measures, which could not be easily achieved in the short-term. After discussing which of these factors would be most practical to control and potentially result in the highest seedling survival, participants identified three ecological factors: mammal herbivory, herbaceous (understory) plant competition, and overstory canopy conditions. Manipulations of these factors were then translated to possible restoration actions as management alternatives. Furthermore, participants expressed interest in planting two stock types of live oak saplings (15-gallon vs 100-gallon containers) under different overstory canopy conditions. When watering stress is reduced and nutrient needs are met after planting, larger containerized trees have demonstrated higher growth rates and can better compete with surrounding vegetation, than their smaller counterparts (Baehre, 2020; Haase et al., 2006).

2.3 Steps 4 and 5: Evaluating consequences and determining trade-offs

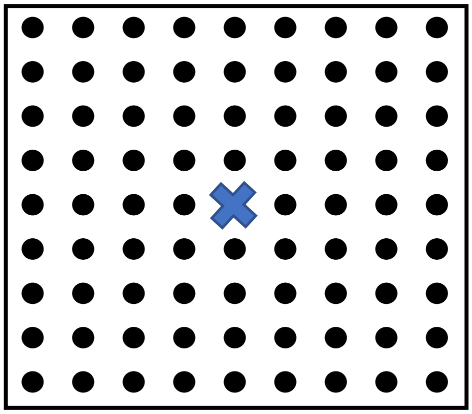
2.3.1 Decision context

The initial goal of this SDM process was to address the question “Are maritime live oak forests on barrier islands in peril? If so, what restoration activities are required?” Throughout the first two workshops, we identified fundamental objectives and a suite of management alternatives that can help meet those objectives. However, most of the participants committed to finding management alternatives were interested in active live oak restoration, specifically by planting juvenile trees. Therefore, we re-evaluated our decision options so we could tailor the final decision support tool to those participants. Our new research question is: “What live oak planting treatments are the most cost-effective and will result in the highest probability of recruitment into the sapling size class?”

Stakeholders interested in active restoration are primarily from Jekyll Island and Sapelo Island. Therefore, we held group interviews with participants from each island, individually, to finalize the problem summary and decision context. With each island, we discussed the ultimate objective in the context of a spatially-defined establishment unit (EU), the number of potential EUs within a site, and other site-associated contextual information that would help develop decision variables for the decision support tool. We also spoke with live oak propagators and environmental consultants to gather information about site preparation and live oak planting strategy feasibility. After these discussions, we finalized the type of information required and available to address this live oak regeneration problem using alternatives discussed from the previous workshops.

The final group of stakeholders—participants from the second workshop—agreed that the main objective for the decision support tool was to achieve the highest probability of recruiting at least one live oak into the sapling size class (> 1.5m, the height above which saplings escape heavy browse damage, referred to herein as "above-browse height") per establishment unit (18m x 18m) at least cost. The EU size was chosen as best approximating the canopy area of an adult live oak tree. We then agreed that planting stock used in each EU would be a choice among three alternatives of containerized seedlings and saplings at specific ages and/or heights (identified according to sizes used by nurseries): larger saplings of 4-inch stem diameter (100 gallon container), smaller saplings of at least 1 ¾-inch stem diameter (15 gallon container), and seedlings that were 30-50cm in height. For either sapling alternative, one sapling would be planted at the center of each EU. For the seedling alternative, up to 81 seedlings (9x9 grid at 2m spacing) would be planted within each EU. The seedling alternative linked to a set of other decision variables that included browse protection, competing vegetation suppression, and overstory removal, all of which were key ecological factors listed by these participants as highly influential to live oak regeneration. Each decision applies to all EUs in a particular site context, and a site's context could influence cost of an action but not the likelihood of established outcomes. Some site contexts we considered were the spatial arrangement of EUs within a site (i.e. scattered, grouped, or grid), public visibility (public or remote) of the site on Jekyll Island, and location of site within or outside existing MLO forest on Sapelo Island, as they could influence cost and utility values. We also decided that general cost estimates for each management alternative would include cost of individual seedling and sapling stock, planting labor, overstory removal, browse protection (materials and labor to install), and competing vegetation suppression (materials and labor per application).

Figure 3.2. Each establishment unit is an 18m x 18m cell. One EU holds a single sapling at the center or a maximum of 81 seedlings on a 9x9 grid at 2m spacing.



2.3.2 Demographic modeling of consequences for each management alternative: live oak seedlings and saplings

2.3.2.1 Transition matrix model to simulate seedling survival and growth

To evaluate management alternatives, we needed to decide the type of information required and available to address this live oak regeneration problem. After the second workshop and during a series of interviews with island managers, live oak propagators, and ecological consultants and stewards, we decided to use a demographic transition matrix model to predict seedling survival and growth. Transition matrix models project population growth based on the probabilities that individuals will survive and stay in a certain size or stage class or survive and grow from one size or stage class to another. Over the last couple of decades, matrix models are increasingly used for management purposes (Crone et al., 2011), and some have proven effective in projecting tree dynamics (Davis et al., 2011; Evans & Keen, 2013). Although these types of models may not provide predictions at resolutions as high as those from models that include more refined life history and environmental detail, matrix models can “calculate the logical outcomes of observed environmental conditions and experimental manipulations...[and] examine what-if scenarios that explore possibilities outside the range of observed conditions" (Crone et al., 2011). Furthermore, matrix models can easily be informed by multiple knowledge sources including field research and monitoring, empirical data, and managers' and stakeholders' direct experience and expertise (Kuhnert et al., 2010; Reed, 2008). Although there are many forest dynamics and growth models that can simulate forest and individual-level dynamics, many are data-intensive or are not appropriate for the scale and nature of restoration treatments. This transition matrix model will be directly incorporated into a decision-making tool that managers can use to evaluate how different management alternatives meet their fundamental objectives.

Alternatives that are practical to implement, likely to influence seedling performance, and will impose varying cost include: limiting mammal herbivory, limiting understory plant competition, and planting in created or existing canopy gaps. Our transition matrix model projects seedling growth and survival rates for manipulations of each of these factors (i.e. management alternatives), ultimately providing probability of achieving a specified height (1.5m, 2m, and 2.5m) at each year up to five years. We parameterized our model from results of an experimental planting study conducted on St. Simons Island (Thyroff, 2018). Chapter 2 of Thyroff (2018) explored the effects of deer herbivory and understory vegetation suppression intensity on growth and survival of live oak seedlings planted in a clearcut or in full sun. Chapter 3 of Thyroff (2018) observed the effect of different overstory treatments on growth and survival of seedlings that were protected from deer browse.

Because all combinations of herbivory protection, understory vegetation suppression, and overstory removal were not manipulated in the Thyroff (2018) work, we used marginal data summaries from that study to parameterize a pair of models: a linear-logit model of survival and a linear model of height growth. The height growth model included main effects of the three management treatments, the three 2-way interactions among treatment effects, and a variance term for an individual random effect (8 parameters). The survival model contained the same terms except the 2-way interactions (5 parameters). Given an array of values for the full set of 13 parameters, we used the models in sequence to simulate survival and height growth of a group of seedlings over time. Our models produced the expected number of survivors and their average height at any arbitrary point in time.

Using the pair of models, we conducted a search to find the array of parameter values that minimized the sum of squared differences between a set of marginal means of height from the Thyroff (2018) study (Table 3.3) and the corresponding summaries from simulated individuals. We defined as solution “fitness” the negative value of this criterion, and we used the GA package in R (Scrucca, 2013) to implement a genetic algorithm to maximize the fitness function (i.e., to minimize the sum of squared differences). This package is a stochastic search algorithm that simulates the evolution of a population of artificial chromosomes. Each chromosome codes for a potential solution and is associated with a value of fitness, and the algorithm mimics genetic recombination and biological mechanisms of evolution to find one or more chromosomes (solutions) with high fitness after many simulated generations (Scrucca, 2013). We assumed real-valued data where linear model effects represent real numbers, a chromosome population size of 100, and 1000 evolutionary steps (generations). We also specified relevant design information from the Thyroff (2018) studies, which would pass through the fitness function. Information included initial seedling height at planting (0.47m), number of seedlings per treatment group (80 in each of 8 groups, which represent combinations of overstory condition, herbivory protection, and competition vegetation control), and time period of observation (9 or 23 months, depending on study component; Table 3.3). To judge whether solutions provided by the genetic algorithm were within reasonable numerical bounds, we performed simple arithmetic operations on the marginal means reported in Thyroff (2018) to approximate the model quantities we would expect to see (Table 3.4).

Table 3.3. Model parameters that were used as optimization targets within the genetic algorithm package.

Model parameter	**Study from Thyroff (2018)**	**Optimization target (cm)**
Clearcut, BA=0m^2/ha, height of seedling after 9 months	Chapter 3: Overstory BA vs vegetation competition, excluding deer	48.37
No thin (full canopy), BA=33.9m^2/ha, height of seedling after 9 months	Chapter 3: Overstory BA vs vegetation competition, excluding deer	30.34
Fenced, annual vegetation removal, height after 23 months	Chapter 2: browsing treatment vs vegetation competition control	119.80
Fenced, no vegetation removal, height after 23 months	Chapter 2: browsing treatment vs vegetation competition control	92.28
Not fenced, annual vegetation removal, height after 23 months	Chapter 2: browsing treatment vs vegetation competition control	37.58
Not fenced, no vegetation removal, height after 23 months	Chapter 2: browsing treatment vs vegetation competition control	40.60

Table 3.4. Model parameters optimized that best replicate data summaries in Thyroff (2018) and their corresponding naïve values derived from manipulation of the reported marginal means.

Model parameter category	**Specific model parameter to be optimized**	**Naïve estimates**	**Optimization solution**
Mean rates under ideal condition (no overstory, no browse, no competition)	Mean probability of annual survival	0.780	0.974
	Mean height growth (m)/year, conditional on survival	0.380	0.363

Additive effects (logit scale) of treatments on annual survival, relative to ideal conditions	Effect of dense overstory	-0.670	-0.475
	Effect of herbivory	0	-0.541
	Effect of competing understory vegetation	0	-0.461
Additive effects of treatments, relative to ideal, on annual height growth rate (m/year)	Effect of dense overstory	-0.520	-0.566
	Effect of herbivory	-0.421	-0.698
	Effect of competing vegetation	-0.278	-0.229
2-way interactive effects of treatments on annual height growth rate	Overstory x herbivory	*	-0.033
	Overstory x competing vegetation	0.240	-0.162
	Herbivory x competing vegetation	0.270	0.182
Individual variation (normal standard deviation)	Annual survival (logit scale)	*	0.454
	Height (m)	*	0.311

* not estimable from results provided in Thyroff (2018)

The genetic algorithm produced a solution (Table 3.4) that achieved a maximum fitness value of -0.046 (sum of squared differences between target and simulated means = 0.046). The values in the solution were generally in agreement with corresponding quantities derived naively from the marginal means (Table 3.4). Model code for this optimization tool is presented in Appendix A.1.

We used the optimized linear models to estimate the probability of a seedling achieving thresholds of height at each of 1, 2, …, 5 years post-planting under each of eight treatment combinations. We used height thresholds of 1.5m, 2m, and 2.5m, provided by stakeholders, to represent alternative above-browse heights. From a group of *n* seedlings planted (and assuming seedling height of 0.47m at planting), we computed the proportion achieving each of the height thresholds under each treatment combination at each year of the simulation. For purposes of the decision support model, we retained estimated probabilities of achieving a height threshold of 1.5m at the 5-year time horizon. Model code for the simulation is shown in Appendix A.2.

We then sought to compute EU-wise success probability (i.e., that at least one seedling in the EU would succeed) by considering that fates of seedlings in an EU may not be independent. Assuming independence among n seedlings planted in the EU (assumed = 81, maximum of seedlings planted/EU), and given the probability p of achieving 1.5m sapling height in a given time period, then the binomial model yields the probability Y of an EU producing at least one sapling in the time period: $Y = 1 – (1-p)^n$. However, more likely, the fates of individual seedlings are not independent, so we also considered a beta-binomial model to portray overdispersion of counts of surviving seedlings. With $\varphi > 0$ representing the intraclass correlation among seedling fate ($\varphi = 0$ for independent fates), we used the model $Y = 1 – \mathrm{Beta}(\alpha, n+\beta)/\mathrm{Beta}(\alpha, \beta)$, where $\alpha = p\,(1-p-\varphi+p\varphi) / (\varphi(1-p))$ and $\beta = (1-p-\varphi-p\varphi) / \varphi$ (Kim & Lee, 2017). As φ increases, the probability of at least 1 of n seedlings surviving to the sapling stage in the time period approaches p, regardless of n. The seedling model and its predicted correlation with other planted seedlings are directly incorporated into our decision support tool.

2.3.2.2 Sapling survival estimates

Because there is little empirical data on planting live oak saplings in a Southern maritime live oak forest, we elicited stakeholder knowledge to obtain survival estimates. We interviewed a few coastal land managers, nurserymen, and restoration professionals, synthesizing and combining their knowledge. These stakeholders emphasized that light and water availability would be the main deterrents to sapling survival as saplings are past browse height and will not heavily compete with understory vegetation; however, they require additional maintenance via irrigation. Larger trees require greater volumes of water for transpiration and metabolism and take a longer time after transplanting to establish healthy extensive root systems to harvest sufficient water from surrounding soil. Thus supplemental watering reduces damage or death due to water stress. (Fernández et al., 2016; Pecknold, 2022). Therefore, we obtained sapling stock (larger vs smaller sapling sizes) survival predictions for different overstory canopy and watering conditions after the first, second, and fifth year post-planting. Survivorship for each sapling stock-light availability scenario is presented in a graph in Appendix A.3.

2.3.3 Cost estimates

After the second workshop, we interviewed stakeholders from Jekyll and Sapelo Islands to elicit cost estimates for each management alternative. Costs were estimated by EU (18m x 18m) but could be scaled up when considering multiple EUs to reduce cost of some bulk items. Cost of specific materials not confirmed by stakeholders were found through commercial vendors (Forestry Suppliers, The Home Depot). All cost estimates are presented in Appendix A.4.

2.3.4 Utility function

Utility functions map the attributes of the fundamental objectives – here, costs of actions and probabilities of sapling establishment (i.e. at least 1 planted seedling entering the sapling stage after five years or a planted sapling surviving one year post-planting) – to stakeholder satisfaction or contentment with outcomes (Ferguson et al., 2015). We measured utility on a 0-10 scale, 0 as the least content and 10 as the most content for an action given a probability of achieving tree response at a given cost per unit. After finalizing cost per management alternative, we elicited utility values from key stakeholders using scenario-planning techniques. For varying costs, we asked stakeholders to report their anticipated level of satisfaction with achieving at least one surviving sapling for each establishment unit. We also requested utility values for specified probability-cost combinations according to different site contexts. Both Jekyll and Sapelo Island managers have expressed interest planting in both publicly visible and more remote locations. We then created a utility function for each stakeholder and an aggregate utility function for all stakeholders in R, fitting elicited values to a predictive polynomial regression in cost and success probability and projecting the regression surfaces onto contour plots. The most preferred management alternative among a set of candidate alternatives was the combination of live oak treatments yielding greatest expected utility.

2.3.5 Evaluating uncertainty

Within our seedling simulation model and elicited sapling survival parameters, there are three primary areas of uncertainty: stochasticity in seedling performance, correlation of seedling fate, and sapling estimates. Stochasticity in seedling performance refers to the fact that seedling fate is a stochastic outcome, even if treatment conditions do not vary. Low versus high correlation of seedling fate affects the probability of ≥1 seedlings successfully reaching the sapling stage. We also addressed uncertainty in sapling survival expressed by stakeholders who provided estimates of these quantities.

To evaluate the uncertainty due to stochasticity in seedling performance, we extracted the probability of a seedling entering the sapling stage after 5 years for each combination of treatments on seedlings. Our main objective was to identify when a change in this model output would change the most preferred management alternative when planting seedlings. As annual survivorship was relatively similar for all treatments, we used the 2.5 percentile (25th highest growth increment) and 97.5 percentile (975th highest growth increment) out of 1000 seedlings per treatment group to evaluate whether a change in average height growth would alter the probability of seedlings reaching the sapling stage after 5 years. We altered this value under ideal conditions (i.e. open canopy, protected from deer, and no understory vegetation competition) using these percentiles, which the model then incorporated additive effects of treatments on annual height growth rate (m/year), relative to the ideal.

Regarding correlation of seedling fate, we noted the difference in the probability of ≥1 planted seedlings reaching browse height for each treatment combination by assuming varying values of the intraclass correlation coefficient (φ) within the beta-binomial model. We had initially assumed φ=0.3 as a likely estimate of correlation of tree seedling fate. Therefore, we compared the probabilities of ≥1 planted seedlings successfully reaching the sapling stage assuming φ=0.3 against assumptions of higher fate dependence (φ=0.8) (Yao et al., 2016) and full independence (φ=0). The former represents the "worst-case" scenario while latter represents our "best-case" scenario.

We also obtained the "worst-case" and "best-case" scenario estimates for sapling survival. As we interviewed our stakeholders, we asked for a "most likely", "highest realistic", and "lowest realistic" survival rate for each sapling stock-overstory canopy combination. Survivorship for all scenarios and treatment combinations are presented in Appendix A.3.

To note whether an increase or decrease in stochasticity in seedling performance, correlation of seedling fate, and sapling survival estimates changed the most preferred management alterative, we created eight scenarios (Table 3.5) that could help us identify areas of uncertainty that most influenced decision-making.

Table 3.5. Eight scenarios used to determine whether uncertainty with seedling simulation, seedling correlation, or sapling survival estimates altered the most preferred management alternative.

Scenario	**Performance stochasticity**		**Seedling correlation**		**Sapling survival**	
	High	**Low**	**High**	**Low**	**High**	**Low**
1	√		√		√	
2	√		√			√
3	√			√	√	
4	√			√		√
5		√	√		√	
6		√	√			√
7		√		√	√	
8		√		√		√

3 Results

3.1 Decision support tool

The decision support tool was designed to accommodate different management scenarios selected by stakeholders. We used Excel and incorporated R code to create an interface through which stakeholders can clearly see the decisions to be made as well as trade-offs associated with those decisions. There are 16 management alternatives that affect ecological outcomes, each alternative associated with four parts of a single decision action that land managers and coastal stewards will face during the decision-making process when planting juvenile live oaks (Table 3.6). The action taken at a planting site for one site context (i.e. publicly visible vs remote or within MLO forest vs not within MLO forest) reflects a combination of nested sub-actions with respect to overstory removal, type of planting stock, browse protection, and understory vegetation suppression/removal (Table 3.6). Individual sub-actions may be conditional on other sub-actions taken (i.e., the choice to plant saplings will remove choices about browse protection), and each one is associated with further detail such as number of seedlings planted and sapling water intensity. Each sub-component of the decision (e.g., overstory removal) induces a resulting state (increased light to forest floor), and their combined effects are linked to an expected outcome through an appropriate model (the seedling growth model or the sapling survival model). Costs of alternatives vary depending on the suite of sub-actions taken, and they also vary by island due to differences in management conventions and availability of personnel and material resources. Because cost minimization is one of the fundamental objectives of the decision, specification of costs aids stakeholders in evaluating trade-offs among alternative actions.

Table 3.6. 16 management alternatives comprised of four decision points that drive ecological outcomes.

Alternative	Overstory (open, closed)	Stock type (3 types)	Browse protection (Y/N)	Vegetation control (3 options)
A	Open	100-gallon sapling	-	-
B	Open	15-gallon sapling	-	-
C	Closed	100-gallon sapling	-	-
D	Closed	15-gallon sapling	-	-
E	Closed	Seedlings	No	None
F	Closed	Seedlings	No	Once
G	Closed	Seedlings	No	Recurrent
H	Closed	Seedlings	Yes	None
I	Closed	Seedlings	Yes	Once
J	Closed	Seedlings	Yes	Recurrent
K	Open	Seedlings	No	None
L	Open	Seedlings	No	Once
M	Open	Seedlings	No	Recurrent
N	Open	Seedlings	Yes	None
O	Open	Seedlings	Yes	Once
P	Open	Seedlings	Yes	Recurrent

Although sub-actions are executed simultaneously as parts of a single action, stakeholders will select these sub-actions and other relevant details in a specific order within the decision support tool according to the descending order of decision points presented in Table 3.7. This is to ensure ease of use and tool simplification. The four parts that comprise each management alternative in Table 3.6 are the only decision points that determine ecological outcomes (marked as '*' in Table 3.7). Other decision points only influence cost. First, managers will evaluate the current overstory state to determine if there is enough light availability to support live oak growth, which was listed as the fourth most-cited ecological concern about live oak regeneration in the first workshop (Table 3.1). Creating canopy gaps has proven to be an effective practice for many forest managers when planting tree seedlings (Vilhar et al., 2015). Because Jekyll Island managers have expressed interest in creating canopy gaps for the potential of improving live oak seedling growth and survival, the decision tool includes this management alternative (light availability/gap creation).

Table 3.7. Decision points that will be chosen by stakeholders in the decision support tool. The four main parts of a single decision action that influence ecological outcomes (*) include: overstory treatment, live oak stock, browse protection, and understory vegetation control. Other decision points only influence cost.

Decision Point	Choice Type	Decision point choice could alter:
Number of establishment units (EU)	Number entered	Total cost for all EUs
Overstory treatment*	(A) No overstory treatment or (B-F) options of single-tree overstory treatment x # trees removed	Cost for all EUs; overstory canopy condition, which could influence live oak performance
Live oak stock*	(A) 100-gallon sapling, (B) 15-gallon sapling, (C) Seedlings (number entered)	Other decision points available, cost per EU
Watering method (saplings only)	(A) Water buffalo (portable tank) (B) Gravity-fed pump	Cost per EU

	Optional: planting gel	
Labor for planting	Number entered for each labor type (staff vs volunteer)	Cost per EU
Browse protection* (seedlings only)	Yes or no	Seedling performance
Caging material	(A-C) Different material options	Cost per EU
Understory vegetation control* (seedlings only)	(A) None (B) herbicide one time (C) herbicide one time, continued treatment via manual removal	Seedling performance, cost per EU
Labor for vegetation control	Number entered for each labor type (staff vs volunteer)	Cost per EU

Stakeholders will also decide whether to plant live oak seedlings or saplings. Planted seedlings will require a different type of maintenance during and after planting than saplings. Saplings will not require browsing or competing understory vegetation treatments because they have already reached above-browse height (1.5m) and are not shaded by neighboring understory plants. However, saplings require additional irrigation to reduce the risk of mortality from water stress. Because stakeholders have expressed interest in planting saplings of different ages/sizes to accommodate for cost and site-specific limitations, stakeholders will also have the option to plant one larger sapling (100 gallons) or one smaller sapling (15 gallons) per establishment unit. In the evaluation of consequences and trade-offs, the decision model links each live oak stock decision alternative to the appropriate demographic model (i.e. seedling or sapling) to inform the fundamental objective of survival to (from a planted seedling) or beyond (from a planted sapling) the sapling stage at the scale of the EU.

For the seedling planting alternative, subsequent sub-actions include whether to protect live oak seedlings from mammal herbivory and whether to treat understory vegetation based on an assessment of competing understory vegetation status. Choosing to protect live oak seedlings or suppress understory vegetation incurs more cost to stakeholders, but not choosing to do so may lessen live oak seedling growth and survival, as mentioned as a top concern for live oak regeneration by all stakeholders in the first workshop (Table 3.1). Within the understory vegetation suppression sub-action, stakeholders will also decide the level of suppression. Stakeholders may opt to choose one-time treatment of herbicide application or recurrent control, which includes one-time herbicide application and annual manual removal of understory vegetation.

3.2 Most effective management alternative

After running each seedling and sapling model individually, we found the most effective or optimal management alternative for 1) planting a sapling and 2) planting a seedling. Here, “most effective” is defined as the scenario that results in the highest probability of sapling survival after one year or the highest probability of a seedling entering the sapling (1.5m) stage after five years.

(1) Both the 100-gallon and 15-gallon sapling planted in partial sun to full shade were estimated to have 90% survival during the first year. Therefore, we also assessed survival rates 5 years post-planting. The strategy that resulted in the highest survival (87%) when planting a sapling is the planting of a smaller sapling (15-gallon) in partial sun to full shade. Planting a larger sapling in partial sun to full shade will most likely result in 85% survival, planting a smaller sapling in full sun will most likely result in 83% survival, and planting a smaller sapling in full sun will most likely result in 80% survival.

(2) For seedlings, the management alternative that resulted in the highest probability of at least one seedling entering the sapling stage after five years includes sub-actions of browse protection and suppressing understory vegetation recurrently. This strategy also assumes an open

canopy and a slight correlation of survival fates among planted seedlings (φ=0.3) within the EU. After five years, for a single EU with 81 seedlings, the probability that at least one seedling reaching above-browse height (1.5m) is 54%.

Ultimately, the most effective management alternative that results in at least one surviving sapling per EU one year post-planting is the planting of a smaller sapling in partial sun to full shade.

3.3 Most desirable management alternative

Figure 3.3 presents management alternatives that are less than $2000 and higher in utility, which include those of lower labor costs and limited to no overstory canopy removal. Appendix A.5 reports the entire range of cost, including varying overstory canopy treatment, for each management alternative. Management alternatives are labeled according to Table 3.5.

The most desirable management alternative is dependent on which live oak treatment meets the optimum utility value for each island (Jekyll and Sapelo). For both islands, the most desirable management alternative, regardless of site-specific costs differences (i.e. public location vs. remote location and canopy openness) is planting a 15-gallon sapling in partial sun to full shade (Figure 3.3, Appendix A.5). This sapling will most likely survive after one year post-planting (90%) and five years post-planting (87%). Although our main objective was for at least one seedling within an establishment unit to reach sapling height five years post-planting or one sapling to survive one year post-planting, all sapling stock-canopy condition combinations resulted in the same survival for the first year. Therefore, we used the five years post-planting estimate to compare sapling planting strategies. All seedling treatment combinations resulted in less than 54% probability of at least one seedling within an EU reaching sapling height (Figure 3.3, Appendix A.5).

The most desirable alternative, planting a 15-gallon sapling, is consistent regardless of cost of labor. When volunteers are enlisted, the minimum cost for this alternative is $205.48. However, even if no volunteers are enlisted, and island managers utilize solely paid staff members to plant saplings, the preferred management alternative does not change.

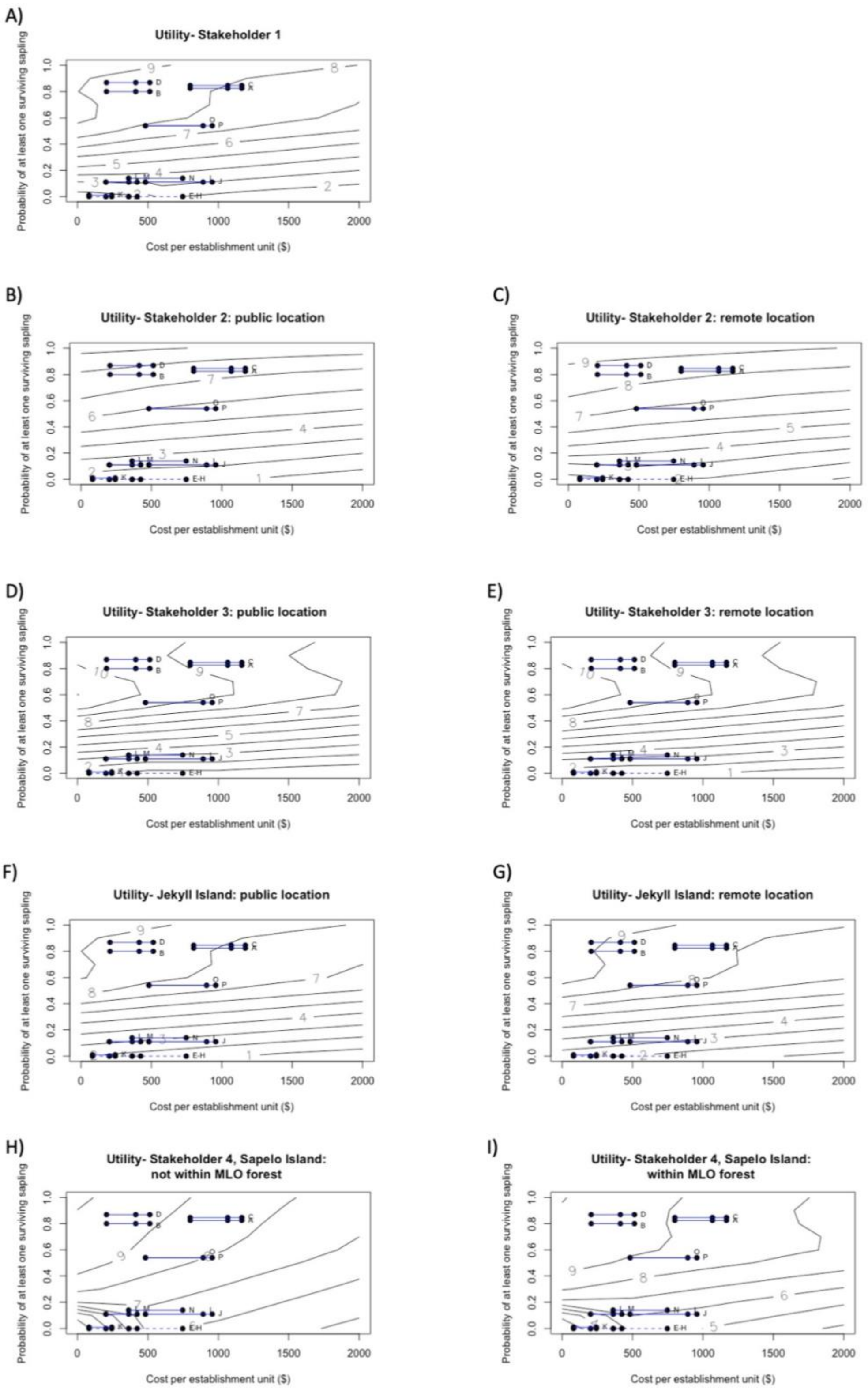


Figure 3.3. Management alternatives on utility contours for each individual stakeholder and island. Alternatives are labeled according to scenarios A-P in Table 3.6, and each line segment corresponds to the range of cost estimates possible for a single management alternative (i.e.

minimum and maximum cost of labor, no overstory canopy removal cost is assumed). Utility contours for full minimum and maximum costs, including overstory canopy removal, are presented in Appendix A.5. **A-E:** Contour plots that contain utility information for each individual stakeholder interviewed from Jekyll Island. Pairings of B-C and D-E show utility values for the same stakeholder but at sites that have different public visibility. **F-G:** Aggregated contour plots that contain utility information for all stakeholders from Jekyll Island. This pairing demonstrates utility values for the same island but at sites that have different public visibility. **H-I:** Contour plots that contain utility information for one stakeholder interviewed from Sapelo Island. This pairing demonstrates the utility values for the same person but at sites that represent different MLO habitat value.

3.4 Evaluating uncertainty

We assessed whether stochastic uncertainty in seedling fate, uncertainty in seedling fate correlation, and uncertainty in sapling survival would affect the most desirable management alternative using the 8 combinations presented in Table 3.5.

Initially, the most desirable management alternative for any site visibility or accessibility on both islands was planting a 15-gallon sapling in partial sun to full shade. Regardless of the 8 combinations, the most desirable management alternative does not change. However, higher predictions of seedling height growth significantly improved treatment combinations, especially when planting in an open canopy, with browse protection, and while suppressing understory vegetation. High seedling performance and high correlation among seedlings (φ=0.8) resulted in a higher probability (83%) of at least one seedling entering the sapling stage after five years post-planting. High seedling performance and low correlation among seedlings (φ=0) resulted in an even higher probability (87%), which is comparable to the lowest estimate of the 15-gallon sapling survival when planted in partial sun to full shade (90%). However, this seedling management alternative is still more costly and retains a lower utility compared to the sapling alternative (Appendix A.5).

4 Discussion

4.1 Applying SDM in a data deficient system

Extensive knowledge gaps and uncertainty in information is often a barrier to restoration success (Cortina-Segarra et al., 2021), often stalling the decision-making process as there are disagreements about priorities and optimal management actions (O'Donnell et al., 2017). However, the recent upturn in incorporating stakeholder' direct experience and expertise into ecological models (Kuhnert et al., 2010; Reed, 2008) paves a way for scientists, land managers, and other collaborators to explore management options when there is deficient data.

Little is known about the complexities of southeastern MLO forest dynamics. However, instead of allowing scarce data and uncertainty to impede our progress in supporting MLO forest restoration, we harnessed stakeholder and expert knowledge and values within our live oak demographic models and through other steps of the SDM process. We began structuring our decision support tool by first evaluating the wealth of experiential ecological knowledge stakeholders hold about their MLO forests. Island managers and other coastal stewards identified multiple salient concerns about the MLO forest ecosystem, which provided a diverse and complementary knowledge base from which to begin understanding MLO forest ecology and live oak life history. We also identified fundamental objectives and designed a suite of live oak planting treatments as management alternatives. We then created live oak demographic models using both empirical data and expert opinion, incorporating their ecological outcomes and stakeholder priorities and costs of different live oak treatments directly into the decision support tool. Ultimately, we synthesized and combined different sources of information to both begin understanding MLO forest ecology and help with decision support for barrier island managers along the Georgia coast interested in MLO forest restoration.

Many other studies have also informed ecological models (King & Franz, 2016) and decision-making frameworks (Ogden & Innes, 2009) using expert opinion when there are extensive knowledge gaps, often combining that information with available empirical and field data (Cohen et al., 2016; Moore & Conroy, 2006; O'Donnell et al., 2017; Robinson et al., 2016b). While supplementing limited data with expert judgements during the decision-making process may prove internally inconsistent or reflect partial pieces of information (Czembor & Vesk, 2009), there are multiple ways to address this uncertainty. Conducting sensitivity analyses can help determine which ecological model variables or parameters and functions respond to changes in other parameter perturbations (Barabás et al., 2014). These analyses can help evaluate model robustness (Barabás et al., 2014), note limitations of the result and the dependence of the optimal outcome on model variables and stochastic factors (Chu-Agor et al., 2012; Conroy & Peterson, 2013), and help prioritize data collection and research (Biek et al., 2002; Chu-Agor et al., 2012). To begin assessing the sensitivity of the decision support tool, we evaluated the effect of uncertainty in empirically-derived seedling growth and survival rates and expert-elicited sapling survival rates, and found that plausible best-case and worst-case scenarios did not affect the most preferred management alternative. This suggests the decision recommendations for Jekyll and Sapelo are not dependent on these sources of large uncertainty.

4.2 Call for an adaptive management strategy: limitations and recommendations for the future

Although identification of the most desirable management alternative was seemingly robust to uncertainties within our ecological models, we emphasize that we evaluated management alternatives for the planting of seedlings based on short-term data and not long-term estimates of live oak survival and growth, which could misinform decision-making. For each live oak treatment combination, we simulated 5-year survival and growth estimates based on a 2-year study, and sapling estimates were solely informed by expert opinion. There is still little known about the stage-specific growth and survival rates of live oaks or the community-level dynamics of MLO forests. While we and others have conducted some field studies on live oak seedlings, there is inadequate formal scientific knowledge to construct reliable demographic models and make sound management decisions using this one iteration of SDM. Effects of different treatments on live oak seedling growth and survival are uncertain, especially those regarding seedling correlation and survival rates in the long-term. Although we found that some of the richest sources of knowledge rest with island managers, environmental stewards, and ecological consultants, efforts to reduce uncertainty need to be implemented.

We suggest applying an adaptive management strategy to better inform actions being undertaken to restore MLO forests through the actions themselves. Rapid SDM prototyping has proven effective in identifying areas of uncertainty (Blomquist et al., 2010; Moore et al., 2011; Neckles et al., 2015) and addressing those concerns in another iteration. Neckles et al. (2015) developed their first prototype decision framework during a week-long workshop. Results then guided preliminary monitoring of salt marshes, which later informed future workshops, refined predictive models, and evaluated trade-offs in the second prototype (Neckles et al., 2015). Continued monitoring several years post-planting and field research on the effects of a wider variety of treatments on live oak seedling and sapling growth and survival should provide more accurate estimates and reduce uncertainty in decision-making. Furthermore, incorporating other main ecological factors cited as highly influential to live oak regeneration including fire and salt stress (Table 3.1) in future research could better improve our understanding of MLO forest ecology and meet island- and site-specific ecological concerns. Fire is a keystone process that could benefit live oak seedlings by creating fluctuations in resource availability, and preventing competitive exclusion (Kerns & Day, 2017), but intense fire has also increasingly been observed as a main factor influencing mature live oak mortality on many barrier islands (Helm et al., 1991). Noting how tolerant and resistant live oaks are to fire at different life history stages will help inform restoration efforts. As MLO forests are often experiencing hurricane and storms that fell or damage adult trees, saltwater intrusion, salt spray, and increased bouts of drought (Bellis, 1995; Conner et al., 2005; Helm et al., 1991; Jones et al., 2013), it is imperative that future research explore the complexities of stochastic events and soil-water-plant dynamics on live oak regeneration.

Using SDM as an iterative process can also better refine fundamental objectives and identify the suite of MLO forest restoration alternatives available. Most participants during the first workshop were committed to finding management alternatives through active live oak restoration so we continued working with these stakeholders (primarily from Jekyll and Sapelo Islands) during the SDM process. However, the diversity of management objectives for all island managers could be better met through another iteration of SDM. For example, Blomquist et al. (2010) initially incorporated expert opinion and available information during the first iteration of SDM to address how different actions would influence the persistence of an invasive species, *Adeleges tsugae* (hemlock woolly adelgid). They then revised the problem statement and prioritized specific fundamental objectives while treating others as model constraints. Identifying common ecological and social concerns among island managers could not only meet their management objectives while supporting those of Jekyll and Sapelo Island, but could also increase the applicability and relevancy of our decision support tool to multiple coastal stewards along the Georgia coast.

4.3 Application to support decisions on Jekyll and Sapelo Islands

As this report demonstrates one iteration of SDM, the full decision support model is a rapid prototype and could be improved through adaptive management by incorporating additional empirical data and field data from monitoring planted seedlings and saplings. This will allow us to build a better inventory of juvenile live oak performance, hopefully reducing uncertainty when making restoration decisions. Also, as we discuss specific cost estimates and their associated seedling and sapling survival probabilities, we can further refine utility functions to best reflect satisfaction with different management alternatives in terms of meeting the fundamental objectives. Trade-offs will inevitably arise regarding costs associated with creating the most favorable conditions for seedling and sapling success, and our aim is to continue facilitating the stakeholders' use of modeling outputs to find optimal combinations of actions for their budget, risk tolerance, and priorities for certainty and time frames for realizing restoration success.

5 Conclusions

Southeastern maritime live oak forests are experiencing many environmental stresses including climate change, land development, and altered wildlife abundances, many of which may be causing low live oak regeneration. To address this live oak regeneration problem and find potential solutions for restoration, we used the SDM framework to define fundamental objectives and identify management alternatives. We assess consequences to specific management actions by constructing ecological models using available empirical data and eliciting juvenile live oak survival estimates. Finally, we explored optimizations between actions and different management objectives by obtaining cost estimates and considering model outputs to evaluate trade-offs.

We found a few management strategies that would both be cost-effective and result in the highest seedling or sapling survival. However, there is still uncertainty regarding the accuracy of estimates used to predict the effect of treatments on juvenile live oaks, so we encourage adopting an adaptive management strategy by continuing to synthesize available empirical data and to collect field data, and incorporating parameters into the ecological models used to inform the decision support tool. Our ongoing commitment to supporting restoration decision-making on Jekyll Island, Sapelo Island, and other barrier islands includes updating our models with emerging research findings, technical advice on logistics and methods for sourcing, and developing monitoring plans for restoration actions. Specifically, both Jekyll and Sapelo have exceptional capacity to use adaptive management to accelerate restoration success, and we look forward to further addressing management needs in this poorly understood forest ecosystem.

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CHAPTER 4

INFLUENCE OF DEER BROWSING ON INVASIVE AND NATIVE VEGETATION ON A GEORGIA BARRIER ISLAND[5]

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[2] Benson, D.L. and E.G. King. To be submitted to *Natural Areas Journal*.

Abstract

The camphor tree (*Cinnamomum camphora*) was introduced from Asia to the subtropical portions of the southeastern United States more than 100 years ago and is naturalized in many areas. In recent decades, however, it has become increasingly abundant in maritime forests on Jekyll Island, an Atlantic Ocean barrier island in Georgia. Native white-tailed deer (*Odocoileus virginianus*) populations have also increased during this period. We sought to experimentally explore whether deer herbivory may be limiting native understory vegetation cover and abundance of native hardwood tree seedlings, and whether camphor seedlings in turn increase in abundance and growth due to competitive release. In April 2018, within a 10ha forest stand with heavy camphor proliferation, we established 22 6m x 6m plots, of which 11 were fenced to exclude deer and 11 were not. At the initialization of the experiment, we counted, tagged, and measured height of each camphor seedling. We also recorded total understory vegetation cover, cover by species, and abundance of hardwood tree seedlings. Plots were re-measured in July 2018, September 2018, May 2019, and May 2020, also tagging and measuring newly emerged camphor seedlings at each census.

Deer exclusion was associated with increased native understory vegetation cover but did not have an immediate effect on the abundance of native tree seedlings or species richness. Vine species, especially *Vitis rotundifolia,* benefitted from excluding deer, yet camphor seedling growth and survival also increased when deer were excluded. Although longer-term herbivory effects on camphor versus native species in this environment are not yet known, these results suggest that controlling deer herbivory may not tip the balance of apparent competition balance back toward native vegetation, and other restoration efforts are likely needed to control camphor invasion and support the native tree and plant community.

1. Introduction

Rapid and ongoing environmental change and additional anthropogenic stress including climate change, altered land use, and introduced species can severely alter native tree and plant abundance and community structure and dynamics in many forest ecosystems. Two common environmental stressors of major concern in many forests in the eastern United States are intense herbivory by white-tailed deer (*Odocoileus virginianus*) and introduction of invasive plant species. Both of these stressors pose a threat to native plant and tree communities, and without management action, they can alter ecological functions, native plant abundance, composition and structure, and biodiversity (Averill et al., 2018).

In many forests throughout eastern North America, dense populations of white-tailed deer have caused major ecological change, affecting native plant communities directly through biomass loss and plant and tree mortality (Thyroff et al., 2019; Woolery & Jacobs, 2011), which can result in a loss of native plant abundance, reduce tree regeneration and plant establishment (Cooper & McCann, 2011; Perrin et al., 2011), and alter community diversity and species richness (Averill et al., 2018; Morrison, 2017; Nishizawa et al., 2016).

One prevalent effect of deer herbivory is its influence on interspecific plant competition and resulting community composition through selective herbivory (Averill et al., 2018). Deer feeding preferences for different plant species and growth forms can ultimately determine the what species can persist and thrive and thus influence successional trajectories (Averill et al., 2018). Some plant species are preferentially browsed by deer because they are more abundant or palatable or have less chemical or physical defenses (Wiegmann & Waller, 2006). Reduced abundance and regeneration of browsed plants can allow other less abundant, non-palatable, or browse-tolerant species to increase in abundance. Many studies have shown that intense deer herbivory can homogenize the native plant community, reduce plant diversity, and allow for less deer tolerant species to persist and dominate (Holmes & Webster, 2011; Kain et al., 2016; Nishizawa et al., 2016; Wiegmann & Waller, 2006).

Invasive plant species are also a growing concern in many forest ecosystems. Invasive plants are non-native or exotic plants that are introduced to a new environment and live outside their native range but have now begun proliferating and displacing native plant species (Society for Ecological Restoration, 2004). Many invasive plants have traits including rapid growth, environmental plasticity, ability to capture resources, and high proliferation and long-distance dispersal mechanisms that allow them to easily colonize and outcompete native plants (Holzmueller & Jose, 2009; McNeish & McEwan, 2016; Mitchell et al., 2006). Once established, invasive plants can threaten native plant abundance and biodiversity by disrupting species interactions, influencing ecosystem processes and functions, and shifting ecosystems to an alternative state where native plant species cannot persist (Prior et al., 2018; Vitousek et al., 2007). Invasive trees and shrubs have increasingly become a major threat to many ecosystems around the world (Dickie et al., 2014). In comparison to short-lived herbaceous invaders, invasive trees and shrubs differ in that they are slower-growing, long-lived, and large (van Wilgen & Richardson, 2014), and tend to rely on prolific seed production and dispersal, escape from pathogens and herbivores in their home range, and strong competitive traits to dominate in new environments (Rejmánek, 2014). Although they may prove easier to control because of their visibility, they are notoriously difficult to eradicate, and reducing their spread becomes increasingly more expensive compared to other invasive plants because of their size (van Wilgen & Richardson, 2014).

A range of studies have assessed the role of deer herbivory in mediating the interactions between invasive species and native plant communities (Averill et al., 2016). Some studies indicate that deer can facilitate invasive success of exotic trees by consuming or causing stress to native competitors. Many exotic plants that become invasive have an upper hand over native plants because they are better adapted to soil disturbances from deer trampling, their propagules are more easily transported by ungulates, or they are not as palatable as native tree and plant species, which could release exotic trees from competition (Nuñez et al., 2008; Vavra et al., 2007). Other studies have observed little to no effect of deer herbivory on invasion success. Inconsistencies in the interaction between deer herbivory and invasive trees are common because the effects are dependent on the level of biological organization observed (i.e. individual species, functional group, diversity), duration of study, and species tolerance to deer browse (Christopher et al., 2014; Wright et al., 2019).

Jekyll Island, GA is a state park that conserves about 65% of the island as natural areas while also supporting tourism amenities and a residential community. It contains roughly 650ha of maritime forests (Jekyll Island Authority, 2020). Jekyll Island managers (Jekyll Island Authority or JIA) are concerned about how environmental stresses like white-tailed deer herbivory and invasive plant species can alter the state of their small forests. Of growing concern Jekyll Island is camphor (*Cinnamomum camphora*), an Asian evergreen tree that was once introduced to the southeastern United States more than 100 years ago for horticulture. It is naturalized on Jekyll Island, but in recent decades, it has begun to proliferate extensively on a few areas on the island. Fast-growing and with prolific seed production, camphor may out-compete native plant species and its establishment raises concerns about native plant composition and biodiversity (Schenk, 2009). However, little is known about the effects of camphor on native plant communities especially with the added pressure of deer herbivory.

JIA is pursuing active restoration to preserve their native plant communities. The JIA conservation team began treating mature and juvenile camphor trees with herbicide in 2016 and 2017. However, camphor seedlings continue to emerge, which raises concerns about how to keep camphor under control and preserve the native plant population, especially when native plants and tree seedlings are also facing another stress with deer herbivory. It is possible that the suppression of native vegetation by deer is allowing camphor to proliferate. However, little is known about southeastern maritime forest ecology and dynamics and how restoration strategies like excluding deer could alter native plant community composition and structure. Therefore, to help JIA conservation staff manage the area for invasive control and native plant diversity restoration, we explored whether deer herbivory is affecting camphor seedling regeneration, native understory plant abundance, biodiversity, and abundance and diversity of different plant growth forms. We conducted a two-year deer exclosure experiment to assess effects of deer exclusion on native understory vegetation abundance, native hardwood tree seedling abundance, and camphor seedling survival and growth. We hypothesized that deer exclusion will result in increased native plant and tree seedling abundance. We also predicted that deer herbivory may improve camphor performance by suppressing other native tree and plant species and releasing the exotic tree from competition.

2. Methods

2.1 Study site

This study was conducted on Jekyll Island, one of the southernmost barrier islands in Georgia. The site is a 10ha mixed oak-pine hammock (N 31.05484367, W 81.41614811) located south of the Jekyll Island Golf Course and is isolated by two paved roads, an unpaved walking trail, and a coastal marsh (Figure 4.1). Soils consist of mandarin fine soil at 0-5% slope (Natural Resources Conservation Service, n.d.). Adult tree composition is dominated by *Pinus* (pine) species, *Quercus virginiana* (live oak), *Quercus hemisphaerica* (laurel oak), *Liquidambar styraciflua* (sweetgum), and *Magnolia grandiflora* (Southern magnolia). The site's herbaceous and shrub layer is dominated by dense saw palmetto (*Seneroa repens*) that nearly excludes other plant species. However, there are distinct clearings without saw palmetto throughout the site, each about 3-12m across, that contain little native plant and shrub vegetation. Each clearing contains evidence of deer utilization.

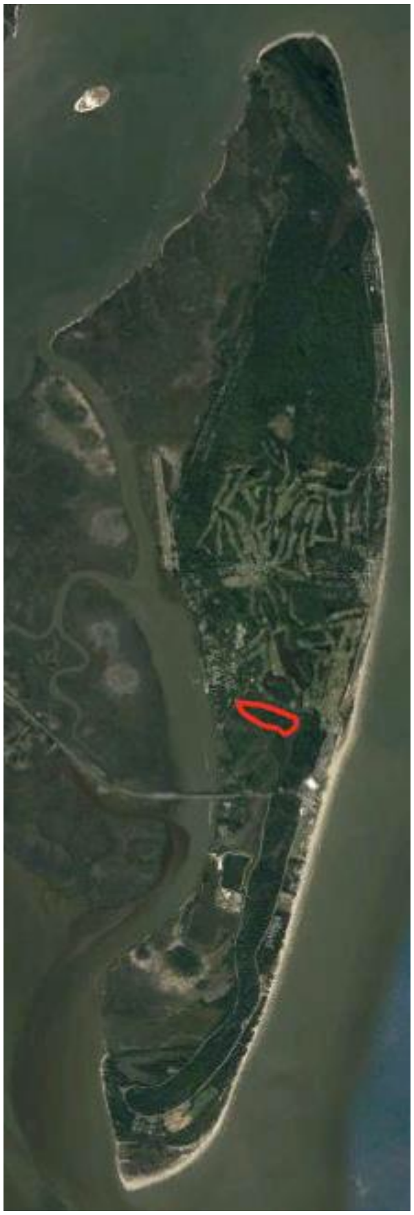

Figure 4.1. Study site is a 10ha mixed oak-pine forest on Jekyll Island, Georgia (*Google Earth Pro 7.3.4.8248*, n.d.).

2.2 Experimental design

In March 2018, we surveyed the entire site by walking parallel linear transects 5m apart to identify clearings in the saw palmetto that were greater than 6m x 6m in size and contained less than 5% saw palmetto cover. We found 32 clearings met these criteria. Each clearing had camphor seedlings present and evidence of either an adult or sapling. The clearings contained less than 15% shrub and herbaceous vegetation cover and contained plant species typical of a maritime forest including *Pteridium aquilinum* (bracken fern) and *Vitis rotundifolia* (muscadine grape). Each clearing had similar canopy composition typical of a maritime forest including *Quercus virginiana*, *Q. hemisphaerica*, *Liquidambar styraciflua*, *Magnolia virginiana*, and *Pinus* species.

In April 2018, we randomly selected 22 of the 32 potential clearings as study sites in which to establish plots. At each site, we marked a 6m x 6m area for study plots. We randomly chose 11 sites to build deer exclosure fences (2.5m height, 6m x 6m in size) and 11 sites where deer would have access, as demonstrated in Figure 4.2. Each site (fenced and unfenced) contained a 5m x 5m plot marked by PVC pipes. Each 5m x 5m plot was divided into 25 1m x 1m subplots, marked by row and column as shown in Figure 4.3.

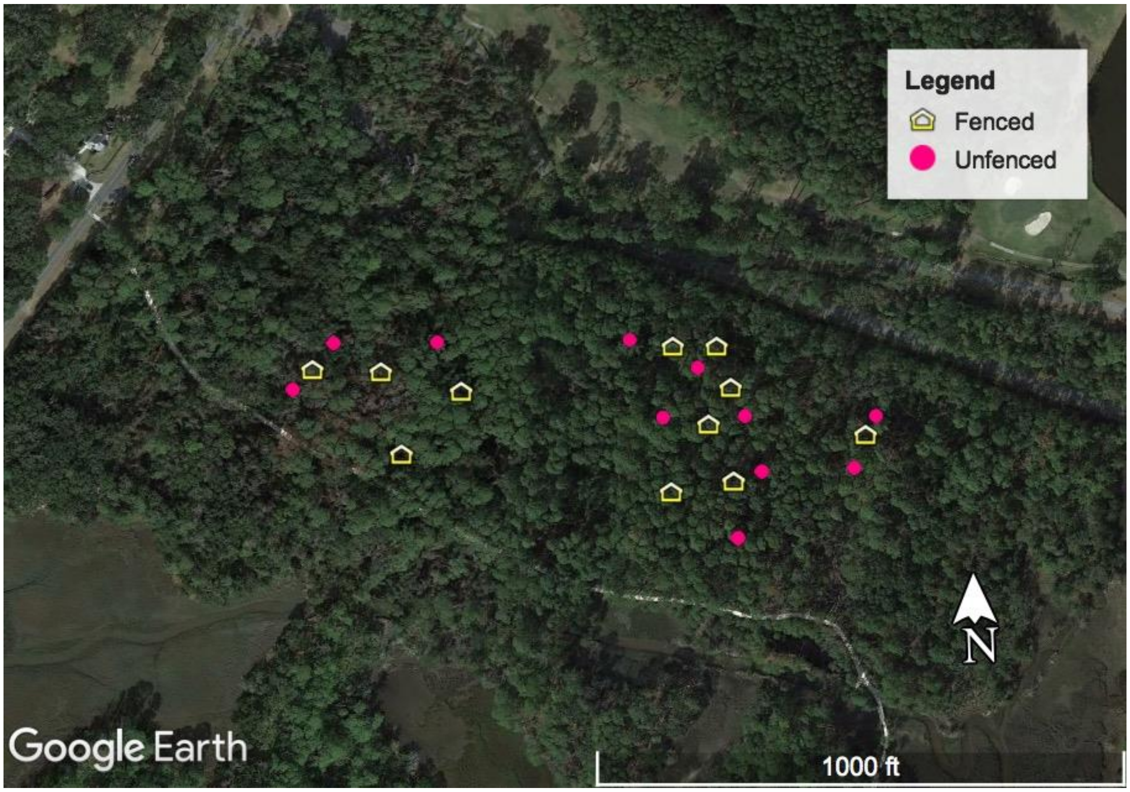

Figure 4.2. The experiment had 22 plots total, including 11 fenced deer exclosures (yellow) and 11 unfenced plots, open to deer herbivory (pink). They were randomly selected from an assortment of 32 clearings, 6m x 6m or larger in size. Each plot is 5m x 5m (Google Earth Pro 7.3.4.8248, n.d.)

2.3 Sampling

Immediately after fences were built in April 2018, each of the 22 plots were surveyed for its baseline vegetation and number of camphor seedlings.

2.3.1 Vegetation surveys

For each 1m x 1m subplot, we recorded total and species percent cover. Percent cover was recorded as less than 1, 1, 2, 3, 4, 5, then increasing by increments of 5. Within each subplot, we also counted the number of native hardwood tree seedlings under 1.5m height. Vegetation surveys were repeated in September 2018, May 2019, and May 2020.

2.3.2 Camphor seedlings

To determine camphor seedling abundance, we tagged all camphor seedlings, measured their height (cm), and noted if there was mammal or insect damage. Each camphor seedling was assigned a camphor ID and (X,Y) coordinates corresponding to its location within the 1m x 1m subplot. Each camphor seedling found in April 2018 was tagged using a red flag pinned to the ground 10cm below the seedling. All flags were labeled with an aluminum tag and looped with a colored zip-tie. Height was measured as the length from the base of the stem to the highest point of woody growth.

We revisited the plots in July 2018, September 2018, May 2019, and May 2020 to note camphor seedling survival and remeasure camphor seedlings found in April 2018. For seedling survival, seedlings were listed as present if they were present and had living tissue and dead if they were present and dead or clearly not found at their location. Seedlings were listed as missing if a tag and seedling were found separately without confidence the tag belonged to the seedling. This first cohort of camphor seedlings were remeasured for height (cm) and presence of mammal or insect damage.

2.4 Analysis

Analyses were performed using JMP® Pro 15 (SAS Institute, 2019) and RStudio version 1.2.5042 (RStudio Team, 2020).

We first used 1-way ANOVA to determine the effect of fencing treatment on total understory plant cover and percent cover of growth forms per plot (averaged across subplots) for the April 2018, May 2019, and May 2020 censuses. We categorized native understory vegetation into six growth forms: ferns, shrubs, palms, vines, forbs, and grasses or sedges. Other studies have also assessed the effects of deer herbivory on plant communities by categorizing them into growth forms, stage-classes, families, and functional groups (Augustine & DeCalesta, 2003; Hegland et al., 2013). We then conducted repeated measures ANOVA and Friedman rank sum tests on responses that demonstrated a significant difference between fencing treatments in Spring 2020 to assess annual variation and the interaction between fencing treatment and year. Because individual species data did not conform to ANOVA assumptions, we analyzed fencing treatment effects on cover by species using the non-parametric Kruskal-Wallis test for each of the three spring censuses. To evaluate the effect of deer exclusion on the change in species richness, we counted the total number of species present in each plot, calculated the absolute difference in species change over time between plots, and analyzed effects of fencing treatments using 1-way ANOVA.

We used Kruskal-Wallis tests to test the effect of fencing on camphor seedling abundance (summed across subplots) and cover for each year. We also performed Friedman rank sum tests to evaluate annual variation and the interaction between fencing treatment and growing season on camphor abundance. For each plot, we calculated plot-level survival rate and average log response ratio of camphor seedling growth over the two year study duration. A Kruskal-Wallis test was performed on survival and growth to test for differences between fencing treatments.

3. Results

3.1 Effects of deer on native vegetation

There was no difference in total understory plant cover between fencing treatments when plots were established in Spring 2018 ($F_{2,21}$= 0.7735, p =0.3901). After both the first (Spring 2019) and second year (Spring 2020), total understory plant cover was higher in fenced plots than unfenced plots (Figure 4.3A), and the difference was greater in the second year ($F_{2,21}$=8.332, p=0.010) than the first year ($F_{2,21}$=3.663, p=0.071). There was also a statistically significant difference in cover between years ($F_{2,21}$=29.417, p<0.001) and a significant interaction between fencing treatment and year ($F_{2,21}$=7.337, p<0.001). Although both fencing treatments experienced an increase in cover during the first year, fenced plots had higher increase in cover by about 63%. After the second year, the difference between fencing treatments became increased as total understory plant cover in fenced plots remained about the same and cover in unfenced plots decreased slightly.

When we examined vegetation change by growth form, only vine and forb species showed a significant response to fencing treatment after the first and second year (Figure 4.3: B, C; Appendix B.1). Both vine and forb species showed no difference in cover when the experiment began in 2018 (p=0.307 and p=0.260, respectively). After one year, fenced plots had a higher cover in vine species in fenced plots compared to unfenced plots (p=0.038) but did not have a higher cover in forb species (p=0.245). However, after the second year, both vine (p=0.027) and forb (0.007) species had higher percent cover in fenced plots than unfenced plots. When assessing the difference in percent cover by species within each of these growth forms, *Vitis rotundifolia* (Muscadine grape) accounted for most of the change in vine cover after the first (p=0.046) and second year (p=0.040). No one species contributed heavily to an increase in forb cover. All other growth forms including ferns, shrubs, palms, and grasses/sedges did not show a significant difference between treatments after either year (Appendix B.1).

Although fencing treatments resulted in a change in total understory plant cover, there was no observed effect on native hardwood tree seedling abundance or species richness (Figure 4.3: E and F). The number of native tree seedlings in both fenced and unfenced plots increased after two years but there was no difference between treatments (p=0.751) (Figure 4.3: E). This was a result of a heavy increase in *Liquidambar styraciflua* (sweetgum) seedlings in both fenced and unfenced plots after the second year. However, a Friedman rank sum test performed on the effect of fencing treatment ($F_{2,21}=1.073$, $p=0.313$), year ($F_{2,21}=2.518$, $p=0.094$), and their interaction on sweetgum seedling abundance was not significant ($F_{2,21}=0.650$, $p=0.530$). After two years, average species richness in fenced plots increased by 2.4 species/plot, while unfenced plots increased by 4 species/plot, although this difference was not significant ($p=0.124$) (Figure 4.3: F).

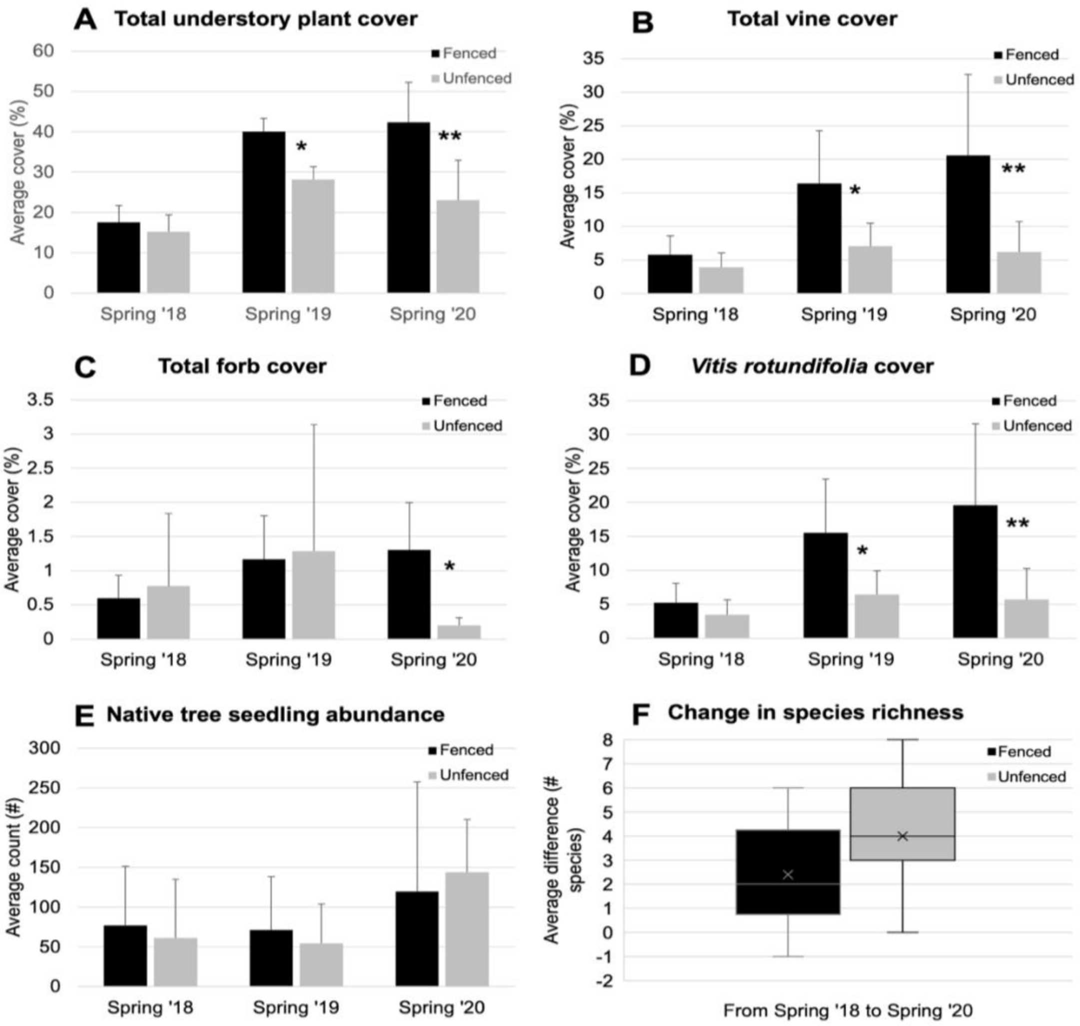

Figure 4.3. Bar plots and box plots summarizing the response of understory vegetation variables to deer exclosure treatments. (A) Total understory plant cover (ANOVA, *$F_{2,21}$=3.663, p=0.071; **$F_{2,21}$=8.332, p=0.010); (B) total vine cover (Kruskal-Wallis, *p=0.038, **p=0.027); (C) total forb cover (Kruskal-Wallis, *p=0.007); (D) *Vitis rotundifolia* cover (Kruskal-Wallis, *p=0.046, **p=0.040); (E) native tree seedlings abundance (Kruskal-Wallis, not significant; and (F) change in species richness from Spring 2018 to Spring 2020 (ANOVA, not significant). Results are considered significant when $\propto < 0.05$.

3.2 Effects of deer on camphor seedlings

In Spring 2020, after two years of deer exclusion, camphor seedling cover (p=0.023) and abundance (p=0.002) were greater in fenced plots (Figure 4.4: C, D). However, camphor cover and abundance were also greater in fenced plots in at the beginning of the experiment (Spring 2018 cover: p=0.023, abundance: p=0.026) and one year post-deer exclusion (Spring 2019 cover: p=0.009, abundance: p=0.012). A Friedman rank sum test was performed to detect annual variation in camphor seedling cover and abundance. For camphor cover, there was a slightly significant effect for fencing treatment ($F_{2,21}$=3.590, p=0.073) and a significant effect of year ($F_{2,21}$=12.896, $p < 0.001$), but no significant interaction between the two ($F_{2,21}$=1.606, p=0.214). For camphor seedling abundance, there was a significant effect for fencing treatment ($F_{2,21}$=10.179, p=0.005) and year ($F_{2,21}$=9.752, $p < 0.001$) but no interaction ($F_{2,21}$=1.561, p=0.223).

Camphor seedlings in fenced plots demonstrated a greater increase in height (p=0.004) and survival (p=0.006) (Figure 4.4: A, B). Camphor seedling growth was more than double in fenced plots than unfenced plots, and camphor survival in fenced plots was about four times more than unfenced plots.

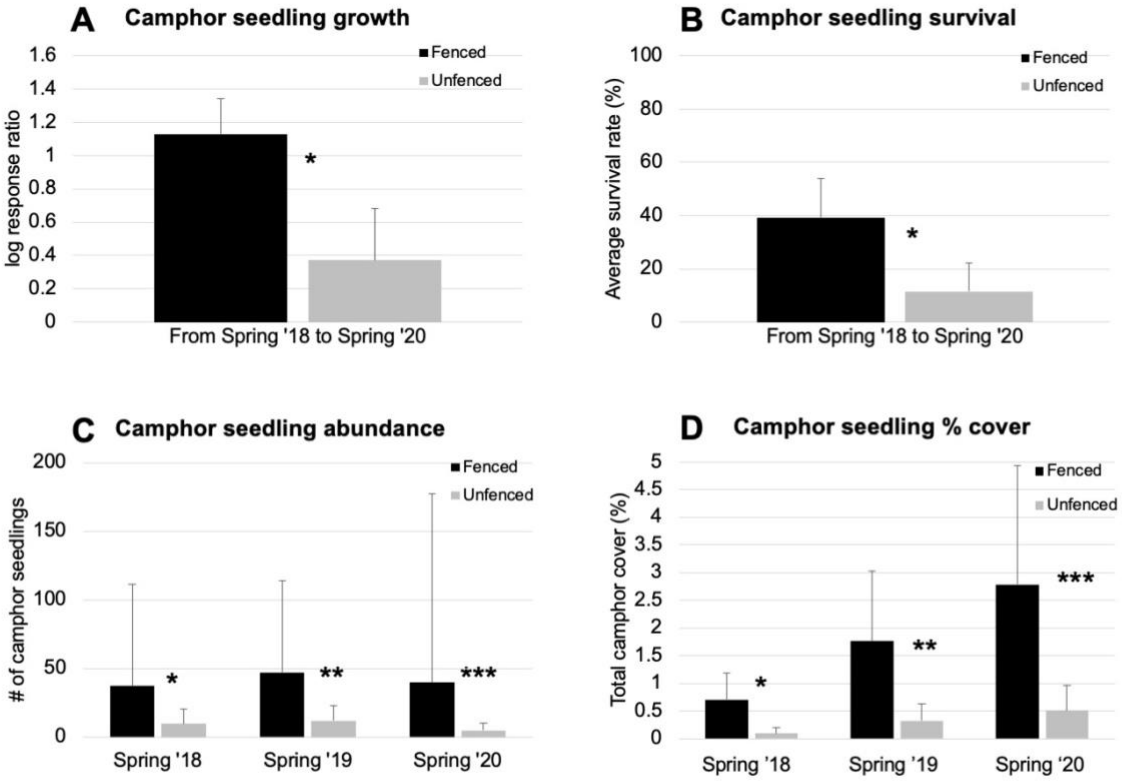

Figure 4.4. Bar plots summarizing Kruskal-Wallis nonparametric tests of fencing treatment effects on camphor performance variables. (A) Camphor seedling growth (*p=0.004); (B) camphor seedling survival (*p=0.006); (C) camphor seedling abundance for each year (*p=0.026, **p=0.012, and ***p=0.002); and (D) camphor seedling percent cover for each year (*p=0.023, **p=0.009, ***p=0.017). Results are considered significant when ∝ < 0.05.

4. Discussion

4.1 Influence of deer browsing native and invasive vegetation

We hypothesized that deer would preferentially consume more palatable plants and tree species, benefitting less palatable or more browse-tolerant species and potentially influencing total species richness. Total understory cover increased in fenced plots after two years of deer exclusion, but this was primarily due to a significant increase in vine species cover, specifically

Vitis rotundifolia (Figure 4.3). Many vine species such as *Smilax* spp., *Gelsemium sempervirens*, and *Vitis* spp. are often consumed by white-tailed deer, especially when other preferred foods including hardwood tree seedlings, shrubs, and other flowering plants are absent or in low abundance (Arceo et al., 2005; Blair & Brunett, 1980; Broz, 2019; Wright et al., 2002). *Vitis rotundifolia* is a fast-growing, high-climbing perennial that can tolerate a wide range of environmental conditions (Andersen et al., 2020). In high light and excluding deer, *V. rotundifolia* may have increased in abundance more quickly than other more slow-growing plants such as native tree seedlings and shrubs. Although there was no immediate effect of fencing on species richness or cover of most other functional groups and species, our findings of positive vegetation response to deer exclusion are consistent with results from other short-term studies (Aronson & Handel, 2011; Begley-Miller et al., 2019).

Although we did not observe an immediate effect of deer herbivory on the abundance of native hardwood tree seedlings, other deer exclosure studies support that intensive browsing can significantly reduce the number of tree seedlings (Blossey et al., 2017; Rooney & Waller, 2003; Slater & Anderson, 2014). Trees are slow-growing, and recovery following herbivore exclusion often takes longer than a few years (Begley-Miller et al., 2019; Bourg et al., 2017), and many smaller tree seedlings are likely eaten before they are surveyed (Blossey et al., 2017), which may prevent the detection of herbivory effects in short-term studies. We also did not measure browsing intensity or individual seedling growth and survival, both of which could have provided insight to deer preference on native tree seedlings and resulting effects on their performance. For example, Aronson and Handel (2011) found that the mean relative growth rate of height and cover for seedings in deer exclosures was about 38% greater than seedlings exposed to deer herbivory (Aronson & Handel, 2011). Therefore, deer herbivory at our site could have reduced native tree seedling performance via effects on growth rather than numbers of seedlings.

The camphor tree is allelopathic (Chen et al., 2013; Schenk, 2009) and can be toxic to specific ungulates, birds, and other consumers (Chen et al., 2013; Friend, 2006). Camphor has also shown to have plasticity in physiological traits such as leaf toughness and surface leaf area in response to damage or defoliation (Friend, 2006; Wan & Bonser, 2016). Therefore, we anticipated camphor seedlings to be more competitive and more resistant and/or tolerant to deer herbivory compared to native plant and tree species. We hypothesized white-tailed deer on Jekyll Island would therefore prefer more palatable, native tree and plant species, which could either maintain or improve camphor abundance and performance in unfenced plots. However, the observed vegetation responses to fencing treatment did not suggest that deer are facilitating camphor invasion through competitive release. There was no difference in camphor seedling abundance between fencing treatments, and camphor cover, survival, and growth were higher in fenced plots where deer were excluded (Figure 4.4).

4.2 Management Implications

According to our findings, excluding deer promotes native understory plant abundance while also improving camphor performance. Jekyll Island management may need to explore restoration efforts other than deer exclusion to reduce camphor performance. A combined strategy may be needed, for instance using deer exclosures in target areas to increase native plants as well as herbicide application or manual removal of larger camphor seedlings and saplings (Catterall, 2016). The camphor tree resprouts heavily after cutting, especially in high light conditions, so invasive management should prioritize treating larger stumps to reduce camphor’s resprouting and competitive abilities (Imaoka et al., 2019).

Environmental factors not assessed in this study could also be influencing plant-plant interactions and camphor performance. The forest where this study was conducted lies on an elevation gradient, and initial measurements indicated that soil moisture content, temperature, pH, and other soil characteristics vary with elevation. Understanding which local environmental conditions favor the native species and which favor the invasive will help JIA conservation staff manage the area for invasive control and native plant diversity restoration. For instance, a study in Australia found that camphor seedlings can dominate and exclude native plant and tree species in moist areas (Coutts-Smith & Downey, 2006), which is especially important to consider when managing maritime forests. Leaf litter depth, which often increases with deer exclusion (Bressette et al., 2012; Heckel et al., 2010), can also alter soil fertility and quality, both of which could be more or less favorable to specific native and invasive plants (Heckel et al., 2010). Furthermore, Jekyll Island has experienced decades of fire suppression, which has led to a heavy accumulation of leaf litter in their maritime forests. Fire suppression has been known to promote camphor invasion in native plant communities in Florida (Daubenmire, 1990; Laessle, 1958; Panetta, 2001), so although it has not been extensively tested, use of controlled burns could reduce camphor abundance and allow native understory plants to regenerate. An adaptive management plan with burns would help reduce dangerous and stressful leaf litter accumulations while also testing whether fire can help control camphor proliferation and/or facilitate native vegetation and tree seedlings.

5. Conclusion

While we did not observe an immediate recovery in native plant and tree seedling abundance and species richness post intensive deer browsing, our data suggest that *Vitis rotundifolia* and camphor benefited from deer exclusion in the short-term. Deer preference and browse severity of specific plant species depends on multiple factors including deer density, deer legacy effects, time of year, resource availability, and relative abundance and density of plant species (Blossey et al., 2017; Heckel et al., 2010). Therefore, longer-term studies are needed to understand which species are likely to benefit more in the long run and to determine if increased camphor performance has a negative effect on native plant and tree seedling abundance. Nevertheless, these results suggest that controlling deer herbivory may not tip the balance of apparent competition balance back toward native vegetation, and other restoration efforts are likely needed to control camphor invasion and support the native tree and plant community.

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CHAPTER 5

MULTIVARIATE ANALYSES OF NATIVE PLANT COMMUNITY AND EFFECTS OF DEER EXCLUSION[4]

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[4] Benson, D.L.; King, E.G.; O'Brien, J.J. To be submitted to *Forest Ecology and Management, Journal of Vegetation Science, Restoration Ecology,* or *Conservation Biology*

Abstract

Many coastal forest ecosystems are experiencing environmental stresses that could alter ecological functions and native plant and tree communities. Two stresses of concern on Jekyll Island, a barrier island in Georgia, are intense herbivory by white-tailed deer (*Odocoileus virginianus*) and introduction of invasive plant species. The camphor tree (*Cinnamomum camphora*) was introduced from Asia to the southeastern United States more than 100 years ago, and it has become increasingly abundant in maritime forests on Jekyll Island in recent decades. Native deer populations have also increased during this period. Furthermore, plant and tree communities on Jekyll Island have heterogeneous abiotic microsite conditions that could affect growth and survival. Therefore, we sought to explore how local abiotic and biotic environmental conditions influenced understory native plant and tree abundance and composition, as well as vegetation response to deer exclusion. We established 22 6m x 6m plots in a 10ha maritime forest with heavy camphor proliferation, of which 11 were fenced to exclude deer and 11 were not. For two years, we recorded total understory vegetation cover, cover by species, and abundance of hardwood tree seedlings, and we counted, tagged, and measured height of each camphor seedling. We also measured environmental conditions of soil moisture and temperature, elevation, leaf litter depth, adult tree composition, and light availability in each plot. We then used multivariate analyses to observe how plant community composition varied across the heterogeneous landscape, and with deer exclusion over two yars. Plant community composition, including abundance of camphor seedlings, varied with environmental conditions and deer exclosure, though due to the scale of the study, ecological interpretations of patterns are tentative. Still, our findings pointed to the value of using environmental conditions to provide helpful contextual information for ecological restoration and invasive species control.

1. Introduction

Many small forest managers seek to preserve and restore native plant and tree communities, especially those that are rare or are undergoing rapid environmental change and stress. However, effective management and restoration strategies depend on understanding how local environmental conditions and biotic interactions influence native plant composition and biodiversity. There is plenty of evidence that variations in habitat and microsite characteristics including light availability, forest fragmentation and edge effects, and soil composition and structure (Hess et al., 2019; Holmes & Webster, 2011; Ozinga et al., 2004) can influence biotic and abiotic factors such as plant-plant competition, herbivory, and resource availability, which in turn determine the favorability of conditions for a suite of plant species (Stephens & Quintana-Ascencio, 2015).

One concept often used to evaluate how environmental conditions and biotic interactions influence community assembly and dynamics is the ecological filter theory, which refers to metaphorical, hierarchical "sieves" or "filters" that can promote or prevent establishment and persistence of specific species (Kraft et al., 2015; Menninger & Palmer, 2006; Poff, 1997; Temperton et al., 2004) (Figure 5.1). After considering regional processes such as initial species pool and introduction order, each ecological filter represents abiotic and biotic conditions that can influence community structure. The abiotic or environmental filter often includes environmental conditions, habitat characteristics, and disturbances regimes that can favor or inhibit species growth, survival, and reproduction while the biotic filter incorporates the effect of herbivory, competition, and other trophic interactions (Menninger & Palmer, 2006). This framework is especially beneficial when planning for restoration because it emphasizes that the combination of these filters determines the *resistance* of an ecosystem to specific restoration activities, and therefore the *successional trajectories* or community assemblages possible for restoration (Temperton et al., 2004).

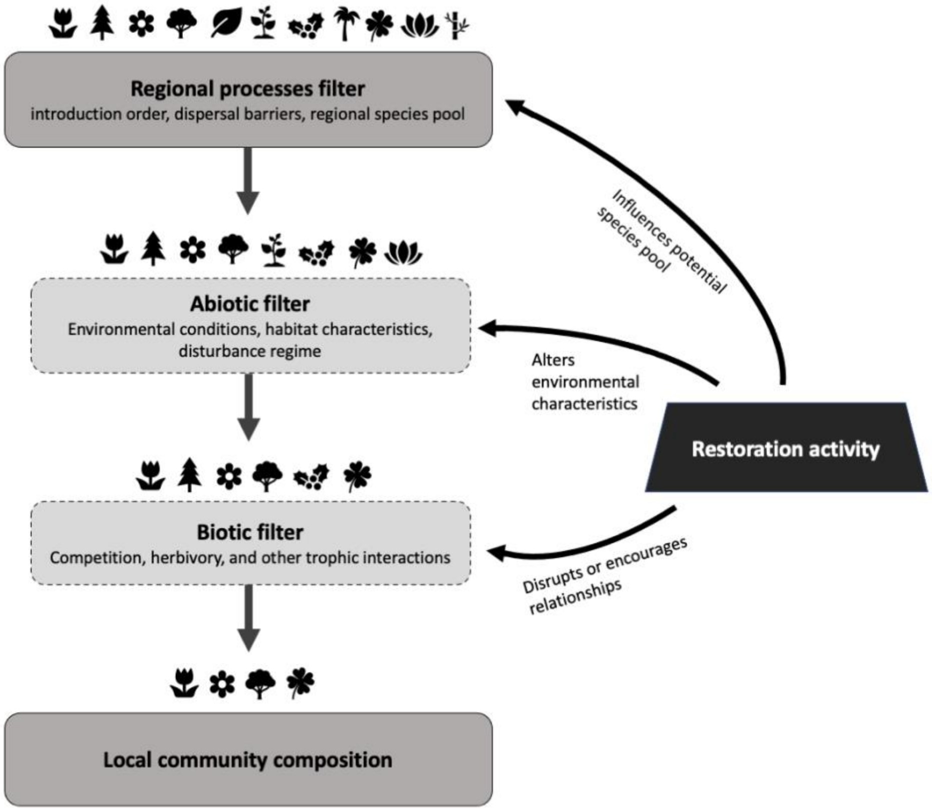

Figure 5.1. General conceptual framework of the ecological filter theory. Regional processes and abiotic and biotic ecosystem components influence which species become established, persist, and reproduce. Restoration activities can help guide the impact of these filters.

Jekyll Island is a state park on the Georgia coast that contains roughly 650ha of maritime forests (Jekyll Island Authority, 2020). Jekyll Island's maritime forests are facing environmental stresses that could affect plant-plant competition and microsite conditions, possibly changing the trajectory of native plant community composition. The deer population on Jekyll island has not fallen below about 30 deer/km^2 since 2014, although Georgia Department of Natural Resources advises no more than a population of about 12 deer/km^2 to maintain a healthy herd (Jekyll Island Authority, 2020). Deer pose a critical constraint on native plant abundance and tree seedling establishment and survival to maturity, and thus are a management concern. Another concern of the Jekyll Island Authority (JIA), the body responsible for environmental management on the island, is invasive plant species, especially camphor (*Cinnamomum camphora*). Camphor is an Asian evergreen tree that was once introduced for horticulture but has now invaded a few natural areas on the island. Fast-growing and with prolific seed production, camphor may out-compete native plant species and its establishment raises concerns about native plant biodiversity (Schenk, 2009). A third concern on Jekyll Island is the ecological consequence of long-term fire exclusion, which has led to a thick shrub layer of saw palmetto (*Seneroa repens*) and a heavy accumulation of litter and duff. Fire is a keystone process that maintains forest biodiversity by creating fluctuations in resource availability and preventing competitive exclusion (Kerns & Day, 2017). Therefore, fire exclusion creates an additional stress for tree species and the herbaceous layer that rely on periodic reduction in litter and shrub cover to regenerate and reach above the shrub layer (Kerns & Day, 2017). Furthermore, many of the native plant communities that are facing these stresses have heterogeneous abiotic microsite conditions including soil moisture and temperature, elevation, and light availability—all of which can affect plant growth and survival. This heterogeneous environment creates an additional challenge for JIA when restoring native plant communities because plants may respond differently depending on their local environment and biotic interactions.

Understanding which local environmental conditions affect which native and invasive plant species can help JIA conservation staff manage forests for native plant diversity restoration. Therefore, in this chapter, I will evaluate three different research questions. I will first assess whether the variation in plant community composition and biodiversity across a small, camphor-invaded forest on Jekyll is associated with environmental variables relating to topography, soil conditions, and overstory canopy conditions. I will then determine if different environmental conditions affect camphor abundance and performance. Because JIA is currently eradicating camphor populations and is considering deer exclusion to enhance forest diversity and tree regeneration, I will also investigate how excluding deer can change native and invasive plant abundance and alter native plant composition across a heterogeneous landscape.

Research questions:

- **Q1:** Is vegetation heterogeneity within the site associated with known environmental variables?
- **Q2:** Does camphor seedling abundance, growth, or survivorship vary with environmental conditions?
- **Q3:** Lastly, do we see any shifts in understory composition in response to two years of deer exclusion?

2. Methods

2.1 Study site and experimental design

This study was conducted on the same study site, array of plots, and vegetation survey data as Chapter 4 (Figure 5.2). There were 22 plots, each 6m x 6m, 11 of which were fenced to exclude deer in April 2018, and 11 were left unfenced. Vegetation surveys were conducted in Spring 2018 (before exclosures were erected), 2019, and 2020. These surveys yielded the average cover (%) for each understory species, the number of camphor seedlings, and the number of seedlings for each native tree species in each plot. These values populated the plot by species matrix used in multivariate analyses.

Figure 5.2. The study site is the same one used in Chapter 3. The site generally slopes downhill in the direction of the arrow (*Google Earth Pro 7.3.4.8248*, n.d.).

2.2 Environmental factors

We measured several environmental factors in each plot, as described below. These data made up the plot by environmental variable matrix used in multivariate analyses.

2.2.1 Elevation

We obtained submeter GPS coordinates for the corner of each 6m x 6m plot, using an Archer II handheld computer paired with a Geode GPS receiver (Juniper Systems, Inc). We then extraction elevation from 2016 LiDAR digital elevation model for the Southeast coast (NOAA;

https://coast.noaa.gov/dataviewer/#/lidar/search) for these coordinates and averaged them to determine a representative elevation for each of the 22 plots.

2.2.2 Soil characteristics

We recorded litter depth in all 22 plots in April 2018, before the deer exclosures were built. We also remeasured leaf litter depth for each plot in May 2020, two years after deer exclusion. For each survey, we took measurements in all 1m x 1m subplots in the upper two rows (1-2) and lower two rows (4-5) of each plot, excluding the middle row (3) to allow movement between subplots (Figure 5.3). We averaged subplot litter depths for each plot.

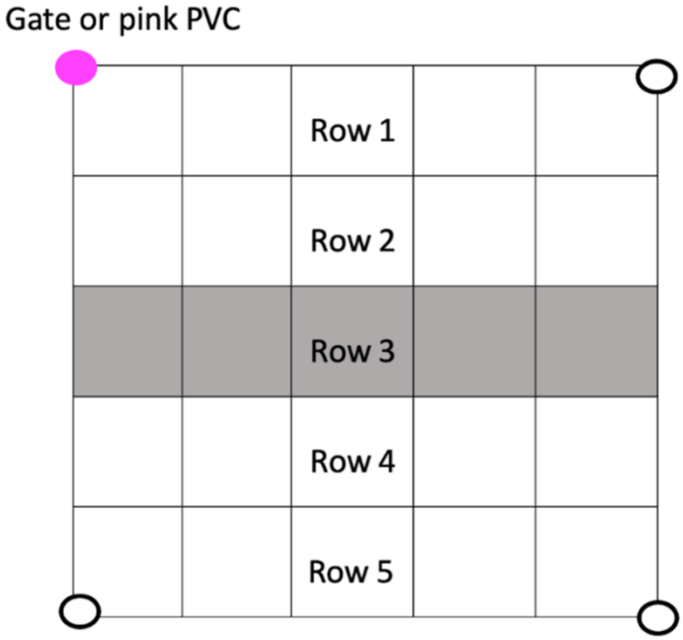

Figure 5.3. Leaf litter depth was recorded in all 1m x 1m subplots within the upper two rows (1-2) and lower two rows (4-5) of each plot, totaling 20 subplots. Subplots that were excluded are in grey.

In May 2019, May 2020, and May 2021, we recorded soil temperature for each of the 22 plots using an EC-350 Aquaterr Digital probe. We measured temperature at the center of 3 of the 4 plot quadrants (Figure 5.4). If there was a tree or plant root at the location, we recorded temperature 30cm toward the center of the plot. We then averaged measurements for each year to obtain one soil temperature value per plot and compared each year for annual variation in temperature. Because there was no change, we used the temperature recorded during May 2019 when conducting multivariate analyses of our species abundance data.

In May 2021, we extracted five surface soil samples (about 15cm below duff layer) from each plot using a soil probe and emptying them into sterile, 4-oz Whirl-Packs. We extracted one sample from the center of the plot and four from the center of each of the four quadrants (Figure 5.4). If there was a tree or plant root at the location, we extracted a sample 30cm toward the center of the plot. To obtain gravimetric soil moisture content, we weighed each wet soil sample, air dried bags for 72 hours, dried bags in 48 hours at 105 degrees Celsius, and weighed each dry soil sample. We averaged the five soil content measurements for each plot to obtain a final soil moisture content estimate. We then extracted 10ml of soil from each of the 5 soil samples per plot and combined them to create a composite sample per plot. We sent the 22 composite soil samples to the Laboratory for Environmental Analysis at the University of Georgia to determine pH, electrical conductivity (EC), and total % soil C and N.

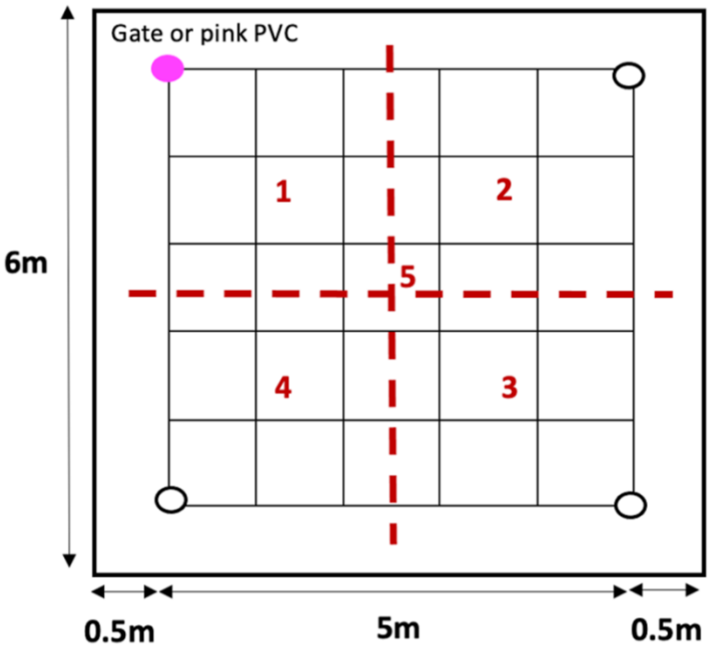

Figure 5.4. Plot with quadrants for corresponding soil measurements. Soil temperature measurements were taken at the center 3 of the 4 plot quadrants (red). Soil samples were extracted from the center of each of the four quadrants and at the center of each plot (5).

2.2.3 Canopy characteristics

For each of the 22 plots, we recorded the number and species of adult trees greater than 10cm DBH and within 5m of the 6m x 6m plot perimeter (Chen et al., 2019). We noted if each tree was living or dead standing, which we defined as a recently-alive tree (within the year) that is upright at least 45 degrees above the ground. We categorized each tree into one of the following five size classes (DBH, cm): 10-25, 25-50, 50-75, 75-100, and 100-125. For trees that were 10, 25, 50, 75, or 100cm DBH exactly, we noted their exact measurements. Then, we calculated average basal area (m^2) for each plot using the average size class DBH and number of trees.

We used hemispherical photography (Kodak PIXPRO SP360) and WinSCANOPY software (Regent Instruments Inc., 2021) to obtain canopy openness and gap fraction values for each plot, which are fraction of open sky unobstructed by vegetation in the canopy above the lens in a 3D and 2D dimensional space, respectively. In July 2021, we took three hemispherical images per plot: one photo at the center of each plot and randomly chose the center of two quadrants diagonal from one another to take the remaining two photos. Each photo was taken at 1.5m height with one side of the camera consistently oriented north. We took images during overcast days and/or during an interval of 90-minutes centered around sunrise or sunset (Sercu et al., 2017).

2.3 Data analysis

2.3.1 Initial species abundance and composition

We conducted ordination and other multivariate analyses to assess how different sets of environmental conditions influence plant community composition (Leps & Smilauer, 2003).

To evaluate variation in our species dataset and determine if specific environmental conditions or excluding deer contributed to that variation, we used *PC-ORD* v. 6.0 software (McCune & Mefford, 2011) to conduct non-metric multidimensional scaling (NMDS or NMS) ordinations. NMDS ordination reduces datasets with multiple variables and samples to fewer dimensions on a graph, arranging and grouping those variables and samples according to patterns of redundancy and similarity. These patterns are reflected as coordinates that explain how similar variables or samples are to one another based on species composition and relative abundance (Harms & Hiebert, 2006; Peck, 2016). NMDS does not assume any particular model form (i.e. avoids parametric assumptions of normality) and is often used with heterogeneous datasets with zero-rich responses within the species matrix (Peck, 2016).

To address whether heterogeneity was associated with any known environmental variables (Question 1), we first conducted NMDS on the species abundance (percent cover) dataset from April 2018—prior to building deer exclosures—based on the Bray-Curtis or Sorensen distance measure by plot. Prior to the analysis, rare species occurring only in three plots or less were excluded. We also excluded one plot whose deer exclosure fell after the first year due to a fallen camphor tree as deer had access to this location for several months. The final species dataset from April 2018 contained 27 species or taxa in 21 plots, 10 fenced and 11 unfenced. We then relativized the species dataset by general relativization to reduce the influence of highly abundant of species on the ordination result (Kiełtyk & Delimat, 2019). We ran multiple analyses with and without statistical outliers, and they were found to have no significant effect on the ordination. We also applied a Monte Carlo randomization test to determine whether a better-than-random solution was found for each dataset (Harms & Hiebert, 2006).

Species abundance patterns were then linked to environmental data using vector biplot overlays and Pearson correlations (Gottlieb et al. 2006). The latter can help us infer the relative contribution of each environmental variable to the variation that is explained by an ordination axis. When environmental variable vectors were overlain on the plot x species ordination, several environmental variables were closely aligned with elevation, and elevation had the strongest correlation with species and plot locations in the NMDS ordination space. To overcome the multicollinearity among predictor variables and better address Question 1, we reduced the dimensionality of the environmental variables by conducting a principle components analysis (PCA) on environmental data only. PCA ordination reduced the original covarying variables into a few orthogonal composite variables that can still capture much of the original variance in the dataset (O’Brien et al., 2004). We rotated PCA-derived axes through variance maximization (i.e.

varimax rotation) to maximize the association of responses or variance of response loadings along each environmental gradient, reducing low correlations and enhancing high correlations and allowing improved interpretation of the components (Peck, 2016). We then regressed factor loadings with species abundance data from April 2018. To address whether camphor seedling abundance or performance varied with environmental conditions (Question 2), we regressed factor loadings with initial camphor seedling abundance, survivorship after 2 years, and growth after 2 years by plot. We conducted the PCA and axis rotations in IBM SPSS Statistics Version 28.0.1.1 (IBM, 2022) and linear regressions in RStudio Version 1.2.5042 (RStudio, 2022).

2.3.2 Community analysis post-deer exclusion

To initially explore species abundance patterns for May 2020, two years after deer exclusion, we conducted two NMDS ordination analyses of the Bray-Curtis dissimilarly matrix by plot (Question 3). The first NMDS ordination evaluated species abundance data from May 2020. Fenced and unfenced plots were grouped separately using biplot overlays. We then conducted another NMDS ordination on species abundance data from both years (April 2018 and May 2020), also grouping fencing treatments separately using biplot overlays. We applied a Monte Carlo randomization test to determine whether a better-than-random solution was found for each dataset.

To directly assess whether there was a shift in understory composition as a result of two years of deer exclusion, we performed a one-way factorial permutation-based MANOVA (PerMANOVA) procedure on the absolute difference (+5 due to zero-rich data) in species abundance between April 2018 and May 2020. PerMANOVA allowed us evaluate the differences in species composition and relative abundance among the two fencing treatments while accounting for variation among plots. Because PerMANOVAs require balanced group membership or the same number of sample units within each treatment group (Peck, 2016), we excluded one plot that was designated as an outlier during an outlier analysis. Therefore, we conducted a PerMANOVA on 20 plots (10 fenced, 10 unfenced) that contained 26 species or taxa. To assess whether any change in species composition was due to particular plant species, we conducted an Indicator Species Analysis (ISA) that assessed the contribution of each species relative abundance and frequency to the treatment groups (Dufrêne & Legendre, 1997; Peck, 2016). Indicator values are the percentage of perfect indication (i.e. IV= 100%) (Selonen et al., 2011) of whether a species contributed to a change in species composition. We compared the highest-ranking plant species in the ISA with non-parametric Kruskal-Wallis tests from Chapter 4 that tested the effect of deer exclusion on individual plant species abundance to confirm species that primarily influenced a change in species abundance and composition.

3. Results

3.1 Initial species abundance and composition

We chose to interpret a significant three-dimensional NMDS solution with a final stress of 13.4 after verifying consistency of interpretation among several NMDS solutions. Up to 500 iterations in three dimensions were ordinated for each dataset, which were run with 250 runs of real data and 250 runs of randomized datasets with a stability criterion of $1x10^6$ standard deviations in stress over the last 10 iterations. We applied varimax rotation around the centroid.

The resulting NMDS ordination found that three axes captured 70.8% of the variation within the species abundance dataset. The proportion of variance expressed by each ordination axis is calculated as a proportion of variation in the reduced matrix relative to that in the original data matrix (Peck, 2016). The two axes that captured the most variation were Axis 2 and Axis 3 at 34.5% and 27%, respectively (Figure 5.5, Table 5.1). Axis 1 captured 8% of the total variation within the dataset. Appendix C.1 contains species abbreviations and their corresponding species, genus, or family name. Axis 1 vs. Axis 2 and Axis 1 vs. Axis 3 are presented in Appendices C.2 and C.3, and all NMDS ordination scores are shown in Appendix C.4.

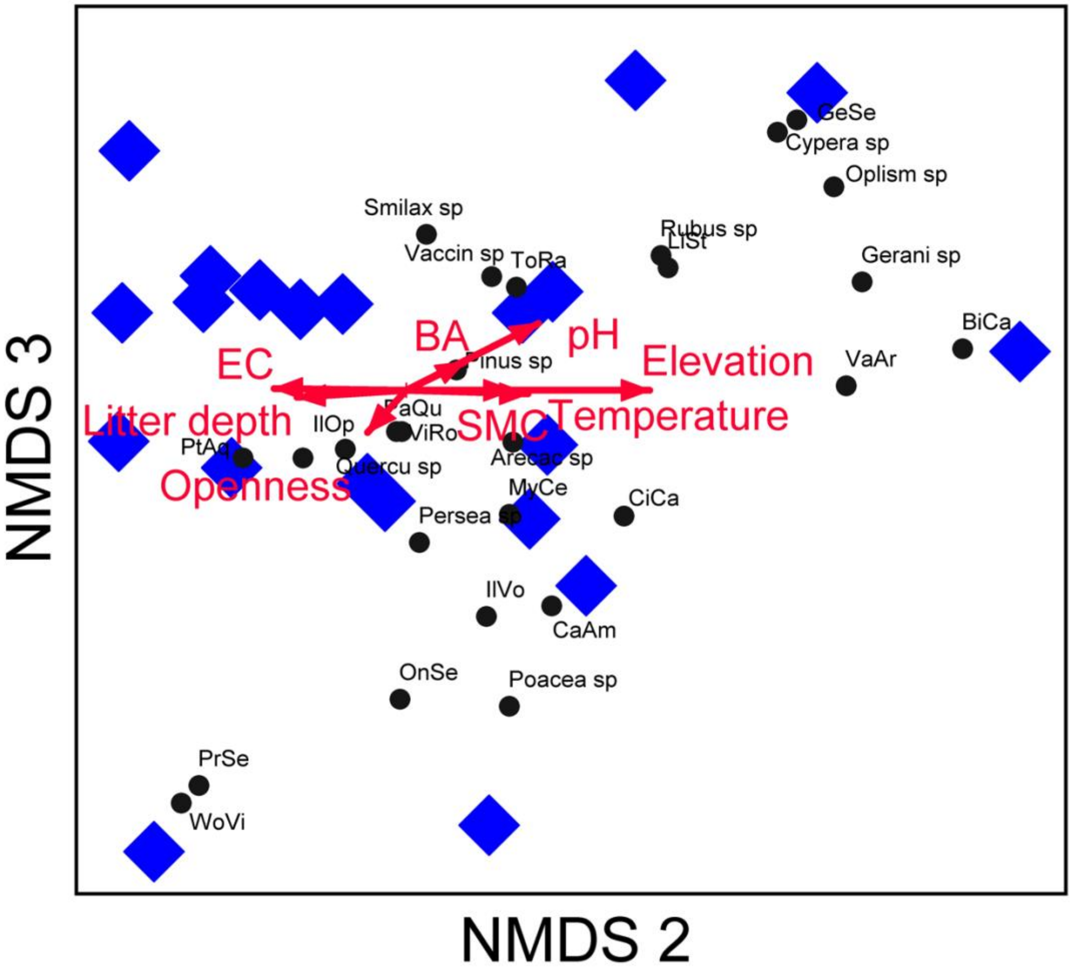

Figure 5.5. Non-metric multidimensional scaling (NMDS) ordination plot of species abundances within sample plot space versus environmental variables. Axis 2 vs. Axis 3 is shown. Environmental variables that had at least a weak or moderate correlation ($r < 0.3$) are shown. Species are coded by the first two letters of the genus and species name (e.g. *Cinnamomum camphora* = CiCa) or the first letters of family classes or genus name (e.g. *Cypera* sp. = *Cyperaceae* family, *Pinus* sp. = *Pinus* spp.). Appendix C.1 contains species abbreviations and their corresponding species, genus, or family name.

Most plots within the site were similar in species composition as they are near one another in ordination space, especially along Axis 2, which represented the highest proportion of variance that is explained between samples and species. However, two distinct plant communities are evident within the second and fourth quadrant. The second quadrant represents plant communities dominated by *Geranium* spp. and few vine, sedge, and grass species including *Gelsemium sempervirens* (Carolina jessamine), *Bignonia capreolata* (crossvine), sedges within the *Cyperaceae* family, and *Oplismenus* spp grasses. The fourth quadrant contains high abundances of *Prunus serontina* (black cherry) seedlings and *Woodwardia virginica* (Virginia chain fern).

These patterns are also present in the individual species' Pearson correlations with NMDS ordination axes (Appendix C.5). We noted moderate ($0.3 < |r| < 0.5$) and high ($0.5 < |r|$) correlations as significant associations between species and axis scores (Kent State University, 2022). Species that demonstrated a moderate correlation with Axis 2, the axis associated with the highest variation within the species dataset, included *Pteridium aquilinum* (Western bracken fern), *Myrica cerifera* (Southern wax myrtle), *Vaccinium* spp., and *Parthenocissus quinquefolia* (Virginia creeper). Strong correlations with Axis 2 included *Vitis rotundifolia* (Muscadine grape), *Pinus* spp. seedlings, and *Ilex opaca* (American holly) seedlings. Many of the same species that are found in the second quadrant also demonstrated a moderate or high correlation with Axis 2. Species that had a moderate or high correlation with Axis 2 were *Toxicodendron radicans* (poison ivy), *Rubus* spp., and *Pinus* spp. seedlings and *P. aquilinum*, *Liquidambar styraciflua* (sweetgum) seedlings, and *Cinnamomum camphora* (camphor) seedlings. There were also many species that showed a moderate to high correlation with Axis 3. Species with moderate correlations included *Callicarpa americana* (beauty berry), *Ilex vomitoria* (yaupon holly), *Oplismenus* spp., *Liquidambar styraciflua* (sweetgum tree seedlings), and *C. camphora* (camphor tree seedlings). Species with high correlations included a few in the fourth quadrant of Figure 5.5 but also *Smilax* spp. and *Cyperaceae* spp.

The NMDS ordination revealed that the heterogeneity within the species abundance dataset is partially associated with a few measured environmental variables. Axis 1 was significantly associated with elevation, temperature, and leaf litter depth. Axis 2 was also significantly associated with elevation, temperature, and leaf litter depth but also significantly associated with pH, electrical conductivity (EC), and soil moisture content (SMC). All canopy characteristics and total soil % C and N were not found to be associated with any NMDS axis. Although Axis 3 explains 27% of the species dataset, no measured environmental variables were significantly associated with Axis 3. NMDS ordination results and Pearson correlation coefficients of environmental variables with ordination axes are presented in Table 5.1.

Table 5.1. Non-metric multidimensional scaling (NMDS) ordination results with Pearson correlations of environmental variables. NMDS was conducted on April 2018 species abundance data.

Proportion of variance represented by each axis R^2	**Axis 1**		**Axis 2**		**Axis 3**	
Increment	0.084		0.354		0.270	
Cumulative	0.084		0.354		0.708	
Correlation of environmental variables with axes	**Axis 1**		**Axis 2**		**Axis 3**	
Environmental variable	r^a	r^2	r^a	r^2	r^a	r^2
Elevation	0.410*	0.168	0.734**	0.539	-0.020	0
Temperature	0.601**	0.361	0.483*	0.234	-0.033	0.001
Leaf litter depth	-0.520**	0.271	-0.494*	0.244	-0.120	0.014
pH	-0.205	0.042	0.541**	0.292	0.383*	0.147

Electrical conductivity (EC)	-0.217	0.047	-0.540**	0.292	0.075	0.006
Soil moisture content (SMC)	0.167	0.028	0.520**	0.271	-0.089	0.008
Total soil % C	0.169	0.029	0.055	0.003	0.041	0.002
Total soil % N	-0.060	0.004	0.124	0.015	0.221	0.049
Total basal area	0.262	0.069	0.361*	0.130	0.252	0.063
Canopy openness	0.048	0.048	-0.291	0.085	-0.309*	0.096
Gap fraction	0.184	0.034	-0.264	0.070	-0.281	0.079
Adult tree species richness	0.006	0.079	0.027	0.001	0.133	0.018

[a]= r, Pearson correlation coefficient
*= significant association between environmental variable and axis score, moderate correlation (0.3 < |r| < 0.5) (Kent State University, 2022)
**= significant association between environmental variable and axis score, high correlation (0.5 < |r|) (Kent State University, 2022)

Although Axis 1 is significantly associated with three environmental variables, it only explains about 8.4% of the total variation within the dataset. Therefore, we focus on the patterns demonstrated by Axis 2 vs. Axis 3 in Figure 5.5. Axis 2 is strongly associated with elevation and at least weakly associated with temperature, leaf litter depth, pH, EC, SMC, canopy openness, and total basal area. Plant species including those in the distinct plant community in the second quadrant, *Geranium* spp., *Rubus* spp., *L. styraciflua* (sweet gum), *Vaccinium arboreum* (sparkleberry), and *C. camphora* are positively associated with higher elevations, higher temperatures, lower EC and leaf litter depth, lower soil moisture content, and less acidic soils than plant species at lower elevations. Plant species such as ferns *W. virginica* and *Pteridium aquilinum*, *P. serontina*, *Quercus* spp., and *Ilex opaca* (American holly seedlings) have higher abundances at lower elevations. The NMDS presented in Figure 5.5 therefore supports that the difference in species composition is strongly correlated with a few known soil characteristics, most of which are ecologically related to elevation.

The PCA reduced the number of variables within the environmental dataset from 11 to three. The component loadings of the environmental variables for the first three PCA-derived axes are shown in Table 5.2. Loadings are similar to Pearson correlation coefficients, and we interpreted loadings greater than 0.6 (O'Brien et al., 2004). The first rotated PCA axis was mostly driven by elevation and environmental variables often highly associated with elevation: soil temperature, soil moisture content, and electrical conductivity. The second and third rotated PCA axes were driven by soil chemistry characteristics (i.e. total soil % N and C) and forest canopy cover, respectively.

Table 5.2. Component loadings, or correlation strengths, of the environmental variables on the first three PCA axes. High loadings (greater than 0.6 and marked with * and bolded) were used in interpretation and naming of the factors. The names in parentheses demonstrate our interpretation of the dominant variables explaining component loading structure (O'Brien et al., 2004).

Environmental variable	**Component 1 (elevation)**	**Component 2 (soil chemistry)**	**Component 3 (forest structure)**
Elevation	**0.937***	0.035	-0.005
Temperature	**0.777***	0.430	-0.116
Leaf litter depth	-0.317	-0.273	-0.065
pH	0.118	0.101	-0.155
Electrical conductivity (EC)	**-0.745***	0.280	0.208
Soil moisture content (SMC)	**0.776***	-0.518	0.025
Total soil % C	0.021	**0.961***	0.093
Total soil % N	-0.137	**0.904***	-0.120
Total basal area	0.588	-0.011	-0.219
Canopy openness	-0.099	-0.015	**0.970***
Gap fraction	-0.110	-0.010	**0.967***
Adult tree species richness	-0.019	-0.033	-0.162

The spring 2018 species abundance dataset (Appendix C.5) used to conduct the NMDS ordination in Figure 5.5 was then regressed with the first three component loading ordination scores (Appendix C.6). For Question 1, we found that the strongest environmental gradient (i.e. Component 1 or elevation and corresponding environmental variables) is linearly associated with Axis 1 ($F_{1,19}$=9.19, p = 0.007) and Axis 3 ($F_{1,19}$=4.153, p=0.058). Component 1 is not linearly associated with Axis 2 ($F_{1,19}$= 0.289). We also regressed Component 2 (i.e. soil chemistry) and Component 3 (i.e. forest structure) with all three NMDS axes, but none of these combinations were significantly linearly associated with one another. Linear equations, R^2 values, and p-values for each combination are presented in Appendix C.7.

After log transforming the camphor abundance dataset, we found that the strongest environmental gradient (Component 1 or elevation) was significantly linearly associated with camphor abundance ($F_{1,19}$=4.184, p=0.055) (Question 2) (Appendix C.8). However, elevation is not significantly linearly associated with camphor survival ($F_{1,19}$=0.083, p= 0.777) or growth ($F_{1,19}$=0.351, p=0.561). Camphor abundance, survival, and growth are also not significantly linearly associated with the second strongest environmental gradient (i.e. Component 2 or soil chemistry) or the third strongest environmental gradient (i.e. Component 3 or forest structure) (Appendices C.8-C.10) (Question 2). Linear equations, R^2 values, and p-values for each combination are presented in Appendices C.8-C.10.

3.2 Plant community response to deer exclusion

For the first NMDS ordination that explored the difference in fencing treatment within species data from May 2020 (Appendix C.11), we chose to interpret a significant two-dimensional NMDS solution with a final stress of 24.917 after verifying consistency of interpretation among several NMDS solutions. Some ordination parameters included: up to 500 iterations in two dimensions were ordinated for each dataset, 250 iterations were run with real data and 250 with randomized datasets, and a stability criterion of 1x10^6 standard deviations in stress over the last 10 iterations. We applied varimax rotation around the centroid. This ordination captured about 47.9% of the variation within the species abundance dataset, of which Axis 1 captured 19.7% and Axis 2 captured 28.2%. NMDS ordination (Axis 1 vs. Axis 2) is shown in Appendix C.11, and ordination scores are presented in Appendix C.12.

We used the same parameters from the April 2020 NMDS ordination for the second NMDS ordination that explored the difference in species data between fencing treatments from both April 2018 and May 2020 (Appendices C.13-C.15). We chose to interpret a significant three-dimensional NMDS solution with a final stress of 18.925. This analysis captured about 59.9% of the variation within the dataset. The two axes that captured the most variation are Axis 2 and 3 at 16.4% and 33.7%, respectively (Appendix C.15). Axis 1 captured 9.8% of the total variation within the dataset. All NMDS ordination scores are shown in Appendix C.16.

Each NMDS ordination presented in Appendix C.11 and Appendices C.13-15 contain many of the same species as the species abundance dataset from April 2018. However, these two NMDS ordinations demonstrate that not only is there high variation of species composition within each group, but that species composition becomes more distant in ordination space or more dissimilar over time for fenced plots versus unfenced plots. This is evident in a shift in the centroids of each group in the NMDS ordination in Appendix C.11 and NMDS ordination in Appendices C.13-C.15. This pattern is especially evident the NMDS ordination in Appendix C.11 for Axis 2, which represents the most variation within that species dataset and in Axes 1 and 2 for the NMDS ordination in Appendices C.13-C15, which is associated with about 26.2% of the variation within the dataset.

The PerMANOVA, whose results are in Table 5.3, allows us to more directly address Question 3. The test was significant, which points to a difference in species composition between fenced and unfenced plots. Thus, there is a shift in species composition after two years of deer exclusion. Although there is high variation within treatment groups as presented in Appendices C.11 and C.13-C.15, PerMANOVAs are insensitive to heterogeneity in dispersion in balanced designs so we can confidently attribute the differences in the group centroids rather than the spread of variation within each treatment group (Fahey et al., 2018). The ISA results presented in Appendix C.17 suggest that *Vitis rotundifolia* (muscadine grape) (p=0.037), *Toxicodendron radicans* (poison ivy) (p=0.039), and *Rubus spp.* (p=0.043) are primarily responsible for the shift in species composition. Vine species, along with forb species, are the main contributors of change. Although not a statistically significant result, *Cinnamomum camphora (*camphor tree) has a relatively low p-value (p= 0.077) that hints this species may also contribute to the difference between fencing treatments.

Table 5.3. PerMANOVA results based on Bray-Curtis dissimilarities using the absolute difference (+5) in species abundance between April 2018 and May 2020. Evaluation is for differences in species between fencing treatments.

Source	**Degrees**	**SS**	**MS**	**F**	**p***
Fencing	1	0.023	0.023	2.929	0.0498*
Residual	18	0.139	0.008		
Total	19	0.162			

Non-parametric Kruskal-Wallis tests from Chapter 4, which also tested the effect of deer exclusion on species abundance, confirm that *V. rotundifolia* (p=0.032), *Rubus* spp. (p=0.029), and *C. camphora* (p=0.002) abundances are significantly different in fenced plots compared to unfenced plots. These tests do not demonstrate a significant effect of deer exclusion on *T. radicans* (p=0.098). However, the data used was from May 2020 and not the absolute difference between species abundance between April 2018 and May 2020. Thus, effect of deer exclusion on the absolute difference in *T. radicans* abundance between the two years may be more ecologically significant than statistically significant (p=0.0619).

4. Discussion

Through multivariate analyses and ordination techniques, we found that variation within the plant community across a small forest on Jekyll Island was associated with a few known environmental variables (Question 1). Specifically, there was evidence to support that the strongest environmental gradient—elevation—could predict differences in species composition. Environmental variables often associated with elevation on this site such as soil moisture content (SMC), electrical conductivity (EC), and temperature also contributed to this pattern. This environmental gradient also influences camphor abundance but does not have an immediate effect on camphor growth and survival (Question 2). Then, we performed additional analyses to confirm that two years of deer exclusion led to a significant shift in species composition, which was primarily driven by a change in vine species abundance including *Vitis rotundifolia* (Muscadine grape), *Rubus spp.*, and *Toxicodendron radicans* (poison ivy) (Question 3). A change in camphor abundance could have also contributed to this shift. Despite the insignificance of the impact of camphor on this change in species composition, camphor still increased in abundance and cover within the limited recovery time post-deer exclusion.

It is evident that some abiotic components are heavily influencing the presence and relative abundance of individual plant species. Plant communities that contain various grass, sedge, and vine species are more commonly found at higher elevations with higher soil temperatures and SMC and lower EC, which is often a proxy for salinity. Tree seedlings of camphor and *Liquidambar styraciflua* are also found at higher abundances within these communities. This pattern is supported by the fact that many plant and tree species like vines species and camphor prefer wetter and warmer sites and are salt-intolerant (J. Wang et al., 2016; S. Wang et al., 2017) or are at least moderately sensitive to saline conditions (WateReuse Foundation, 2007). However, ferns such as *Pteridium aquilinum* (Western bracken fern) and *Woodwardia virginica* that also prefer these conditions and have a low salt tolerance (*Florida Native Plant Society*, 2021) were also found at lower elevations. Therefore, other microsite conditions measured and those not considered within the analyses could also be influencing plant composition. For instance, *P. aquilinum* and *W. virginica* can often be found in more acidic soils that are rich in organic matter (*Florida Native Plant Society*, 2021), the former of which is more prominent in lower elevations with higher EC. Additionally, a history of long-term fire exclusion on the island has led to a a thick shrub layer of saw palmetto (*Seneroa repens*) and heavy accumulation of litter and duff. Studies have shown divergent responses of exotic plant species and other opportunist and aggressively competitive species to different disturbance regimes and legacies (Kerns & Day, 2017). Prior to reintroducing fire, JIA may need to consider which factors related to burn timing, frequency and season, intensity, and severity favor camphor seedlings and which favor native plant communities.

Many studies have found strong associations with topographic or soil characteristics and plant community assemblages (Begley-Miller et al., 2019; Bonanomi et al., 2005; Weiher & Keddy, 1995), some of which consider these gradients as environmental filters that influence establishment and persistence of particular plant species (Baer et al., 2005; de Bello et al., 2013;

Hough-Snee et al., 2011). Some of these associations are often reflected in dominant plant traits within a community as this environmental filter could "remove" or reduce species that are intolerant to a set of environmental conditions and maintain those that have adequate traits for persisting under those conditions (de Bello et al., 2013; Diaz et al., 1998; Keddy, 1992). Cingolani et al. (2007) found that plants associated with high resource acquisition (i.e. higher surface leaf area (SLA), leaf toughness) often dominated the species pool at elevated soil moisture availability as they took advantage at low stress (Cingolani et al., 2007). As this gradient shifted to lower soil moisture availability, plants with lower SLA and leaf toughness dominated the community. In each case, plants with the most beneficial traits affected their probability of becoming dominant. Increased soil moisture "filtered out" plant species with small, softer leaves, and reduced soil moisture "filtered out" plant species with larger, tougher leaves. This filtering of plant species and plant traits through environmental gradients, especially soil characteristics, is evident in other studies (de Bello et al., 2013; Venn et al., 2011). Thus, plant-soil feedbacks are vital to consider when restoring native plant communities as they are driving factors of plant population and community dynamics (Bonanomi et al., 2005).

The shift in plant community composition following deer exclusion is highly supported by other experiments as herbivory often acts as a biotic filter that can alter plant community composition (Cingolani et al., 2007; Royo & Carson, 2022; Suzuki et al., 2013). Intensive browsing from deer herbivory can promote competitive exclusion of particular plant species by reducing the abundance of abundant, palatable species that do not have chemical defenses, allowing less palatable plants to increase in abundance (Wiegmann & Waller, 2006). As the primary indicator species of this change (i.e. *V. rotundifolia*, *Rubus spp.*, and *T. radicans*) are fast-growing vines that are often preferred by deer (Warren & Hurst, 1981; Williams & Baxley, 2008), their increase was expected in the short-term. Given more time, other slow-growing, palatable species including native tree seedlings may also benefit, further diverging the successional trajectories of fenced and unfenced plots. The future of the camphor population is also dependent on deer preference. Camphor seedlings demonstrated a less significant response to herbivory in this study, but earlier results from Chapter 4 indicate that deer reduced camphor growth and survival. If deer continue to consume camphor seedlings, we can assume that deer may not facilitate camphor invasion if the number of regenerating seedlings remains less than those browsed. However, if deer prefer other palatable tree seedlings, vines, forbs, and shrubs, then this may shift the balance between camphor-native plant interaction, allowing camphor to increase in abundance and competitively exclude other native plants.

Although the independent effects of abiotic conditions and biotic interactions on plant communities are well documented, their interactions as dynamics filters, especially in a site experiencing plant invasion, are less explored (Germain et al., 2018). Neglecting to consider both the relative roles and interactions of different ecological filters can limit true understanding of the underlying mechanisms that shape community assemblages (Chollet et al., 2021). For example, legacy effects from past land use, herbivory, and other disturbances could already be unfavorable and limiting to some plant species. When faced with additional environmental or biotic stresses, these effects can often be overshadowed or not fully realized (Begley-Miller et al., 2019; Chollet et al., 2021; Royo & Carson, 2022) and ecosystem recovery could be postponed or unsuccessful if the appropriate management strategy is not implemented (Temperton et al., 2004). Tree and plant communities on Jekyll Island could be experiencing slow recovery due to past intensive herbivory and other ecological stresses including a lack of fire. Thus, a more holistic view of restoration that considers environmental-biotic interactions could help inform restoration management by prioritizing sites and determining intensity and timing of the intervention.

5. Conclusion

Plant and tree communities on Jekyll Island experiencing camphor invasion have heterogeneous abiotic microsite conditions that are influencing local composition. As multivariate analyses and ordination techniques can help investigate variation in plant community composition across environmental gradients, we sought to explore if specific environmental conditions are associated with specific plant species or assemblages (Baer et al., 2005; Leps & Smilauer, 2003). We found that, due to an elevational gradient, soil moisture content, electrical conductivity, and temperature are highly influencing presence and relative abundance of individual species, including camphor tree seedlings. When we assessed how excluding herbivores affects native plant communities, we observed that vine species strongly benefitted from two years of deer exclusion, , although camphor seedlings and other palatable species may also demonstrate a positive response in the long-term. Although we observed these patterns on one site on Jekyll Island, our findings demonstrate that considering both environmental conditions and biotic relationships as ecological filters can provide helpful contextual information for ecological information and invasive species control.

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CHAPTER 6

CONCLUSIONS

To address management and restoration challenges on Jekyll Island, I used a range of methods to begin understanding small forest ecology and the management consequences of different tools and restoration efforts. Each chapter explored different approaches to conservation and restoration of native tree and plant communities.

(1) First, we evaluated the relevancy and applicability of forest dynamics models to small forest management in Chapter 2. This literature review explored the suitability of 54 existing forest dynamics models. Evaluation was based on characteristics of each model using five criteria with implications for small forest management: spatial resolution, number of species the model can simulate, inclusion of spatial structure, modeling approach, and mechanistic detail. While numerous models can be suitable under certain conditions, the review criteria led us to conclude that two models offered the broadest versatility and usability for small forest contexts, SORTIE and FORMIND. This review can help orient and guide small forest managers like those on Jekyll Island who wish to add modeling to their forest management efforts.

(2) In Chapter 3, we collaborated with JIA and other coastal stewards to use structured decision-making to find potential MLO management actions to evaluate the live oak regeneration problem. We first held workshops to identify: the mangers' long-term objectives and shorter-term success indicators; spatial and temporal scales of likely management actions; a set of potential management options; and data, legal, and resource constraints. We then constructed demographic models using empirical data and expert knowledge to estimate parameters for

juvenile tree growth and survival rates associated with alternative tree-planting strategies. The decision-support tool incorporated the models and associated cost estimates of management alternatives in order to project likely outcomes, costs, associated uncertainties, and the degree to which alternatives would meet different management objectives. This process ensured that we capitalized on diverse understandings and perspectives and that the decision support tool would be directly relevant to stewards' values, objectives, and information needs.

(3) In Chapter 4, we explored the effects of deer on native plant and tree seedling abundance to assess whether deer are facilitating the camphor invasion, using an experiment with deer exclosures in one of the small forests on Jekyll Island. Deer herbivory was associated with decreased native understory vegetation cover but did not have an immediate effect on the abundance of native tree seedlings or species richness. Vine species like *Vitis rotundifolia* especially benefitted from excluding deer, yet camphor seedling growth and survival also increased when deer were excluded. Although longer-term herbivory effects on camphor versus native species in this environment are not yet known, these results suggest that controlling deer herbivory may not tip the balance of apparent competition back toward native vegetation, and other restoration efforts are likely needed to control camphor invasion and support the native tree and plant community.

(4) Finally, we used multivariate analyses to understand how abiotic and biotic environmental conditions like soil moisture, elevation, and adult tree composition affect native plant communities and camphor seedlings on Jekyll Island. Because JIA plans to exclude deer and eradicate camphor populations, we also assessed how deer exclosures affect native plant composition through these analyses. Plant community composition did vary with environmental conditions and deer exclosure, though due to the scale of the study, ecological interpretations of

patterns are tentative. Still, our findings point to the value of using environmental conditions to provide helpful contextual information for ecological restoration and invasive species control.

APPENDIX A: CHAPTER 3 SUPPLEMENTARY INFORMATION

Appendix A.1. R code for optimization. This code simulates data drawn from a linear-logit model of survival and linear model of height growth for *Quercus virginiana* seedlings. The models are parameterized to roughly replace the data summaries in Thyroff's thesis, Chapters 2 and 3 (E. Thyroff, 2018).

```
Library(GA)

## DESIGN AND FITNESS TARGET INFORMATION TO PASS INTO FITNESS
FUNCTION
## Height at planting (m)
size0 <- 0.47

## Number of seedlings per treatment group
##   8 groups – combinations of overstory condition, herbivory defense, competing vegetation
defense
n.group <- 80

## Number of years of observation
n.years <- 2

## Optimization target
##   1:2 – Study 1 (ch 3), clearcut vs no thin (fenced, averaged over veg removal);
##   3:6 – Study 2 (ch 2), fenced/annual, fenced/none, not fenced/annual, not fenced/none (all in
clearcut)
target <- c(48.37, 30.34, 119.8, 92.28, 37.58, 40.6) / 100
names(target) <-
c("Ch3.ClrCut","Ch3.NoThin","Ch2.Fncd.Weed","Ch2.Fncd.NoWd","Ch2.NoF.Weed","Ch2.N
oF.NoWd")

n.samp <- 11

## Construct design matrix
data <- data.frame(over = gl(2,2*2*n.group), herb = gl(2,2*n.group), comp = gl(2,n.group))
design <- model.matrix(~ over + herb + comp + over*herb + over*comp + herb*comp, data)



## MODEL PARAMETERS
```

```
## All roughly estimated based on simple manipulations of means in Thyroff thesis

## Mean rates of annual survival and annual growth under ideal conditions:
##   no overstory, no browse, no competition
surv0 <- 0.78  ## mean probability of annual survival
d.ht0 <- 0.380  ## mean height growth (m) per year, conditional on survival

## Additive effects (logit scale) of treatments on annual survival, relative to ideal conditions
phi.over <- -0.67   ## effect of dense overstory
phi.herb <- 0   ## effect of herbivory
phi.comp <- 0   ## effect of competing vegetation

## Additive effects of treatments, relative to ideal, on annual height growth rate (m/yr)
gam.over <- -0.520   ## effect of dense overstory
gam.herb <- -0.421   ## effect of herbivory
gam.comp <- -0.278   ## effect of competing vegetation

## 2-way interactive effects of treatments on annual height growth rate
gam.over.herb <- 0.5     ## Overstory x herbivory (just a guess … no data to support)
gam.over.comp <- 0.240   ## Overstory x competing vegetation
gam.herb.comp <- 0.270   ## Herbivory x competing vegetation

## Individual variation (normal SD) – only a guess … no data to support
sd.surv <- 0.3   ## annual survival (logit scale)
sd.size <- 0.05  ## height (m)

## Collect the parameters into vectors
# p <- c(phi.over, phi.herb, phi.comp)
# g <- c(gam.over, gam.herb, gam.comp, gam.over.herb, gam.over.comp, gam.herb.comp)
# s <- c(sd.surv, sd.size)



#### FITNESS FUNCTION
####   FIRST 13 ARGUMENTS ARE VARIABLES TO BE OPTIMIZED, LAST 6 ARE
DESIGN AND TARGET VARIABLES
objfn <- function(surv0, d.ht0,
                  phi.over, phi.herb, phi.comp,
                  gam.over, gam.herb, gam.comp, gam.over.herb, gam.over.comp, gam.herb.comp,
                  sd.surv, sd.size,
                  n.samp, n.group, design, size0, target, prt.sim){

  ## START FUNCTION
  ## input: 13 variables (surv0, d.ht0, …, sd.size)
  ##        and 6 fixed quantities (n.samp, n.group, design, size0, target, prt.sim)
  ## return: diff
```

```
  p <- c(phi.over, phi.herb, phi.comp)
  g <- c(gam.over, gam.herb, gam.comp, gam.over.herb, gam.over.comp, gam.herb.comp)
  s <- c(sd.surv, sd.size)

  if(prt.sim==1) {
    cat(“\nDesign values\n -Samples per group: “, n.group, “\n -Initial size (m): “, size0, “\n”)
    cat(“\nParameter values\n -Mean survival probability: “, surv0, “\n -Mean height growth
(m/yr): “, d.ht0)
    cat(“\n -Survival effects (over, herb, comp): “)
    cat(p, sep=”, “)
    cat(“\n -Growth main effects (over, herb, comp): “)
    cat(g[1:3], sep=”, “)
    cat(“\n -Growth interactions (over.herb, over.comp, herb.comp): “)
    cat(g[4:6], sep=”, “)
    cat(“\n -Individual variation (survival, growth): “)
    cat(s, sep=”, “)
    cat(“\n\nTarget values\n”)
    print(target)
    cat(“\n”)
  }

  ## Compute treatment group effects
  surv.eff <- design[,2:4] * matrix(rep(p, n.group*8),ncol=3,byrow=TRUE)
  grow.eff <- design[,2:7] * matrix(rep(g, n.group*8),ncol=6,byrow=TRUE)

  diff <- rep(NA, n.samp)

  for (k in 1:n.samp){

    ## Compute individual annual survival probabilities
    surv <- log(surv0/(1-surv0)) + rowSums(surv.eff) + rnorm(n.group*8, 0, s[1])
    surv.p <- 1 / (1 + exp(-surv))
    surv.p.m <- surv.p^(1/12)    ## monthly survival

    ## Compute individual annual height growth
    grow <- d.ht0 + rowSums(grow.eff) + rnorm(n.group*8, 0, s[2])
    grow.m <- grow/12          ## monthly growth

    ## Initialize time series of individuals
    h.t <- matrix(0, nrow=n.group*8, ncol=3)    ## time series of heights
    h.t[,1] <- size0

    ## Track each each individual through time
    m <- c(9,14)  ## Period lengths (months)
    for (t in 2:3){
```

```
      ## if height in prior period >0 (alive last period), then draw a survival outcome
      surv.t <- rbinom(n.group*8,1,surv.p.m^m[t-1]) * (h.t[,t-1]>0)

      ## if survived to this period, then add height growth
      h.t[,t] <- pmax(0, (h.t[,t-1]>0 & surv.t>0) * (h.t[,t-1] + grow.m*m[t-1]))

    }

    ## Create object for data export
    out <- data.frame(cbind(design[,2:4], h.t))

    ## Overstory treatment x competing vegetation treatment at 9 months under no-browse
(fenced) condition
    ##   (compare to Thyroff Fig. 3.6)
    sel <- out[out[,2]==0,]
    sums1 <- tapply(sel[,5], sel[,1], sum)
    sel[(sel[,5]>0),5] <- 1
    counts1 <- tapply(sel[,5], sel[,1], sum)
    means1 <- sums1/counts1
    means1[is.na(means1)] <- 0

    ## Herbivory treatment x competing vegetation treatment at 23 months under open overstory
condition
    ##   (compare to Thyroff Fig. 2.3)
    sel <- out[out[,1]==0,]
    sums2 <- tapply(sel[,6], list(sel[,2], sel[,3]), sum)
    sel[(sel[,6]>0),6] <- 1
    counts2 <- tapply(sel[,6], list(sel[,2], sel[,3]), sum)
    means2 <- sums2/counts2
    means2[is.na(means2)] <- 0

    if(prt.sim==1){
      cat(k,” “)
      cat(means1,sep=”      “)
      cat(“    “, t(means2), sep=”     “)
      cat(“\n”)
    }

    diff[k] <- sum( (matrix(t(rbind(means1, means2[1,], means2[2,])),nrow=1,byrow=TRUE) –
target)^2 )

  }

  diff0 <- median(diff)
  if(prt.sim==1) cat(“\nMedian distance from target (n =”, n.samp, “): “, diff0, “\n”)
```

```
  return(-diff0)

  ### END FUNCTION
}


## Test fitness function with these parameter values
diff <- objfn(surv0, d.ht0, phi.over, phi.herb, phi.comp, gam.over, gam.herb, gam.comp,
            gam.over.herb, gam.over.comp, gam.herb.comp, sd.surv, sd.size,
            n.samp, n.group, design, size0, target, prt.sim=1)
```

Appendix A.2. R code for seedling transition matrix model. This model simulates data drawn from a linear-logit model of survival and a linear model of height growth for *Quercus virginiana* seedlings. The models are parameterized to roughly replace the data summaries in Thyroff's thesis, Chapters 2 and 3.

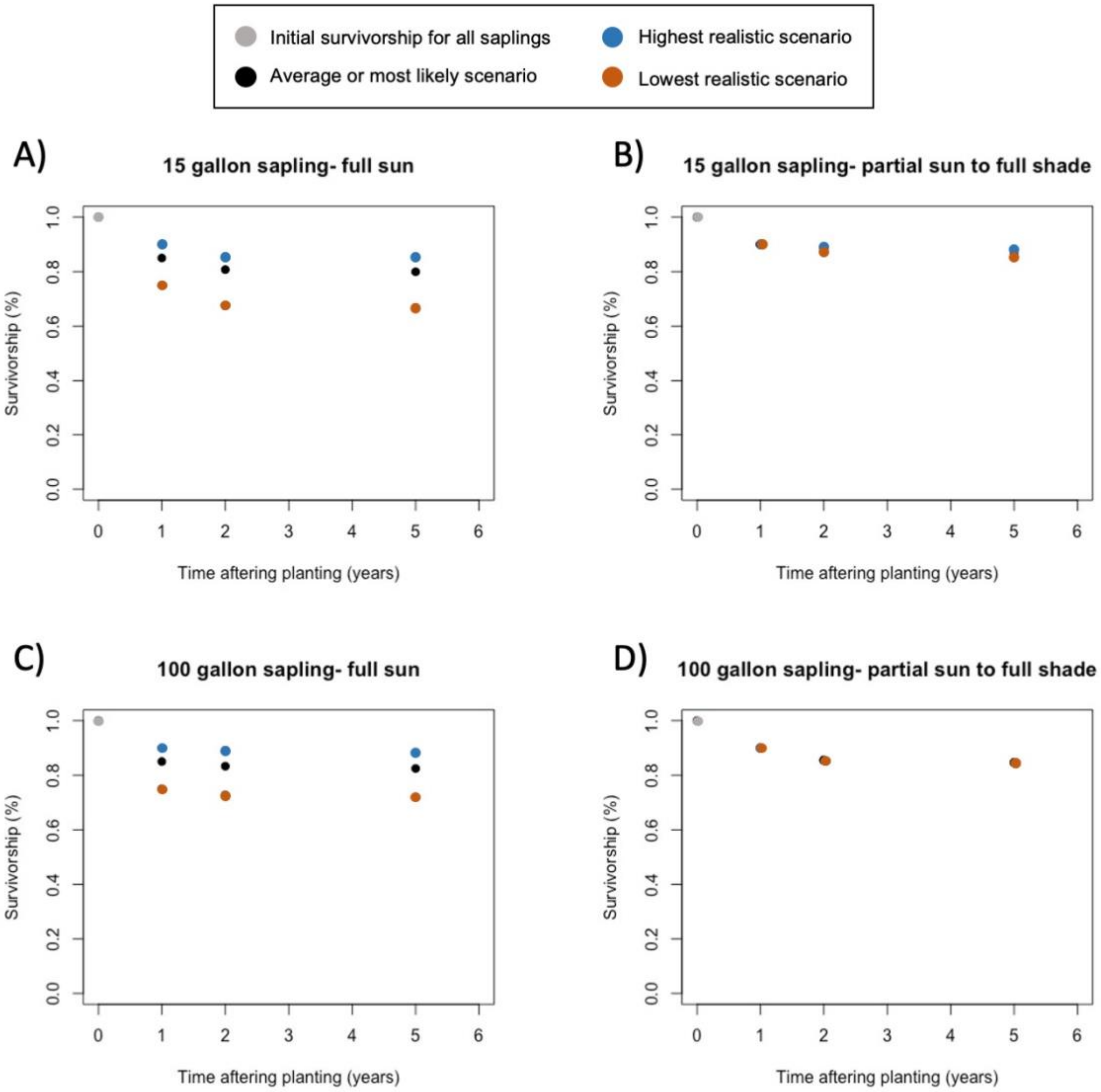
```
## MODEL SETUP
## Height at planting (m)
size0 <- 0.47

## Number of seedlings per treatment group
##   8 groups – combinations of overstory condition, herbivory defense, competing vegetation defense
n.group <- 80

## Number of years of observation
n.years <- 5

## To simulate all treatments, set trt.sel=NA
##   Otherwise, specify treatment as 0/1 triplet: (canopy closed=1, unfenced=1, unweeded=1)
trt.sel <- NA
trt.sel <- c(0,1,1)


## MODEL PARAMETERS
##  13 parameter values loaded into a vector, then named in order in the lines below
```

```
## Initial estimates
##  These are roughly estimated based on simple manipulations of means in Thyroff thesis
x <- c(0.78,     ## mean probability of annual survival
      0.380,    ## mean height growth (m) per year, conditional on survival
      -0.67,    ## (survival) effect of dense overstory
      0,        ## (survival) effect of herbivory
      0,        ## (survival) effect of competing vegetation
      -0.520,   ## (growth) effect of dense overstory
      -0.421,   ## (growth) effect of herbivory
      -0.278,   ## (growth) effect of competing vegetation
      0.5,      ## (growth) overstory x herbivory (just a guess … no data to support)
      0.240,    ## (growth) overstory x competing vegetation
      0.270,    ## (growth) herbivory x competing vegetation
      0.3,      ## (variation) annual survival (just a guess … no data to support)
      0.05)     ## (variation) height growth (m) (just a guess … no data to support)

## Solution from optimization
load(file=”GA_n.samp=101,n.group=80,pop=100,iter=1000.Rdata”)
x <- GA@solution


## Mean rates of annual survival and annual growth under ideal conditions:
##   no overstory, no browse, no competition
surv0 <- x[1]  ## mean probability of annual survival
d.ht0 <- x[2]  ## mean height growth (m) per year, conditional on survival

## Additive effects (logit scale) of treatments on annual survival, relative to ideal conditions
phi.over <- x[3]   ## effect of dense overstory
phi.herb <- x[4]   ## effect of herbivory
phi.comp <- x[5]   ## effect of competing vegetation

## Additive effects of treatments, relative to ideal, on annual height growth rate (m/yr)
gam.over <- x[6]   ## effect of dense overstory
gam.herb <- x[7]   ## effect of herbivory
gam.comp <- x[8]   ## effect of competing vegetation

## 2-way interactive effects of treatments on annual height growth rate
gam.over.herb <- x[9]     ## Overstory x herbivory
gam.over.comp <- x[10]    ## Overstory x competing vegetation
gam.herb.comp <- x[11]    ## Herbivory x competing vegetation

## Individual variation (normal SD)
sd.surv <- x[12]  ## annual survival (logit scale)
sd.size <- x[13]  ## height (m)
```

```
## Collect the parameters into vectors
p <- c(phi.over, phi.herb, phi.comp)
g <- c(gam.over, gam.herb, gam.comp, gam.over.herb, gam.over.comp, gam.herb.comp)
s <- c(sd.surv, sd.size)

## Construct design matrix
data <- data.frame(over = gl(2,2*2*n.group), herb = gl(2,2*n.group), comp = gl(2,n.group))
design <- model.matrix(~ over + herb + comp + over*herb + over*comp + herb*comp, data)

## Compute treatment group survival effects, and individual annual survival probabilities
surv.eff <- design[,2:4] * matrix(rep(p, n.group*8),ncol=3,byrow=TRUE)
surv <- log(surv0/(1-surv0)) + rowSums(surv.eff) + rnorm(n.group*8, 0, s[1])
surv.p <- 1 / (1 + exp(-surv))


## Compute treatment group height effects, and individual annual height growth
grow.eff <- design[,2:7] * matrix(rep(g, n.group*8),ncol=6,byrow=TRUE)
grow <- d.ht0 + rowSums(grow.eff) + rnorm(n.group*8, 0, s[2])

## Identify rows indicating focal treatment, extract corresponding rows from input data
if(is.na(trt.sel[1])){ sel <- rep(1,n.group*8) } else { sel <- apply(trt.sel==design[,2:4],1,prod) }
surv.p <- surv.p[(sel==1)]
grow <- grow[(sel==1)]

## Histograms of individual-level survival probability and growth increment
hist(surv.p, main=paste0("Survival probability, trt.sel = ", toString(trt.sel)))

hist(surv.p, main=paste0("Survival probability of open canopy,browse protection,
                    and suppressed understory vegetation                        "),
    xlab="Probability of survival")
hist(grow, main=paste0("Growth increment, trt.sel = ", toString(trt.sel)))


## Initialize time series of individuals
h.t <- matrix(0, nrow=sum(sel==1), ncol=n.years+1)    ## time series of heights

h.t[,1] <- size0

## Initialize matrix to store height achievement probabilities at each year
##  (1.5, 2.0, 2.5 m thresholds)
h.thresh <- c(1.5, 2.0, 2.5)
alive.at.height <- matrix(0, nrow=n.years+1, ncol=3)
colnames(alive.at.height) <- paste("Ht(m) ", h.thresh, sep="")
rownames(alive.at.height) <- paste("Year ", (0:n.years), sep="")

## Track each each individual through time
```

```
namestring <- "Time.0"
for (t in 2:(n.years+1)){

  ## if height in prior year >0 (alive last year), then draw a survival outcome
  surv.t <- rbinom(length(surv.p),1,surv.p) * (h.t[,t-1]>0)

  ## if survived to this year, then add height growth
  h.t[,t] <- pmax(0, (h.t[,t-1]>0 & surv.t>0) * (h.t[,t-1] + grow))

}


## Plot histograms by year
for (t in 2:(n.years+1)){

  namestring <- cbind(namestring, paste0("Time.",t-1))

  hist(h.t[,t], main=paste0("Height, trt.sel = ", toString(trt.sel),", year ",t-1),
       xlim=c(0,ceiling(max(h.t))), ylim=c(0,nrow(h.t)))

  alive.at.height[t,] <- colSums(outer(h.t[,t], h.thresh, '>')) / length(surv.p)

}

## Print probability of achieving height thresholds at each year
cat("\nProbability of achieving height at each year (trt.sel =", toString(trt.sel), ")\n")
print(alive.at.height)
```

Appendix A.3. A-D: Estimates of sapling survival for each stock-light availability combination. Estimates are elicited from one stakeholder, Clint Gawron, Landscape Superintendent at the Jekyll Island Authority. Survivorship estimates include average or most likely scenario, highest realistic scenario, and lowest realistic scenario. Average or most likely scenario was used to determine the most effective and most desirable management alternative prior to evaluation of uncertainty.



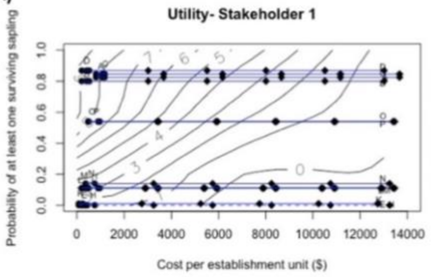
Appendix A.4. Cost estimate assumptions ($). Costs are initially estimated by establishment unit (18m x 18m) but can be scaled up to reduce cost of some bulk items. All information is elicited from stakeholders unless noted from Forestry Suppliers or The Home Depot.

- A) Overstory treatment (removal by individual adult tree). Maximum number of trees that can be removed/establishment unit is 5.
    - a. None—$0
    - b. Jekyll Island staff felling and removing—$500
    - c. Independent contractor felling and removing—$2500
    - d. Independent contractor felling and Jekyll Island staff removing—$1575
    - e. Forestry whole-sale—$0
- B) Tree type purchased
    - a. Larger sapling at 4-inch DBH and 100 gallons—$800/tree
    - b. Smaller sapling at 1 ¾ inch-2 inch DBH and 15 gallons—$100/tree
        - i. Assumption is that protective plastic tree wrapping will be purchased to deter deer rubbing. The Home Depot: $5.48/ 4in. x 20ft. that can wrap up to 4 small saplings.
    - c. Seedling at 12-18 inches tall—$1/tree for first 1000, $0.70/tree for 1000+
- C) Staff and volunteer labor/hour options:
    - a. $40/hour
    - b. $20/hour
    - c. $0/hour (volunteer)
- D) Watering intensity estimates (sapling only)
    - a. Man-hours to water saplings for each watering option
        - i. Water buffalo—at least 5 hours/year (8 minutes/tree/bout. If planting in November, 2 bouts/month November-March. About 4 bouts/week April-October.)
        - ii. Gravity-fed pump—at least 10 hours/year (16 minutes/tree/bout. If planting in November, 2 bouts/month November-March. About 4 bouts/week April-October.)
    - b. Planting gel--$87.50/10-lb bag, Forestry Suppliers
        - i. 1 ounce used/ 5 gallons of tree volume.
            1. 15 gallons = 3 ounces
            2. 100 gallons = 20 ounces
            3. Cost can be reduced if using for multiple establishment units.
    - c. Additional efforts to retain moisture such as mulch or leaves are assumed at no additional cost.
- E) Planting time (man-hours)/tree type purchased. Seedling options include browse protection and no browse protection.
    - a. Larger sapling
        - i. Will require 4 staff members or volunteers. Time to plant = 1 hour.
    - b. Smaller sapling
        - i. 1 person, time to plant = 1 hour
        - ii. 2 people, time to plant = 30 minutes
    - c. Seedling
        - i. No browse protection

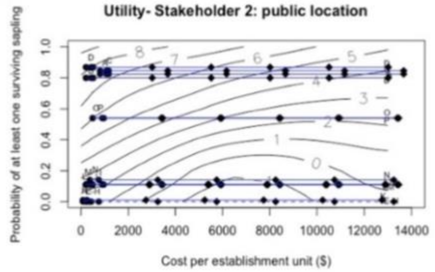
        1. 1 person, seedlings planted per hour= 10
        2. 2 people, seedlings planted per hour= 20
        3. 3 people, seedlings planted per hour= 30
        4. 4 people, seedlings planted per hour= 40
        5. 5 people, seedlings planted per hour= 50
    ii. Browse protection—planting includes applying cages to individual tree seedling
        1. 1 person, seedlings planted per hour = 4
        2. 2 people, seedlings planted per hour = 8
        3. 3 people, seedlings planted per hour = 12
        4. 4 people, seedlings planted per hour =16
        5. 5 people, seedlings planted per hour = 20
F) If browse protection, cost of materials: Forestry Suppliers.
    a. Rigid seedling protector tube, 5'' x 48'':
        i. $281/pack of 150 cages when ordering 1-3 packs
        ii. $259/pack of 150 cages when ordering 4-9 packs
        iii. $242/pack of 150 cages when ordering 10+ packs
    b. Protex pro/gro solid tube tree protector, 48'':
        i. $3.75/1-199 protectors
        ii. $3.50/200-399 protectors
        iii. $3.25/400+ protectors
    c. Tubex tree shelter:
        i. $26.95/pack of 5 (1-9 packs)
        ii. $23.25/pack of 5 (10+ packs)
G) If vegetation control, cost of materials:
    a. $60/gallon on average for glyphosate, assuming a maximum of 2 gallons/EU
    b. Materials that are assumed not costly: herbicide backpack and sprayers, clippers, mowers, and other supplies for manual removal
H) If vegetation control, man-hours (or minutes) for application:
    a. Spraying herbicide:
        i. 1 person- 15 minutes
        ii. 2 people- 7.5 minutes
        iii. 3 people- 3.75 minutes
        iv. 4 people- 1.875 minutes
        v. 5 people- 0.9375 minutes
    b. Manually removing vegetation:
        i. 1 person- 1.5 hours
        ii. 2 people- 45 minutes
        iii. 3 people- 30 minutes
        iv. 4 people- 15 minutes
        v. 5 people- 7.5 minutes

Appendix A.5. Management alternatives on utility contours for each individual stakeholder and island. Alternatives are labeled according to scenarios A-P in Table 3.5, and each line segment corresponds to the minimum and maximum range of cost estimates possible for a single management alternative (i.e. no effect on ecological outcome but could increase cost in overstory tree removal or extensive labor). **A-E:** Contour plots that contain utility information for each individual stakeholder interviewed from Jekyll Island. Pairings of B-C and D-E demonstrate utility values for the same stakeholder but at sites that have different public visibility and accessibility. **F-G:** Aggregated contour plots that contains utility information for all stakeholders from Jekyll Island. This pairing demonstrates utility values for the same island but at sites that have different public visibility and accessibility. **H-I:** Contour plots that contain utility information for one stakeholder interviewed from Sapelo Island. This pairing demonstrates the utility values for the same person but at sites that represent different MLO habitat value.

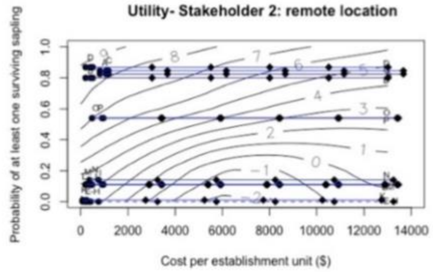
A)


Utility- Stakeholder 1

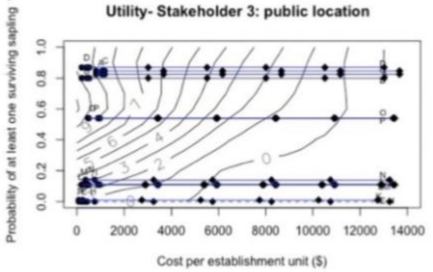
B)


Utility- Stakeholder 2: public location

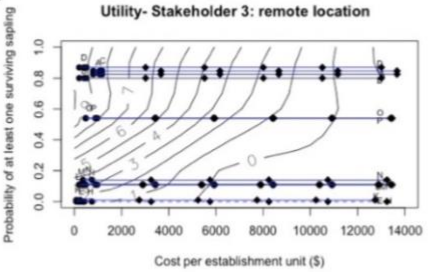
C)


Utility- Stakeholder 2: remote location

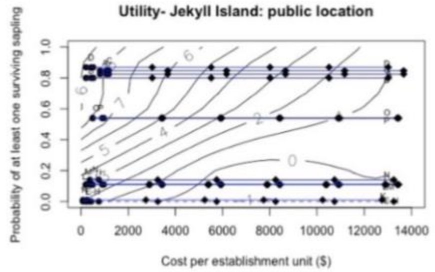
D)


Utility- Stakeholder 3: public location

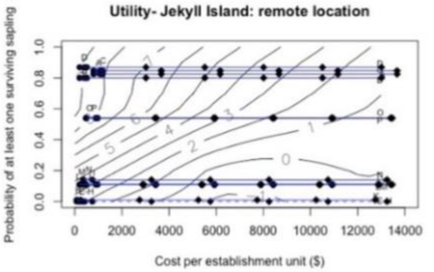
E)


Utility- Stakeholder 3: remote location

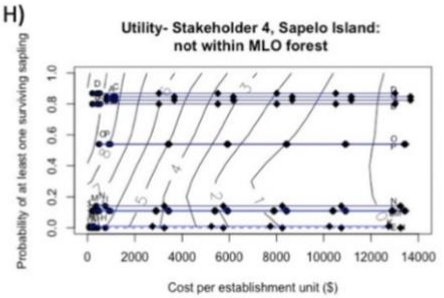
F)


Utility- Jekyll Island: public location

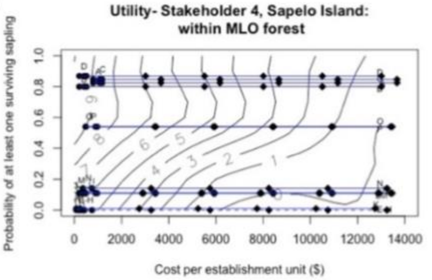
G)


Utility- Jekyll Island: remote location

H)


Utility- Stakeholder 4, Sapelo Island: not within MLO forest

I)


Utility- Stakeholder 4, Sapelo Island: within MLO forest

APPENDIX B: CHAPTER 4 SUPPLEMENTARY INFORMATION

Appendix B.1. ANOVA table for the effects of deer on total understory percent cover and percent cover by growth form in April 2018 before plots and exclosures were established, May 2019, and May 2020 and change in number of species present between April 2018 and May 2020.

	Spring 2018					Spring 2019					Spring 2020				
Source	df	SS	MS	F-ratio	p-value	df	SS	MS	F-ratio	p-value	df	SS	MS	F-ratio	p-value
Total understory percent cover															
Fencing treatment	1	29.650	29.650	0.7735	0.390	1	748.453	748.453	3.663	***0.071****	1	1948.543	1948.540	8.332	***0.001****
Error	19	728.322	38.333			19	3881.924	204.312			19	4443.410	233.860		
Total	20	757.972				20	4630.377				20	6391.953			
Total fern cover															
Fencing treatment	1	3.324	3.324	0.071	0.793	1	14.315	14.315	0.081	0.779	1	142.013	142.013	0.956	0.341
Error	19	890.804	46.884			19	3342.781	175.936			19	2822.079	148.53		
Total	20	894.128				20	3357.100				20	2964.09			
Total shrub cover															
Fencing treatment	1	12.796	12.796	0.991	0.332	1	44.353	44.353	1.247	0.278	1	88.045	88.0493	1.487	0.238
Error	19	245.331	12.912			19	675.927	35.575			19	1124.779	59.199		

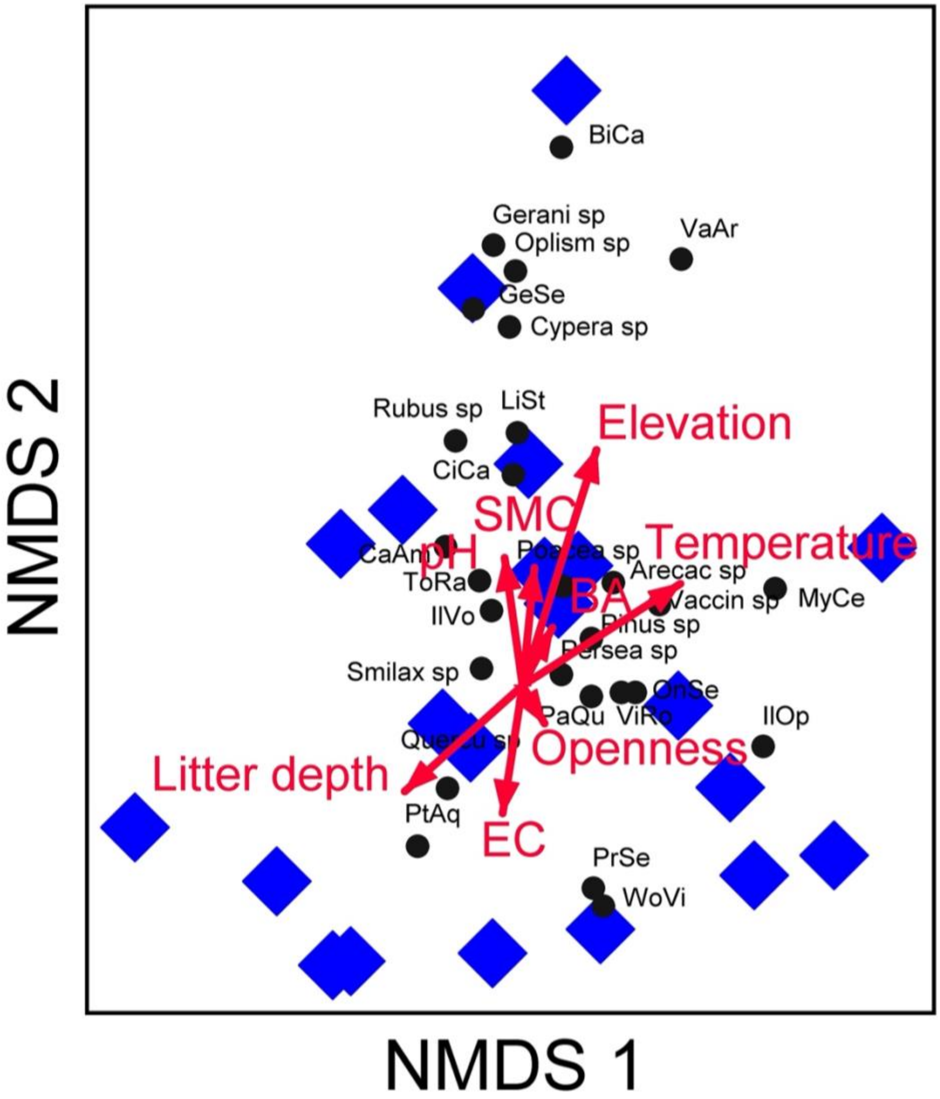
Total	20	258.126				20	720.280				20	1212.823			
Total palm cover															
Fencing treatment	1	0.728	0.728	0.068	0.797	1	0.390	0.390	0.023	0.882	1	0.310	0.310	0.021	0.886
Error	19	203.178	10.694			19	327.000	17.211			19	278.468	14.656		
Total	20	203.905				20	327.389				20	278.778			
Total vine cover															
Fencing treatment	1	17.966	17.966	1.079	0.312	1	456.170	456.169	4.890	***0.040****	1	1085.173	1085.17	5.149	***0.035****
Error	19	316.320	16.648			19	1773.155	93.324			19	4004.346	210.76		
Total	20	334.285				20	2229.324				20	5089.519			
Total forb cover															
Fencing Treatment	1	0.163	0.163	0.0879	0.770	1	0.075	0.075	0.013	0.9096	1	6.434	6.434	10.721	***0.0040 ****
Error	19	35.248	1.855			19	107.952	5.682			19	11.404	0.600		
Total	20	35.411				20	108.027				20	17.838			
Total grasses/sedges cover															
Fencing Treatment	1	1.0178	1.0178	1.261	0.276	1	1.558	1.558	1.206	0.2859	1	1.306	1.306	1.209	0.2854
Error	19	15.340	0.807			19	24.557	1.293			19	20.531	1.081		
Total	20	16.358				20	26.115				20	21.837			

APPENDIX C: CHAPTER 5 SUPPLEMENTARY INFORMATION

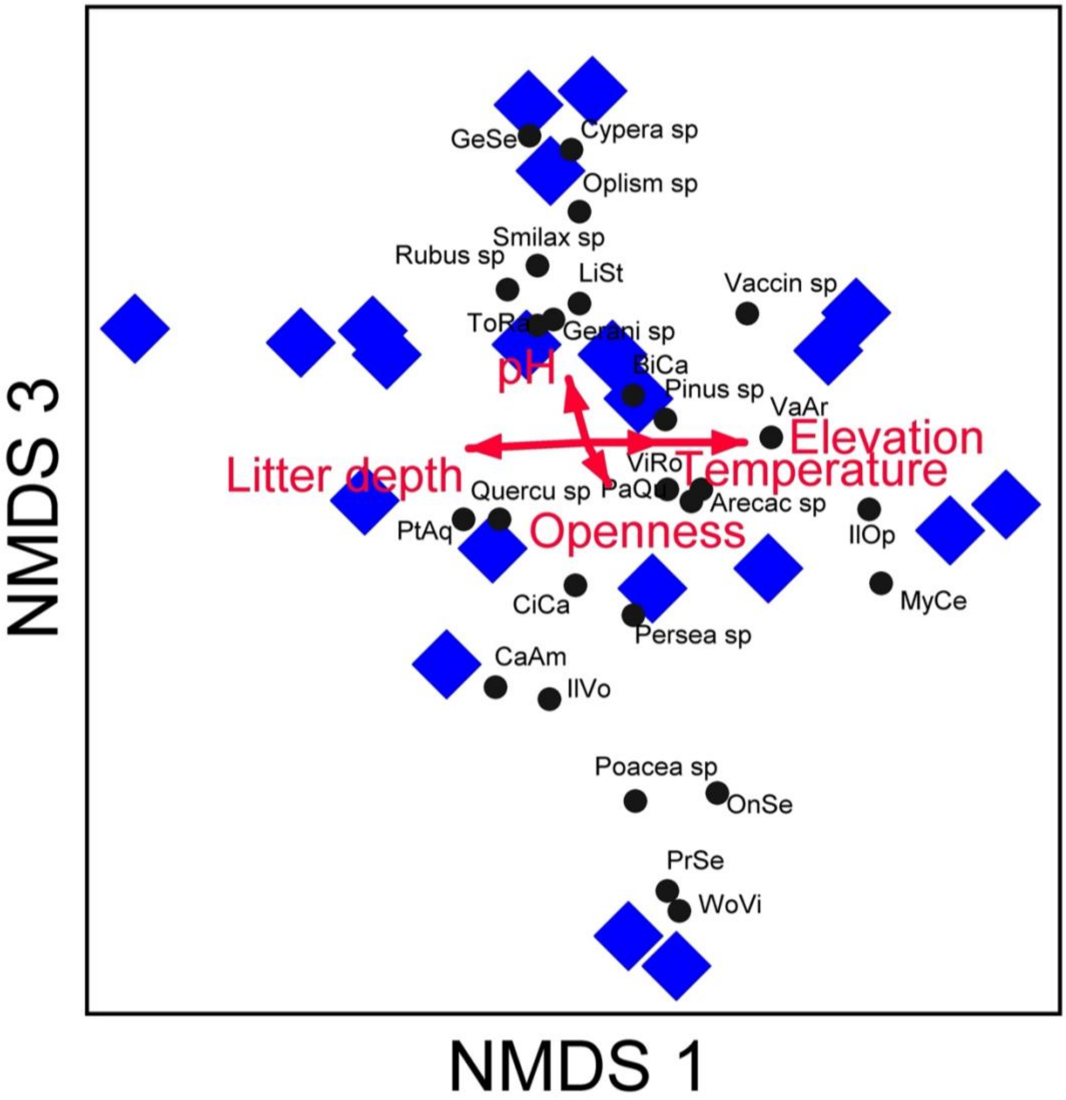
Appendix C.1. Species abbreviations and their corresponding species, genus, or family name.

Species Abbreviation	**Classification**	**Species, genus, or family name**
OnSe	Species	Onoclea sensibilis
WoVi	Species	Woodwardia virginica
PtAq	Species	Pteridium aquilinum
MyCe	Species	Myrica cerifera
CaAm	Species	Callicarpa americana
VaAr	Species	Vaccinium arboreum
Vaccin sp	Genus	Vaccinium
IlVo	Species	Ilex vomitoria
Arecac sp	Family	Arecaceae
PaQu	Species	Parthenocissus quinquefolia
Smilax sp	Genus	Smilax
GeSe	Species	Gelsemium sempervirens
ViRo	Species	Vitus rotundifolia
ToRa	Species	Toxicodendron radicans
Rubus sp	Genus	Rubus
Gerani sp	Genus	Geranium
Poacea sp	Family	Poaceae
Oplism sp	Genus	Oplismenus
Cypera sp	Family	Cyperaceae
IlOp	Species	Ilex opaca
Quercu sp	Genus	Quercus
Persea sp	Genus	Persea
Pinus sp	Genus	Pinus
LiSt	Species	Liquidambar styraciflua
PrSe	Species	Prunus serotina
BiCa	Species	Bignonia capreolata
CiCa	Species	Cinnamomum camphora

Appendix C.2. Non-metric multidimensional scaling (NMDS) ordination plot of species abundances within sample plot space versus environmental variables. Axis 1 vs Axis 2 is shown. Environmental variables that had at least a weak or moderate correlation ($r^2 = 0.16$ as the cutoff) are shown. Species are coded by the first two letters of the genus and species name (e.g. *Cinnamomum camphora* = CiCa) or the first letters of family classes or genus name (e.g. *Cypera* sp. = *Cyperaceae* family, *Pinus* sp. = *Pinus* spp.



Appendix C.3. Non-metric multidimensional scaling (NMDS) ordination plot of species abundances within sample plot space versus environmental variables. Axis 1 vs Axis 3 is shown. Environmental variables that had at least a weak or moderate correlation ($r^2 = 0.16$ as the cutoff) are shown. Species are coded by the first two letters of the genus and species name (e.g. *Cinnamomum camphora* = CiCa) or the first letters of family classes or genus name (e.g. *Cypera* sp. = *Cyperaceae* family, *Pinus* sp. = *Pinus* spp.



Appendix C.4. NMDS ordination scores (3 axes) for species abundance data from April 2018.

Plot	Axis 1	Axis 2	Axis 3
11a	-0.9101	0.4963	0.2512
12	-0.1766	-0.6387	0.0164
14	-1.7381	-0.0587	-0.2601
15	-0.2102	-0.5192	-0.1961
22	1.1088	-0.5263	-0.6413
24a	0.1150	0.3250	-0.5834
29	0.2443	-0.3243	0.1989
30a	0.7070	0.4252	0.4937
8	0.1419	0.1335	0.2237
11b	-0.4977	-0.2463	0.1870
17	-0.5164	0.0364	0.5477
21	-0.3752	-0.3253	-0.9865
24b	0.3996	0.8450	0.3123
25	0.1812	0.5685	-0.5485
27	0.0719	-0.1867	-0.4836
28	0.4112	0.2449	-0.8999
30b	0.7908	0.1197	0.4823
32	0.5020	0.2847	0.7943
33	0.4117	-0.0329	1.0608
37	-1.1846	0.7641	0.0411
7	0.5234	-1.3849	-0.0100

Appendix C.5. Pearson correlations with non-metric multidimensional scaling (NMDS) ordination axes. NMDS was conducted on April 2018 species abundances.

	Axis 1		Axis 2		Axis 3	
Species	**r^a**	**r^2**	**r^a**	**r^2**	**r^a**	**r^2**
OnSe	0.211	0.045	-0.01	0	-0.547**	0.299
WoVi	0.112	0.013	-0.249	0.062	-0.547**	0.299
PtAq	-0.423*	0.179	-0.509**	0.259	-0.249	0.062
MyCe	0.453*	0.205	0.141	0.020	-0.206	0.042
CaAm	-0.124	0.015	0.177	0.031	-0.316*	0.100
VaAr	0.273	0.075	0.588**	0.346	0.007	0.000
Vaccin sp	0.305*	0.093	0.147	0.022	0.238	0.057
IlVo	-0.072	0.005	0.135	0.018	-0.468*	0.219
Arecac sp	0.275	0.075	0.253	0.064	-0.145	0.021
PaQu	0.491*	0.241	-0.062	0.004	-0.270	0.073
Smilax sp	-0.155	0.024	0.053	0.003	0.535**	0.286
GeSe	-0.065	0.004	0.401*	0.161	0.336*	0.113

ViRo	0.578**	0.334	-0.027	0.001	-0.224	0.050
ToRa	-0.190	0.036	0.371*	0.137	0.420*	0.176
Rubus sp	-0.149	0.022	0.431*	0.185	0.277	0.077
Gerani sp	-0.061	0.004	0.717**	0.515	0.207	0.043
Poacea sp	0.070	0.005	0.136	0.019	-0.504**	0.254
Oplism sp	-0.016	0.000	0.754**	0.569	0.435*	0.189
Cypera sp	-0.028	0.001	0.604**	0.365	0.509**	0.259
IlOp	0.618**	0.382	-0.122	0.015	-0.138	0.019
Quercu sp	-0.257	0.066	-0.275	0.076	-0.213	0.046
Persea sp	0.201	0.040	0.052	0.003	-0.736**	0.541
Pinus sp	0.586**	0.343	0.339*	0.115	0.172	0.030
LiSt	-0.018	0.000	0.598**	0.358	0.343*	0.117
PrSe	0.099	0.010	-0.231	0.053	-0.528**	0.279
BiCa	0.054	0.003	0.600**	0.360	0.054	0.003
CiCa	-0.037	0.001	0.582**	0.339	-0.405*	0.164

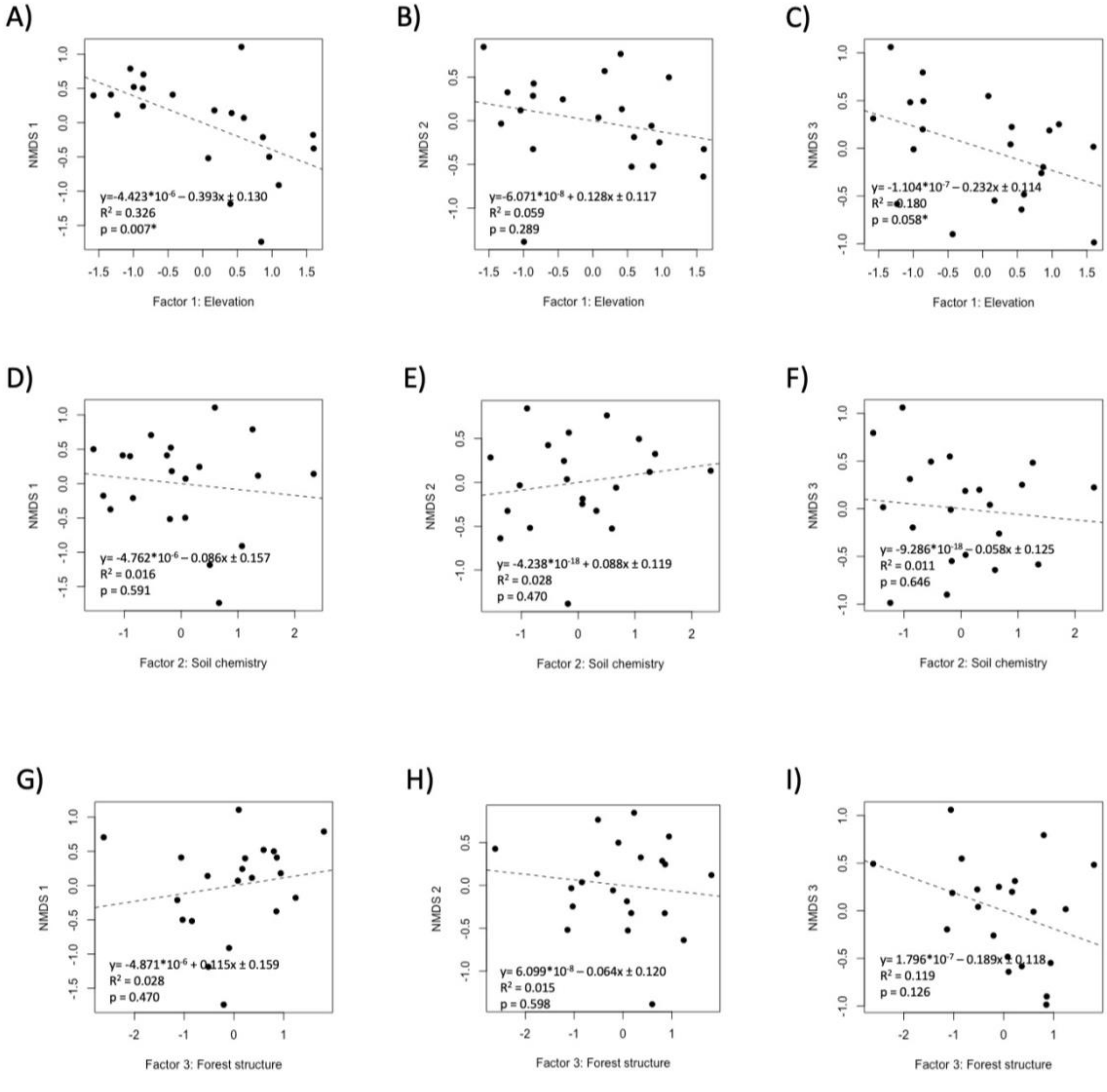
[a]= r, Pearson correlation coefficient
*= significant association between species and axis score, moderate correlation (0.3 < |r| < 0.5) (Kent State University, 2022)
**= significant association between species and axis score, high correlation (0.5 < |r|) (Kent State University, 2022)

Appendix C.6. The ordination scores for the first three axes extracted from polar ordination analysis on environmental variables by plot.

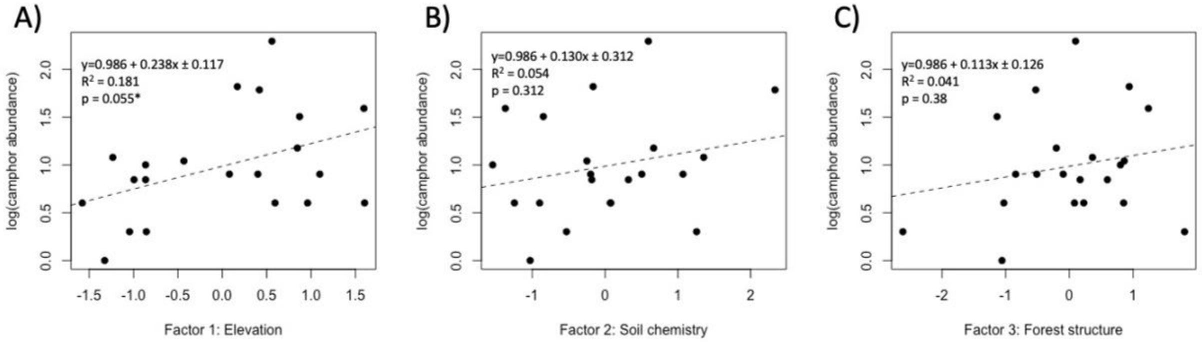
Plot	Factor 1	Factor 2	Factor 3
11a	1.09789	1.07089	-0.09759
12	1.59461	-1.36890	1.24041
14	0.84536	0.66667	-0.20531
15	0.87016	-0.84766	-1.13598
22	0.55899	0.59455	0.09692
24a	-1.23298	1.35434	0.36186
29	-0.86412	0.32113	0.16703
30a	-0.85570	-0.52943	-2.61511
8	0.41724	2.33296	-0.52955
11b	0.96009	0.07244	-1.02976
17	0.08047	-0.19791	-0.84353
21	1.60235	-1.24365	0.85186
24b	-1.57711	-0.89871	0.22472
25	0.16943	-0.16472	0.94007
27	0.59418	0.07847	0.07963
28	-0.43297	-0.24961	0.86086

30b	-1.04459	1.25757	1.80815
32	-0.86405	-1.54294	0.80190
33	-1.32450	-1.02862	-1.05904
37	0.40015	0.50484	-0.51333
7	-0.99491	-0.18171	0.59581

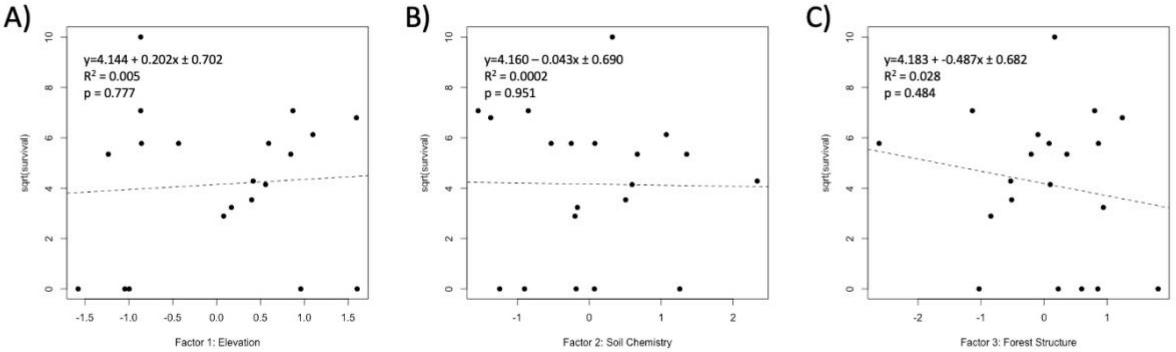
Appendix C.7. A-F: The first three factor loadings from the PCA-derived ordination of environmental variables linearly regressed with the three NMDS ordination axes. NMDS ordination was conducted on April 2018 species abundance data. **A-C:** Factor 1 (elevation) vs NMDS 1-3, **D-F:** Factor 2 (soil chemistry) vs NMDS 1-3, **G-I:** Factor 3 (forest structure) vs NMDS 1-3. Linear equations, R^2 values, and p values (* = significant p value, <= 0.06) are presented on their corresponding graph.



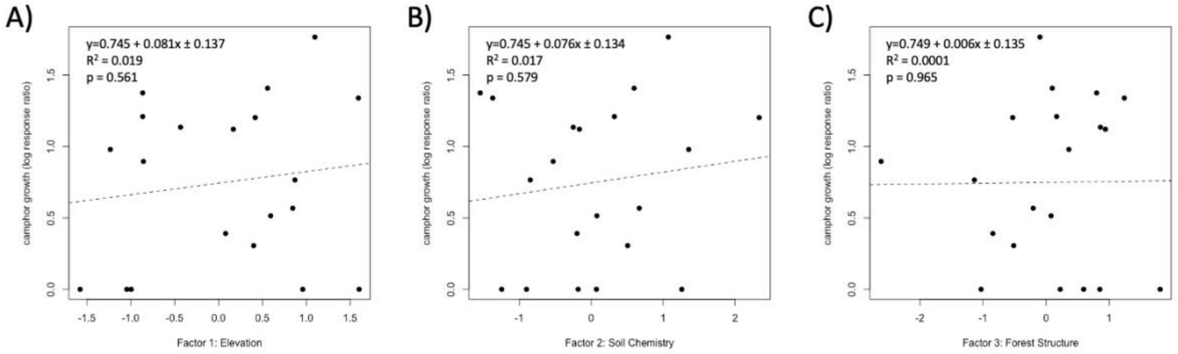
Appendix C.8. A-C: The first three factor loadings from the PCA-derived ordination of environmental variables linearly regressed with initial camphor seedling abundance: (A) elevation, (B) soil chemistry, and (C) forest structure. Linear. Linear equations, R^2 values, and p values (* = significant p value, <= 0.06) are presented on their corresponding graph.



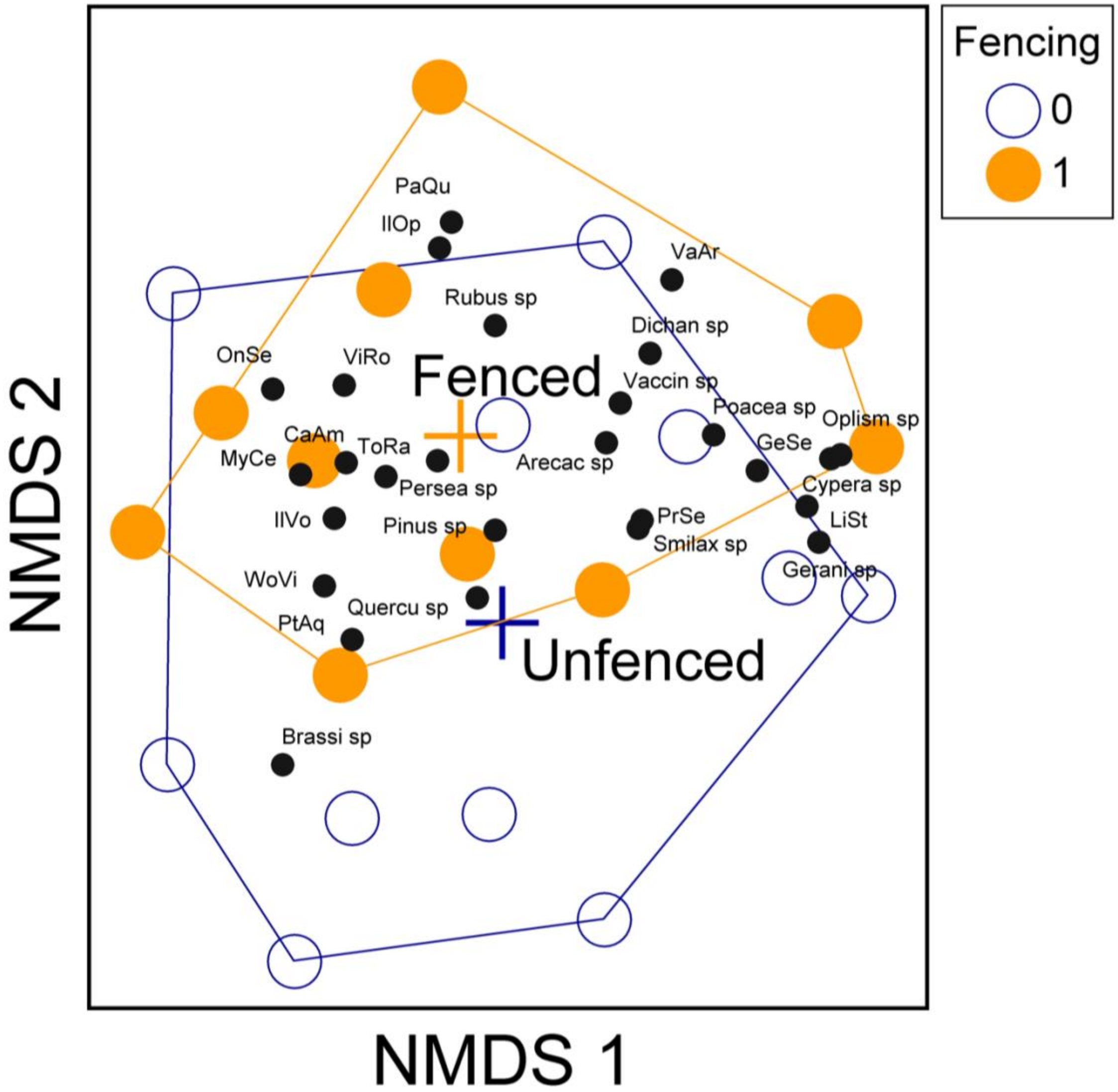
Appendix C.9. A-C: The first three factor loadings from the PCA-derived ordination of environmental variables linearly regressed with camphor survivorship: (A) elevation, (B) soil chemistry, and (C) forest structure. Linear. Linear equations, R^2 values, and p values (* = significant p value, <= 0.06) are presented on their corresponding graph.



Appendix C.10. A-C: The first three factor loadings from the PCA-derived ordination of environmental variables linearly regressed with camphor growth (log response ratio): (A) elevation, (B) soil chemistry, and (C) forest structure. Linear equations, R^2 values, and p values (* = significant p value, <= 0.06) are presented on their corresponding graph.



Appendix C.11. Non-metric multidimensional scaling (NMDS) ordination plot of May 2020 spring abundance, after two years of deer exclusion—fenced=1 (10 plots) vs unfenced=0 (10 plots). Axis 1 vs 2 is shown. Species are coded by the first two letters of the genus and species name (e.g. *Cinnamomum camphora* = CiCa) or the first letters of family classes or genus name (e.g. *Cypera* sp. = *Cyperaceae* family, *Pinus* sp. = *Pinus* spp.



Appendix C.12. Final ordination scores for NMDS ordination in Appendix B.11 (**Tables 1 and 2**). There are 27 species within 21 plots (10 fenced, 11 unfenced). Ordination explains about 47.9% of variance within the dataset. Percent variance explained by each axis is expressed in parenthesis next to corresponding axis.

Table 1. Final ordination scores by plot.

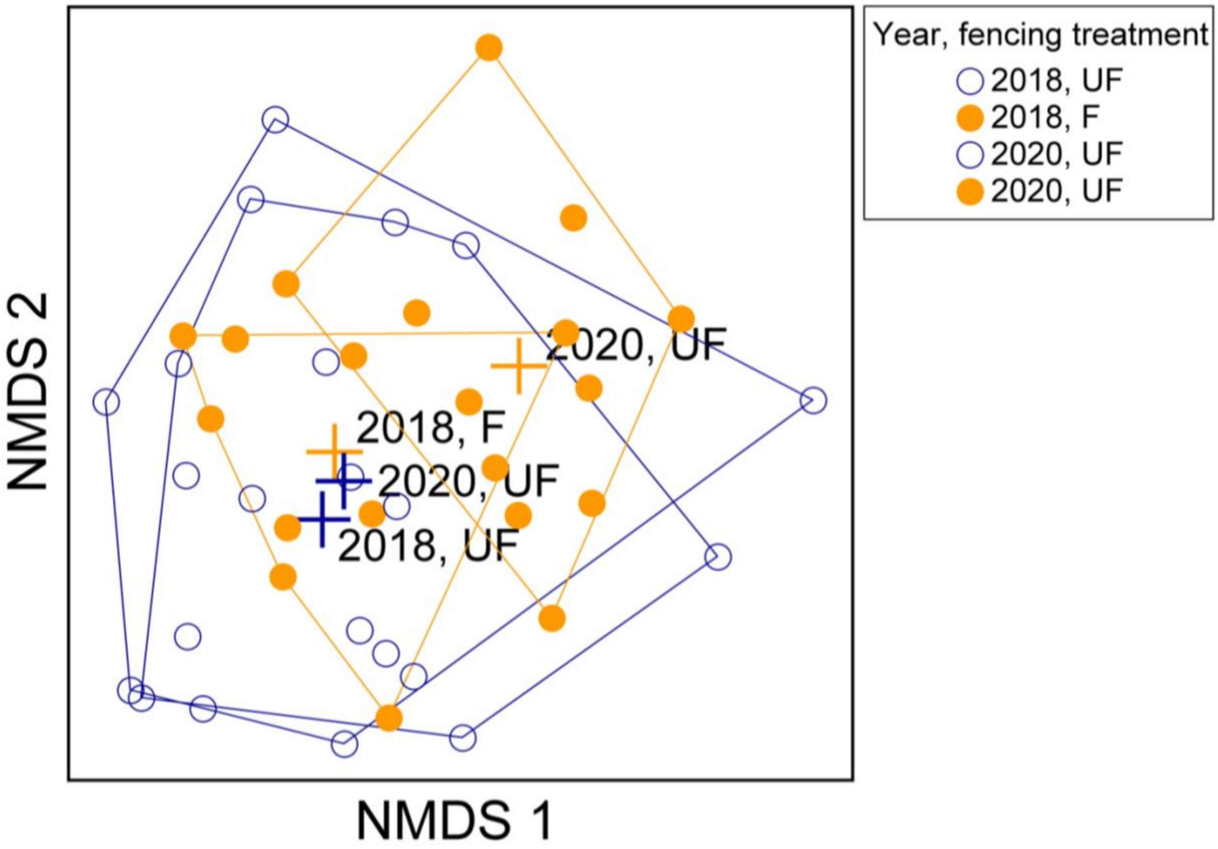
Plot	**Axis 1 (19.7%)**	**Axis 2 (28.2%)**
11a	1.22262	0.27484
12	-0.52421	0.22642
14	1.09373	0.66300
15	0.37046	-0.17273
22	-0.81556	0.37485
24a	-0.13900	1.39159
29	-0.05181	-0.06026
30a	-0.44356	-0.43591
8	-1.07525	0.00334
11b	0.62934	0.30059
17	0.95088	-0.13437
21	0.37838	0.90883
24b	0.37454	-1.19579
25	-0.96107	0.74847
27	0.06421	0.34133
28	-0.30744	0.76017
30b	0.01735	-0.87226
32	-0.40703	-0.88625
33	-0.58893	-1.32676
37	1.19549	-0.19315
7	-0.98318	-0.71595

Table 2. Final ordination scores by species.

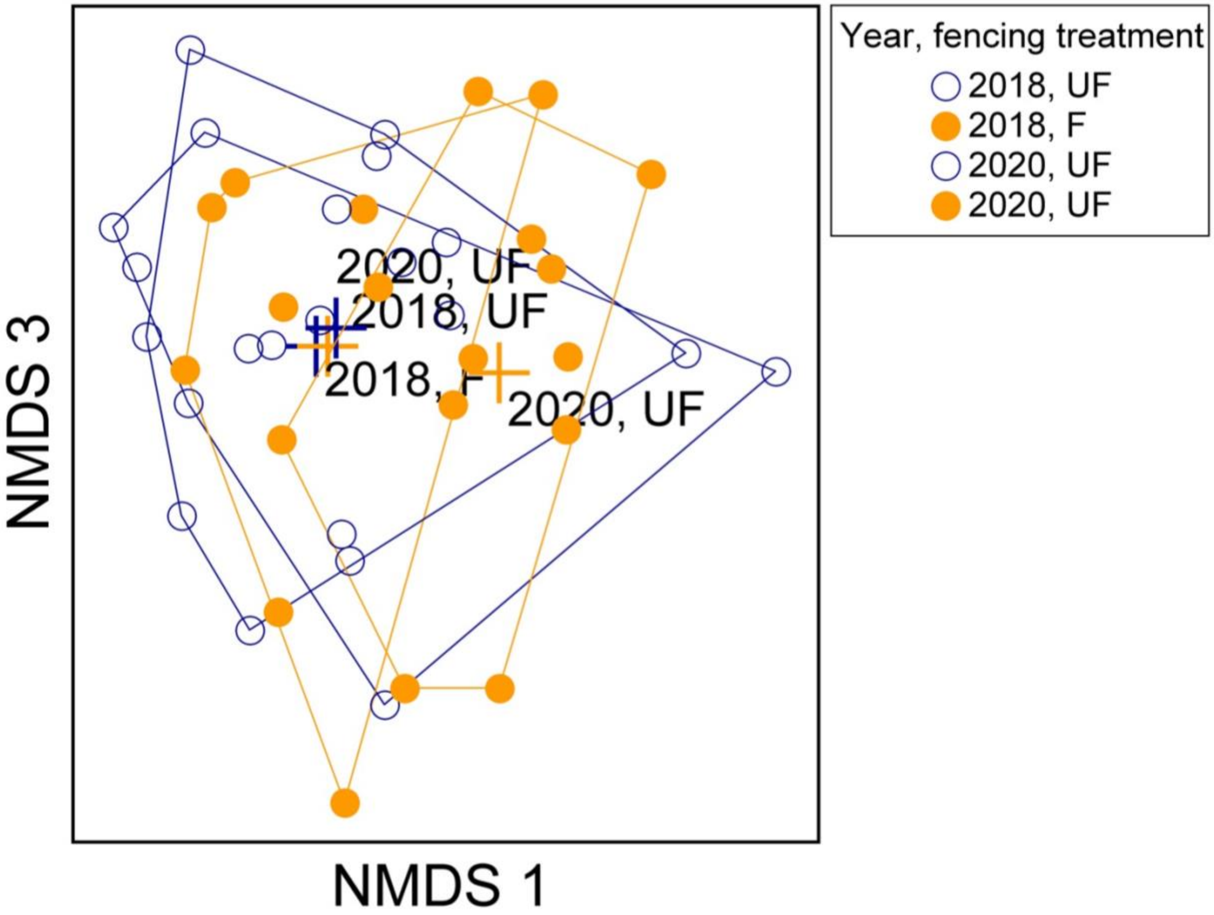
Species	**Axis 1 (19.7%)**	**Axis 2 (28.2%)**
S20chubf	-0.65737	0.44995
S20medf	-0.49193	-0.15890
S20ptaqf	-0.40522	-0.32544
S20myrt	-0.56568	0.18813
S20beaut	-0.42800	0.21980
S20vaar	0.58466	0.79189
S20vasp	0.42755	0.40608
S20ilvo	-0.46044	0.05069
S20palm	0.38414	0.28124
S20vacrp	-0.09756	0.97212
S20smil	0.48467	0.01765
S20caje	0.85329	0.20057
S20viro	-0.43058	0.46147
S20tora	-0.30250	0.17947

S20rubus	0.03412	0.64729
S20geran	1.04469	-0.02724
S20fforb	-0.62357	-0.71662
S20grspp	0.71383	0.31034
S20petal	1.11384	0.24624
S20wisp	0.51684	0.56370
S20sedge	1.08402	0.23587
S20ilop	-0.13529	0.89142
S20que	-0.02089	-0.19503
S20pers	-0.13976	0.22579
S20pinus	0.03998	0.01329
S20list	1.00427	0.08632
S20prse	0.49710	0.04538

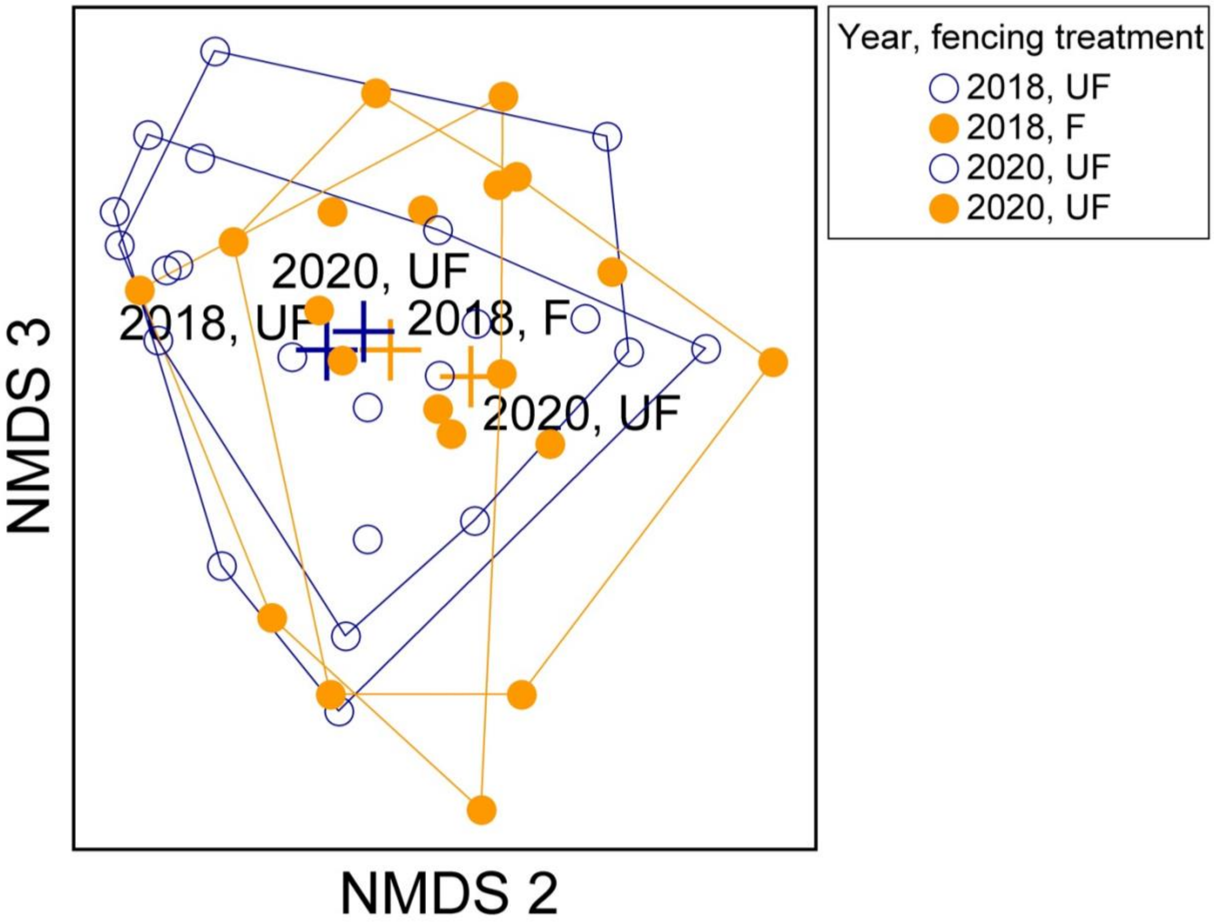
Appendix C.13. Non-metric multidimensional scaling (NMDS) ordination plot of species abundance in April 2018 and May 2020, both fenced and unfenced plots. Axis 1 vs 2 is shown. Species are coded by the first two letters of the genus and species name (e.g. *Cinnamomum camphora* = CiCa) or the first letters of family classes or genus name (e.g. *Cypera* sp. = *Cyperaceae* family, *Pinus* sp. = *Pinus* spp.



Appendix C.14. Non-metric multidimensional scaling (NMDS) ordination plot of species abundance in April 2018 and May 2020, both fenced and unfenced plots. Axis 1 vs 3 is shown. Species are coded by the first two letters of the genus and species name (e.g. *Cinnamomum camphora* = CiCa) or the first letters of family classes or genus name (e.g. *Cypera* sp. = *Cyperaceae* family, *Pinus* sp. = *Pinus* spp.



Appendix C.15. Non-metric multidimensional scaling (NMDS) ordination plot of species abundance in April 2018 and May 2020, both fenced and unfenced plots. Axis 2 vs 3 is shown. Species are coded by the first two letters of the genus and species name (e.g. *Cinnamomum camphora* = CiCa) or the first letters of family classes or genus name (e.g. *Cypera* sp. = *Cyperaceae* family, *Pinus* sp. = *Pinus* spp.



Appendix C.16. Final ordination scores for NMDS ordinations in Appendix B.13-15 (**Tables 1 and 2**). There are 25 species within 21 plots (10 fenced, 11 unfenced) at two points in time (April 2018 and May 2020). Ordination explains about 59.9% of variance within the dataset. Percent variance explained by each axis is expressed in parenthesis next to corresponding axis.

Table 1: Final ordination scores by plot.

Plot	**Axis 1(9.8%)**	**Axis 2 (16.4%)**	**Axis 3 (33.7%)**
11aA	-0.30795	-0.38787	-0.91436
12A	0.29407	0.17953	-0.19219
14A	-0.07943	0.32551	-1.57089
15A	-0.63027	0.39376	-0.07370

22A	0.60375	0.40036	0.88019
24aA	-0.54147	0.12432	0.48852
29A	-0.29396	-0.22878	0.14618
30aA	0.03693	-0.84195	0.21459
8A	-0.01749	-0.18132	0.48192
11bA	-0.61972	-0.06076	-0.18801
17A	-0.06090	-0.56096	-0.73539
21A	-0.33287	1.09302	0.00916
24bA	-0.79999	-0.75377	0.27981
25A	-0.87778	0.17778	0.41800
27A	-0.16850	0.30743	0.09512
28A	-0.46027	0.38328	0.57544
30bA	0.11330	-0.71079	0.29846
32A	-0.10884	-0.92924	0.48119
33A	-0.56401	-0.81265	0.74340
37A	0.06009	-0.15902	-1.23308
7A	1.40609	0.18535	-0.08037
11aB	0.45393	-0.18776	-1.17393
12B	0.68080	0.22145	-0.28276
14B	0.12372	0.46705	-1.17651
15B	-0.29985	0.56325	-0.31792
22B	0.97770	0.44823	0.60324
24aB	0.35946	1.32435	-0.03314
29B	0.68838	-0.14823	-0.02795
30aB	0.56154	-0.52197	0.37673
8B	0.37936	-0.03411	0.88816
11bB	-0.64493	0.30363	-0.58181
17B	-0.09071	-0.06231	-0.64459
21B	-0.41400	0.83307	0.00119
24bB	-0.76398	-0.78088	0.04183
25B	0.05541	0.75965	0.74082
27B	0.28343	0.68469	0.11641
28B	0.62942	0.77492	0.27795
30bB	0.27082	-0.91052	0.36453
32B	0.02597	-0.63546	0.66379
33B	-0.61570	-0.58252	1.03268
37B	-0.40698	-0.13629	-0.97651
7B	1.09545	-0.32350	-0.01618

Table 2: Final ordination scores by species.

Species	**Axis 1(9.8%)**	**Axis 2 (16.4%)**	**Axis 3 (33.7%)**
chubf	0.76717	0.49078	0.53564
medf	0.88709	0.09312	0.02849
ptaq	0.31079	-0.31510	0.39915
myrt	0.10872	0.54100	0.29220
beaut	0.66218	0.23909	-0.15483

vaar	-0.14371	0.62975	-0.77836
vasp	-0.07096	0.44014	-0.33381
ilvo	0.40069	0.21290	0.41107
palm	-0.30357	0.44061	-0.17990
vacrp	0.17120	0.67671	-0.03023
smil	-0.02170	-0.23420	-0.33417
caje	0.31662	-0.11756	-0.90140
viro	0.24871	0.41158	0.28452
tora	0.19807	-0.01569	-0.05611
rubus	0.22526	0.25584	-0.43664
geran	-0.06145	0.00673	-1.24087
grspp	0.41955	0.18728	-0.06194
petal	0.02273	-0.00291	-1.14287
sedge	-0.12686	0.04258	-1.06940
ilop	0.21266	0.80622	0.16156
que	0.20258	-0.13329	0.10478
pers	0.21413	0.27215	0.07037
pinus	0.11635	0.02287	-0.08745
list	-0.08339	-0.00911	-0.86469
prse	1.01135	0.13489	-0.14716

Appendix C.17. Indicator values (IV) (%) for the two fencing treatments (fenced and unfenced). Significant IV are in bold with *. Indicator values derived from same matrix used to conduct PerMANOVA—absolute difference (+5) n species abundance between April 2018 and May 2020. No indication = 0, perfection indication = 100. Significant p value (*) indicates the proportion of randomized trials with indicator value is equal to or exceeding the observed indicator value. Species that have relatively large IV values for one group versus the other and where $p < 0.05$ are generally the most responsible for the observed differences in that group.

Species	**Indicator value for fencing treatment**		**P value**
	Fenced	**Unfenced**	
Onoclea sensibilis	61	39	0.283
Woodwardia virginica	50	50	0.728
Pteridium aquilinum	60	40	0.114
Myrica cerifera	51	49	0.499
Callicarpa americana	58	42	0.162
Vaccinium arboreum	49	51	0.866
Vaccinium spp.	50	50	0.440
Ilex vomitoria	53	47	0.685
Arecaceae spp.	51	49	0.885

Parthenocissus quinquefolia	51	49	0.402
Smilax spp.	51	49	0.444
Gelsemium sempervirens	51	49	0.267
Vitus rotundifolia	73	27	0.037*
Toxicodendron radicans	52	48	0.039*
Rubus spp.	54	46	0.043*
Geranium spp.	50	50	0.938
Poaceae spp.	50	50	0.797
Oplismenus spp.	50	50	0.705
Cyperaceae spp.	50	50	0.927
Ilex opaca	51	49	0.286
Quercus spp.	52	48	0.304
Persea spp.	51	49	0.482
Pinus spp.	50	50	0.131
Liquidambar styraciflua	50	50	0.989
Prunus serotina	50	50	0.930
Cinnamomum camphora	53	47	0.077