PROJECTING FOREST OUTCOMES FOR PRINCE EDWARD ISLAND NATIONAL PARK UNDER CLIMATE CHANGE USING A PROCESS-BASED FOREST LANDSCAPE MODEL

by

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ABSTRACT

Climate change is projected to have profound impacts on the Acadian Forest ecosystem. Large uncertainties (climate and future disturbances effects on stand composition, structure) make it difficult to determine the best course of action (management). Novel forest simulation models allow us to grow the forest under a changing climate and disturbance regimes, assess vulnerabilities, and test different management strategies.

In this project, iLand (v1.1.1), a landscape-scale process-based forest model that offers a novel approach for assessing the feedback between individual trees and their environment (ecosystem processes, climate, and disturbance), was calibrated, and used for the first time in the Acadian Forest Region (AFR). We applied the model to the forest of Prince Edward Island National Park (PEINP), a highly degraded forest with increased vulnerability to climate change. PEINP is an ideal landscape for the initial regional application of this model because of high intensity inventory data available for set up and calibration. The Park is also representative of the heavily disturbed forest found throughout the AFR, providing a framework for future studies to be conducted in the region using iLand.

Forest outcomes were quantified through various stand measures and discussed in relation to the management goals of the Park and implications of climate change for the AFR. As the accessibility and capacity of process-based forests models increases, this project provides a case study for forest managers looking to expand their toolbox to deal with climate change and increasing disturbance activity.

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List of Symbols, Nomenclature or Abbreviations

AFR – Acadian Forest Region

DBH – Diameter at breast height

GDD – Growing degree days

LIF – Light interference field

LIP – Light interference potential

LRI – Light resource index

MADR – Mean annual disturbance rate

NB – New Brunswick

NS – Nova Scotia

PEI – Prince Edward Island

PEINP – Prince Edward Island National Park

PSP – Permanent Sample Plot

RA – Relative abundance

RU – Resource unit

VPD – Vapor pressure deficit

Chapter 1 – General Introduction

1.1 Background

Based on current projections, despite climate mitigation actions, anthropogenic climate change will continue over the coming decades with global average temperatures expected to rise 3–7°C by 2100 (IPCC 2018, Peters et al. 2020). Resulting climatic changes will expose global forests to novel conditions, driving shifts in forest structure and function, and influencing the provision of goods and services we derive from our forestlands (Hoegh-Guldberg et al. 2019).

The Acadian Forest Region (AFR), including the Canadian provinces of Prince Edward Island (PEI), New Brunswick (NB), Nova Scotia (NS), a small portion of Quebec (QC), and extending into the northeastern United States, has already seen a rise in annual average temperature of 0.7°C from 1948 to 2016, while an additional warming of 1.5°C to 5.2°C is expected by 2100 along with a 3–12% increase in precipitation (Zhang et al. 2019), under the moderate and high radiative climate forcing scenarios defined by Representative Concentration Pathways 4.5 and 8.5 (RCP; van Vuuren et al. 2011), respectively. The forest of the AFR may be especially susceptible to the impact of climate change, given it is an ecological transition zone with many of its tree species growing at the northern or southern limit of their ranges. Disturbed and degraded forests, such as that of Prince Edward Island National Park (PEINP), have further vulnerabilities due to low species diversity, even-aged stands and stand conditions (Amero et. al. 2015; PEI 2018). Small islands such as PEI also experience compounding effects of climate change due to their reduced ability to buffer climatic or biological change, limited fresh

water supply, coastal exposure to severe maritime weather, and dramatic erosion (IPCC 2014).

The compounding effects of climate concerns and current forest condition have implications for the long-term management goals of PEINP which include the conservation and restoration of ecological integrity, alongside public access, and recreation opportunities (Overton 2003). Forest restoration to a more natural Acadian Forest condition is a main component of PEINP's participation in the Parks Canada *Conservation and Restoration* (CoRe) program (Parks Canada 2018), however, it is uncertain if using historical forest conditions as a restoration goal is feasible or advisable for long-term forest resilience (Seastedt et al 2008; Taylor et al. 2017; Boulanger et al. 2019).Projecting the long-term effects of climate change and forest management will be vital to guiding future forest conditions and availability of resources.

Fortunately, recent developments in process-based forest landscape modelling, combined with access to more powerful computers, now allow forest managers to assess the joint impacts of management actions and climate change on future forest conditions. Process-based forest ecosystem models use a complex collection of equations and algorithms that interact to reproduce the interactions of ecosystem processes and environmental conditions (Battaglia and Sands 1998). This dynamic response-based approach grounded in the first principles (i.e., core theories) of ecology (Marquet et al. 2014) allows for the simulation and analysis of landscapes under projected climate conditions unlike traditional empirical modelling which is based on historical growth rates and climate conditions.

However, the parameterization, calibration, and validation of process-based models is informationally and technically complex, subject to disagreement, and seldom described in detail (but see: Shifley 2000 et al., Forrester et al. 2021; Suárez-Muñoz et al. 2021). This has dissuaded forest professionals from adopting process-based models, but growth in data availability for model calibration, and improved complimentary software (e.g., spatial data management), has improved accessibility (Shifley et al. 2017). Nevertheless, for such models to fully transition from theoretical research to the forest managers' toolbox, each step of the model preparation requires clarification and examples.

In this project, I used iLand (v1.1.1), an individual-based forest landscape and disturbance model, to present a case study on the calibration and validation of a complex forest model and to simulate forest development under climate change and disturbance for the PEINP. iLand was released in 2012 and offers a novel approach for simulating the interaction between individual trees (demographic processes) and their environment (ecosystem processes, climate, and disturbance) in a scalable manner, bridging previous gaps between the traditional stand and landscape models (Seidl et al. 2012). iLand is of interest for use in the AFR because its fine-scale spatial resolution is designed for highly heterogeneous environments, both in species and environmental variation. As well, the use of daily climate data and the functionality of individual tree competition and disturbance response dynamics are unique to iLand and important for future modelling of an area that is likely to experience dramatic impacts from climate change (Evans and Brown 2017). The iLand software is also open-source and functions with the use of additional open-source software resources.

1.2 Objectives

In Chapter 2 of this study, robust methodology for the parameterization, calibration, and validation of a process-based forest landscape model is demonstrated using iLand as a case study. The specific objectives were:

1. Demonstrate the parameterization of 18 of the most common species of the AFR and calibration and verification of model performance in replicating
    a. individual species population dynamics,
    b. stand structure (growth and yield),
    c. stand dynamics (succession)

In Chapter 3, iLand was used to project forest development under climate change for the Prince Edward Island National Park. The specific objectives were:

1. Initialize the model for PEINP and simulate the park landscape over 100 years under baseline (historical), RCP 4.5, and 8.5 climate without and with wind disturbance and analyze the results to describe the impact of climate change and disturbance on
    a. Species population dynamics
    b. Landscape level forest structure and productivity

The expected benefits of this project are twofold: (1) provision of a ready to use forest model for PEINP to provide a basis for ongoing investigation by Park Management and to provide analysis of model results that can be used immediately by PEINP to help inform forest management decisions going forward; and (2) the resulting parameter set can be utilized to apply iLand to landscapes throughout the AFR for further study.

1.3 Study Design

This study consists of two main research chapters follow by a general discussion of results and implications. The second chapter includes the parameterization, calibration, and validation of the iLand forest model for the species of the AFR. An initial parameter set was obtained for 18 of the most common species of the AFR based on a previous calibration of the individual tree forest gap model PICUS by Taylor et al. (2017), the TRY database (Kattge et al. 2020), and extensive literature review (D. Thom, personal communication, Nov. 11, 2020). A multistep iterative process was then used to calibrate each species beginning with simulations of single species stands through to a full landscape simulation with all 18 species. Analyses of model results were conducted through a combination of visual assessment and descriptive statistics using comparison to empirical data available for the AFR for the calibration and validation process. Parameter adjustments were made until model results conformed adequately with empirical data.

The third chapter presents the creation of an iLand landscape for PEINP using data from the 2015 Management Plan inventory (Amero et al. 2015) and the simulation of that landscape under three climate scenarios (e.g., baseline, RCP 4.5, 8.5) without and with wind disturbance. Each scenario was run for 100 years and replicated 20 times for a total of 120 simulations across 6 scenarios. Scenario results were then summarized and reported as mean values. Analyses of model results were conducted through a combination of visual assessments and descriptive statistics, assessing the magnitude and direction of change for the forest conditions to assess implications for future management guidance.

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Chapter 2 – CALIBRATION OF A COMPLEX PROCESS-BASED FOREST MODEL: A CASE STUDY FOR THE ACADIAN FOREST REGION

Willis, S.; Taylor, A.R.; Thom, D.; D'Orangeville, L.

2.1 Introduction

Projecting the long-term effects of forest management efforts under climate change, and increasing disturbance is vital to guiding future forest conditions and availability of resources. Fortunately, recent developments in process-based forest landscape modelling, combined with access to more powerful computers, now allow forest managers to assess the joint impacts of management actions and climate change on future forest conditions. Process-based models simulate forest landscapes using first principles of ecology (Marquet et al. 2014) to reproduce interactions of ecosystem processes and environmental conditions (Battaglia and Sands 1998). Contrary to empirical models, this approach allows for increased confidence of model results when extrapolating forest response to novel environmental conditions (Cuddington et al. 2013).

Decision making in forest management has grown more complex given changes in climate (Contosta et al. 2019), invasive species (Miller et al. 2021; Gandhi and Herms 2010), and disturbance regimes (Dhar et al. 2016; Wang et al. 2017; Boucher et al. 2018), coupled with a transition in management objectives from high production sustained yield forestry through multi-use sustained yield forestry, to a more holistic approach of "ecological forestry" (Long 2009; Christensen et al. 1996). Under these constraints, forest managers must divide limited forest resources for harvesting (McEwan et al. 2020), carbon storage and climate change mitigation (Zhao et al. 2022; Anderegg et al. 2020),

conservation (Golloday et al. 2016), and social values (Lidestav et al. 2019) while maintaining ecosystem services (Biggs et al. 2012). In the past, management for sustainable yield relied on expert opinion (Drescher et al. 2008) and empirical growth models to project future stand conditions based on historical trajectories (Korzukin 1996; Gustafson 2013). However, changes induced by climate change challenge the traditional empirical management approach based on the fundamental assumption that the past can inform the future (Millar et al. 2007; Achim et al. 2021). To better understand and predict the impacts of these stressors on forest management outcomes, it has become imperative that process-based modelling be added to the managers toolkit (Battaglia and Sands 1998).

Process-based models, also referred to as mechanistic models, combine our understanding of physiological and ecosystem functions through a series of equations and algorithms to represent forest change over time (Taylor et al. 2009). Development of the process-based model type began about 50 years ago with JABOWA, the first functional forest gap model, created to model the mixedwood forests of the northeastern United States (Botkin 1972; Botkin 1993) and FOREST, which used distance dependent competition indices to modify tree growth and mortality (Ek and Monserud 1974). Since that time, innovation in process-based modelling has tracked the exponential increase in computational power, development of complimentary software (e.g., GIS, database management), and continued work in applied ecological science enhancing the empirical data available for model development and calibration (Bugmann 2001; Johnsen et al. 2001; Shifley et al. 2017). The advancements in model applications and efficiency,

combined with more user-friendly software design, have allowed the use of process-based models to begin to bridge the gap between researchers and applied forest managers.

For forest management, models which use combinations of spatiotemporal dynamics and stochastic processes to project forest development, climate response, and disturbances at multiple spatiotemporal scales are most applicable (Shifley et al. 2017). There are many different models available, each with unique design and function, making the task of selecting the appropriate model a major challenge for novice modelers and many forest practitioners (Keane et al. 2019). Resources such as Taylor et al. (2009), which provides a comprehensive review of forest succession models for forest management, including a framework for assessing model suitability based on evaluation of criterion for strategic planning (Table 2.1) or Keane et al. (2019), which speaks more specifically to spatially explicit process-based models and outlines the development of a clear modelling objective along with further review of selection criterion, can provide insight on the selection process. The differences in model structure impact the applicability of each model and care must be taken in matching the objectives and scale of the model to those of the user, in addition to considering the information available for calibration and validation (Blanco et al. 2020).

Process-based models of forest development have historically been divided by spatial scale, such as stand-level models (e.g., JABOWA-3, PICUS) and forest landscape models (e.g., LANDIS, LandClim). Stand-level models are further defined as individual tree or gap but essentially, they represent the forest at a higher resolution using more complex interactions than landscape models (Baker and Robinson 2010). This has benefits for assessing stand dynamics but increases complexity and computational

demand and has traditionally limited the spatial extent to which these models can be applied to < 100 hectares (Baker and Robinson 2010). In comparison, landscape models use a coarser representation of the forest as aggregated cells defined by characteristics such as age class, species composition, or management technique with interactions projected through empirical relationships or mechanistic processes rather than interactions between individuals (Taylor et al. 2009). As a result, they can emulate forest growth and disturbance over a much larger spatial and temporal scale but are limited in the representation of individual species or stand dynamics. Models can also be combined to upscale stand dynamics to larger spatial units (e.g., Boulanger et al. 2017). However, many of the impacts of climate change on the forest will be at the tree level, as well as across the landscape, making the ability to finely integrate dynamic interactions across spatial and temporal scales essential (Boulanger et al. 2018).

After the model has been selected, a time and resource intensive process to parameterize, calibrate, and validate its function against observations must be completed before the model can be applied. The process is informationally and technically complex, subject to disagreement, and seldom described in detail (but see: Shifley 2000 et al., Forrester et al. 2021; Suárez-Muñoz et al. 2021). The growth in data availability for model calibration and improved complimentary software (e.g., spatial data management) has improved accessibility (Shifley et al. 2017). However, for process-based modelling to fully transition from theoretical research to the forest managers' toolbox, each step of the model preparation requires clarification and examples.

Table 2.1 Summary of model evaluation criteria for strategic forest management planning (Taylor et al. 2009).

Evaluation Criteria	Requirements and considerations for strategic planning
Input Data	Must be compatible with data commonly available to management planning
Inference space	Planning horizon: 1-2 forest rotations ~50-200 years Temporal resolution: 1-10 years Temporal capacity: must accommodate planning horizon Planning unit size: variable Small planning units (<1,000 ha): tree/gap level resolution adequate Large planning units (>1,000 ha): coarser resolution required Aspatial and spatial methods both acceptable and commonly used Quantitative reference to estimation accuracy and reliability required
Complexity	Ecosystem representation should be no greater than that essential to accurately project succession within desired inference space Unnecessarily complicated models incur extra direct and indirect costs of implementation
Flexibility	Ability to simulate alternative scenarios for comparison Adaptability for use under varying management and environmental conditions Output should be easily interpretable for planning analysis, and as input for planning models

In this chapter, we will be calibrating iLand (v1.1.1), an individual-based forest landscape and disturbance model. iLand was released in 2012 and offers a novel approach for simulating the interaction between individual trees (demographic processes) and their environment (ecosystem processes, climate, and disturbance) in a scalable manner, bridging previous gaps between the traditional stand and landscape models (Seidl et al. 2012a). It operates at the individual-tree level while simultaneously modelling dynamic ecosystem processes at the landscape scale, allowing for explicit spatial projection of forest succession and disturbance. The development of iLand was

not focused on increasing the complexity of the individual tree processes, but rather on overcoming previous limitations of computational demand in integrating interactions between individuals on a fine spatial resolution and the changing climatic conditions on a landscape scale (Seidl et al. 2012a). Greater detail regarding the function of the model can be found in the Methods section, in Seidl et. al (2012a), and on the comprehensive online resource (iland-model.org).

iLand was initially shown effective in replicating the unique forest conditions of an old-growth forest in the Cascades of Oregon, along an elevational gradient transect in Oregon, USA, and along a second transect in the east Austrian Alps (Seidl et al. 2012a). Since then, it has been used to model forest growth and the impact of climate change and disturbance in the temperate forests of central Europe and western USA (e.g., Old Growth Dynamics - Seidl et al. 2012b; Climate Change and Disturbance – Thom et al. 2017a; Wildfire – Seidl et al. 2014a, Braziunas et al. 2018; Wind disturbance - Seidl et al. 2014b, Bark Beetle - Dobor et al. 2018; and other disturbances - Honkaniemi et al. 2021). iLand is of interest for use in the AFR because its fine-scale spatial resolution is designed for highly heterogeneous environments, both in species and environmental variation. As well, the use of daily climate data and the functionality of individual tree competition and disturbance response dynamics are unique to iLand and important for future modelling of an area that is likely to experience dramatic impacts from climate change (Evans and Brown 2017). The iLand software is also open-source and functions with the use of additional open-source software resources.

The objective of this chapter was to demonstrate a robust methodology for the parameterization, calibration, and validation of a process-based forest landscape model

using iLand as a case study. We parameterized 18 of the most common species of the AFR and calibrated and verified the model performance in replicating (1) individual species population dynamics, (2) stand level dynamics (growth and yield), and (3) forest landscape dynamics (succession). A manual multistep iterative process was used, by repeatedly running simulations at the single and multi-species level, comparing the simulation outputs to observational data from the AFR, and adjusting species parameters until the results conformed sufficiently with the observational data. The resulting parameter set is ready for initial application to modelling scenarios in the AFR.

2.2 Methods

2.2.1 Model Calibration Review

The requirements to set-up and apply a process-based model can be broken down into a few general steps regardless of model specifics. After selecting the appropriate model for your needs, the collection of an initial set of relevant species and environmental parameters must be completed. A test environment is then created which is used in the calibration of the species and environmental parameters. The terms calibration and validation are often used interchangeably but, in this paper, calibration will refer to the iterative process of adjusting model parameters based on repeated output analysis, while the validation will refer to the overall evaluation of the model performance before declaring it fit or unfit for application (Rykiel 1996). The calibration and validation processes must be done over all the spatiotemporal scales that the model operates on, for example examining the dynamics at each the species, stand, and landscape level.

One of the largest hurdles to overcome in using a process-based model is the collection of information required to parameterize, initiate, calibrate, and validate a model before it can be applied to a forest. Species-specific parameter information is highly technical and difficult to obtain from published literature or intensive measurement, often resulting in the need to estimate some parameters (Forrester et al. 2021). Parameterization is further complicated by the temporal and spatial extents over which individuals and species persist, where intraspecific variation may be high (Johnson et al. 2001). Parameter value selection is the first important step and must be done with care as parameters can introduce uncertainty into the model that scales up through the process, ultimately impacting the quality of the results (McKenzie et al. 2019).

Environmental and site data including climate, soils and elevation is also required for model initialization to inform the simulated environment to which the model processes will be responding. The availability and format of that data can vary depending on the collection agency and scale of the data, for example, climate data collected by federal agencies spans coast to coast with standardized formats, while forest inventory data is generally collected by the forest management branch of each provincial or state government and differs greatly in the data collection protocol. For spatially explicit models (i.e., those that account for the distribution of landscape characteristics and spatially dependent biological processes), the necessary data can be difficult to obtain at an appropriate resolution due to cost or logistical constraints, as many environmental conditions such as soils or microclimate can vary greatly over short distances (Petter et al. 2020). In many cases, it will be necessary to gather data from many sources and apply

spatial joins and estimations to form a complete dataset (Ruiz-Benito et al. 2020; Suárez-Muñoz et al. 2021). Climate data available through the long-term monitoring of weather stations often contain gaps and does not identify local variations and microclimates that are altered by vegetation, water bodies, and terrain (Petter et al. 2020). Spatially aggregated data from historical or projected modelling (e.g., BioSIM) is a valuable resource to be used in addition to local observational data. Due to the influence of the input data on model performance and outcome, it is important to maintain transparency in the assumptions and projections used in the initialization process and acknowledge that model outputs depend on the initialized model condition (Temperli et al. 2013).

The calibration and validation of models can be a contentious topic due to subjectivity in the process depending on the assessment method used (Yang et al. 2004). It must be clarified for ecological models that valid does not equal a universal truth, but rather asserts acceptable model conformance with "specified criteria based on the current knowledge and data available for the system of study" (Rykiel 1996). Criteria used to assess model validity can include not only conformance with empirical data but also qualitative assessment of biological realism and consistency with expectations of forest growth and management response (Vanclay and Skovsgaard 1997; Soares et al. 1995). The calibration and validation of a model, or at least portions of the process, must be repeated each time a model is applied with a new condition such as additional species or in a different geographic location.

Empirical data from tree, stand, and landscape development over time are required for calibration and validation purposes. Depending on the jurisdiction or forest

type, this information may be readily available; but if not, it may be expensive and difficult to obtain, particularly for highly complex or remote forests. Often times, there are more data available for commercial species and plantations, mainly because of the historic wide use of empirical growth and yield models (Landsberg 2003; Pitt and Lanteigne 2008).

To permit comparisons with model outputs, forest measurement datasets must be processed and cleaned to conform with model outputs for meaningful comparison, which represents a large investment of time and requires skill and understanding in both data management and interpretation of forest characteristics and dynamics (Shifley et al. 2017). Existing data is also subject to potential quality issues from collection or record errors and may not encompass all the information required, such as poor representation of certain species, stand types, or age classes, or inability to account for confounding impacts such as harvest or natural disturbance. The quality and replication of empirical data available for comparison must be considered when choosing a calibration technique.

Qualitative methods for validation include subjective assessments (e.g., face validty or Turing tests) where model results are judged based on expert opinion or visual comparison of predicted versus observed data, while quantitative methods include statistical testing and measures of deviance (Rykiel 1996; Van Oijen et al. 2005). Qualitative methods are widely accepted, more straightforward to apply, and rely less on the availability of observed data, however, there are concerns regarding misinterpretation and personal bias (Mayer and Butler 1993). Quantitative methods require more refined and independent empirical data for comparison and are viewed by some as a stronger indication of model performance, but they can be heavily influenced by biases present in

the observed data and different tests run on the same simulation results can produce different results, simultaneously validating and invalidating the model (Yang et al. 2004).

2.2.2 Case Study Model: iLand

iLand uses a novel, multi-hierarchical scaling approach based in ecological field theory to simulate the demographic processes (growth, mortality, regeneration) at the individual tree level. Competition for light is modelled through a Light Interference Pattern (LIP) library that is derived for each species during a pre-processing routine from height and crown size relationships (i.e., representation of a tree's field of shading influence). This library is then accessed for trees at each annual time step of the modelling routine, thus reducing the real-time computational load. The LIP of all the trees on the landscape are combined to calculate a continuous Light Interference Field (LIF) representing crown height and structure. The tree's height and location within the LIF determines their Light Resource Index (LRI, i.e., potential to intercept radiation) which is combined with the available radiation, individual leaf area, shade tolerance, environmental modifiers, and tree age to modify their growth.

Light, water availability, and climate are considered on a daily timestep, while nutrient availability and atmospheric CO_2 are used monthly, to calculate annual tree growth and mortality. The default spatial units are 2x2m grid cells for individual tree location and competition for resources, nested within10x10m cells for stand initialization, which are nested within 100x100m cell resource units (soil and climate). More than 60 individual parameters are used for each species to modify these interactions and determine allocation of carbon (C) within the tree. A descriptive list of parameters is

available in the online resource (iland-model.org/species+parameter). Tree mortality occurs intrinsically from age-related decline in C-use efficiency (i.e., productivity potential), through C starvation due to stress, or from disturbance. Growth and mortality outputs are recorded on an annual timestep.

Regeneration is impacted by seed-source availability, seed rain dynamic, spatially explicit seed dispersal, resprouting, environmental constraints, and light availability. Multiple age cohorts of different species may establish on one 2x2m cell (one cohort per species) and are each represented by a “mean tree” method where all stems of each species in a single cohort are the same size. New cohorts may establish on a cell each year until the mean tree of any one cohort exceeds 1.3m tall; at this time shading is considered excessive for additional establishment to occur. Competition between saplings is not calculated explicitly but rather emerges through height growth potential, radiation utilization, and environmental modifiers of sapling growth and survival, such as water and temperature limitations. When the mean tree of any one species reaches >4m in height the cell is “won”, and individuals of that species will be recruited into the tree layer while the rest of the saplings are removed, and the establishment process may begin again. Figure 2.1. represents the flow of interactions within a simulated forest stand: the climate inputs from the top include temperature, precipitation, vapor pressure deficit (VPD), and radiation; the individual processes affecting growth and biomass allocation are indicated in the center; and soil inputs feed in from the bottom (Seidl et al. 2012a).

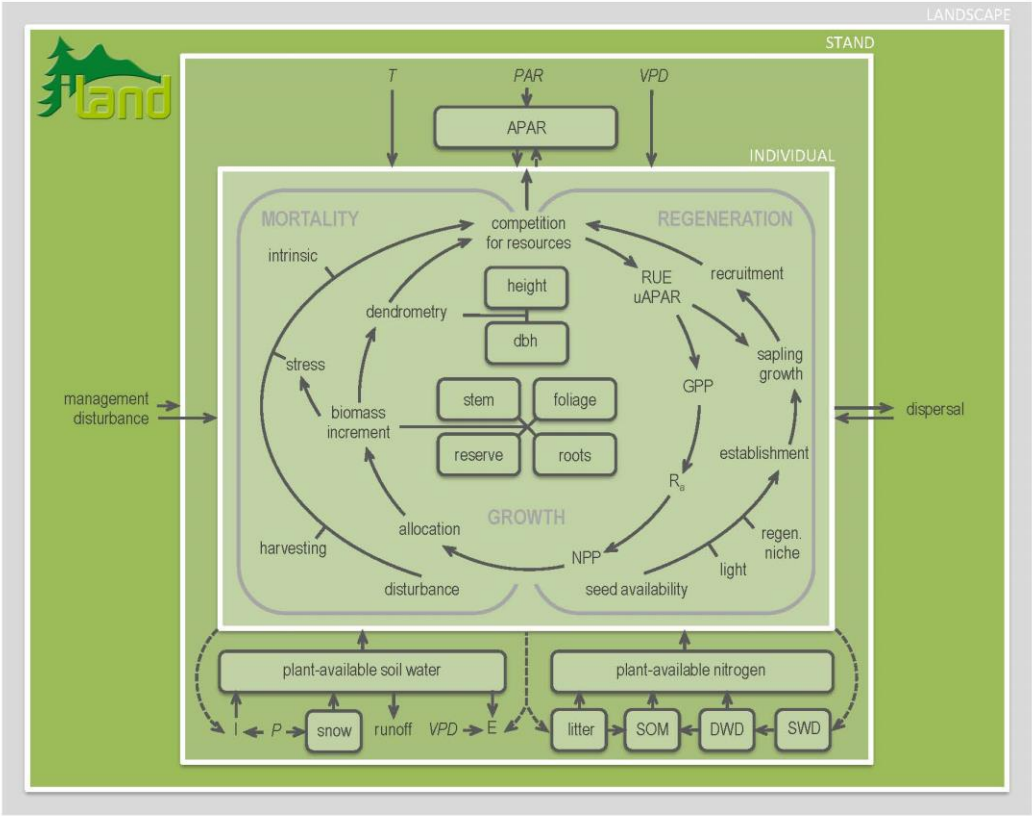

Fig. 2.1 Overview of the physiological processes and their interactions as modeled in iLand at the individual, stand and landscape level (larger square boxes).T = mean temperature, PAR = photosynthetically active radiation, VPD = vapor pressure deficit, APAR = absorbed PAR, RUE = resource use efficiency, uAPAR = utilizable APAR, GPP = gross primary production, R_a = autotrophic respiration, NPP = net primary production, I = interception, P = precipitation, E = transpiration, SOM = soil organic matter, DWD = down woody debris, SWD = standing woody debris(after Seidl et al. 2012).

For initialization iLand requires forest landscape inventory, climate, and soil data. Landscapes can be initialized from “bare ground” (devoid of vegetation) by seed, by species cohort information for trees and saplings, or by individual trees with coordinate

locations. Climate data is required at a daily timescale and includes minimum and maximum temperature (°C), precipitation (mm), solar radiation, and VPD. Basic soil data required includes available nitrogen, effective soil depth, and percent sand/silt/clay for each resource unit. A complex carbon and nitrogen soil cycling sub-model is available, however it requires extensive parameterization and calibration and will not be used as it is outside of the scope of this study. The model can also be run without or with the available disturbance modules which include fire, wind, bark beetles, and other biotic disturbance agents, as well as a generic user-defined "timed" disturbances which are controlled and calibrated individually (Seidl et al. 2014a; Seidl et al. 2014b; Seidl and Rammer 2017; Thom et al. 2017a; Honkaniemi et al. 2021). The disturbance modules are spatially explicit and dynamic, arising from the interaction between individual trees and climatic conditions. Each module requires a separate parameterization and calibration process not included in this study.

iLand offers many pre-specified output tables as well as a user-defined dynamic stand output option. The most relevant outputs to this calibration process included the "trees" table (every tree by resource unit), "stands" (measures aggregated by species and resource unit), and "sapling" (establishment and sapling measures aggregated by species and resource unit). The dynamic stand output was used to assess aging and growth patterns, but no visual or numerical comparisons were based on this output. Additionally for this project Notepad++, SQLiteStudio, and R were used for project file creation, database management, and data analysis respectively.

2.2.3 Study Area

The AFR is composed of 36 tree species in varying abundance according to topographic, soil, and local climate conditions (Rowe 1972). The typical temperate species of the AFR include red spruce (*Picea rubens* Sarg.) along with a significant shade-tolerant hardwood component of sugar maple (*Acer saccharum* Marshall), yellow birch (*Betula alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), and red maple (*Acer rubrum* L.). Other prevalent conifers in the region include eastern hemlock (*Tsuga canadensis* L.), eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.), tamarack (*Larix laricina* (Du Roi) K. Koch), and eastern white cedar (*Thuja occidentalis* L.). Additional hardwood species include white ash (*Fraxinus americana* L.), balsam poplar (*Populus balsamifera* L.), and red oak (*Quercus rubra* L.). Cold-adapted, typically boreal species, also found throughout the AFR include balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* Mill.), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.; Basquill and Baldwin 2020).

Current climatic conditions include relatively mild winters and cool summers with mean temperatures from -2 to -8°C in the winter and 15 to 18°C in the summer; precipitation varies from 800-1,500 mm with higher amounts falling along the coast and drier conditions inland (Environment and Climate Change Canada 2021). The large amount of coastline and general proximity to the Atlantic Ocean does have a moderating effect on both temperature and precipitation, but prevailing westerly winds counter that effect, resulting in frequently fluctuating weather conditions (Loo and Ives 2003). Gap disturbances of small, infrequent fires, windthrow events, and endemic insect damage are

most frequent in the AFR (Basquill and Baldwin 2020), however larger wind events, fires, and insect outbreaks also occur throughout the region and are expected to increase in frequency and severity (Taylor et al. 2020).

2.2.4 Initialization

To calibrate iLand, we used a multi-step iterative process beginning with single species stands and ending with a landscape level assessment of forest dynamics. The initial growth and life history parameters required by each species was obtained for 18 of the most common species of the AFR based on a previous calibration of the individual tree forest gap model PICUS by Taylor et al. (2017), the TRY database (Kattge et al. 2020), and extensive literature review (D. Thom, personal communication, Nov. 11, 2020). A full list of the required parameters with descriptions can be found in Appendix A and at https://iland-model.org/species+parameter. Only the 18 most common species found in the AFR were considered in this study (Table 2.2). At all levels of model calibration, the same representative climate and site condition inputs were used. Daily climate estimates were generated using monthly historical and projected climate data obtained from high-resolution interpolated climate data provided by Natural Resources Canada (McKenney et al. 2011) and daily observed data from Environment and Climate Change Canada weather stations on PEI. For simulations assuming historical climate conditions, the model uses random sampling of years to extend through the simulation extent required. Three stand soil conditions were used, based on Nova Scotia permanent sample plot (NS PSP) observations, with different soil composition and available nitrogen values ($kg \cdot ha^{-1} year^{-1}$) to represent low, moderate, and high productivity sites

(Table 2.3). All simulations were initialized from bare ground conditions using seed from an unlimited "outside" sources; seed remains available from outside sources throughout the simulation in addition to local seed rain as the forest develops.

Table 2.2 List of calibrated species common name, scientific name, four letter iLand code, and shade tolerance class.

Common Name	Latin	iLand Code	Shade Tolerance
Balsam fir	*Abies balsamea*	abba	high
Red maple	*Acer rubrum*	acru	mod
Sugar maple	*Acer saccharum*	acsa	high
Yellow birch	*Betula alleghaniensis*	beal	mod
White birch	*Betula papyrifera*	bepa	low
American beech	*Fagus grandifolia*	fagr	high
White ash	*Fraxinus americana*	fram	low
Tamarack	*Larix laricina*	lala	low
White spruce	*Picea glauca*	pigl	high
Black spruce	*Picea mariana*	pima	high
Red spruce	*Picea rubens*	piru	high
Jack pine	*Pinus banksiana*	piba	low
Red pine	*Pinus resinosa*	pire	low
White pine	*Pinus strobus*	pist	mod
Trembling aspen	*Populus tremuloides*	potr	low
Red oak	*Quercus rubra*	quru	mod
Eastern white cedar	*Thuja occidentalis*	thoc	high
Eastern hemlock	*Tsuga canadensis*	tsca	high

Table 2.3. Varied soil conditions used in stand initialization representing low (1) to high (3) nutrient availability sites based on NS permanent sample plot (PSP) data.

N Class	Site Available N (kg/ha/year)	Sand	Silt	Clay
1	76	63	24	13
2	125	68	22	10
3	174	71	20	9

2.2.5 Calibration

Analyses of model results were conducted through a combination of visual assessment and descriptive statistics using comparison to empirical data available for the AFR for the calibration and validation process. Visual assessments were used to assess population and stand dynamics as time series plots overlaying model outputs with empirical data. Average and maximum model result and observed values were also compared to assess individual species growth. Succession was assessed through the relative abundance (RA) of species by shade tolerance group (Table 2.2). RA was calculated as the percentage of total volume represented by each species on the landscape as:

$$(1)\ RA_{iy} = 100\left(\frac{V_{iy}}{\sum V_y}\right),$$

where RA_{iy} is the relative abundance of shade tolerance group i in year y, V_{iy} is the volume ($m^3\ ha^{-1}$) of shade tolerance group i in year y, and V_y is the total volume ($m^3\ ha^{-1}$) in year y (Ricklefs 2006).

The AFR and adjacent regions have been subject to timber exploitation and land clearing since the 17th century but have only had widespread intensive forest management for less than 100 years (Loo and Ives 2003; Noseworthy and Beckley 2020). As a result, there is substantial growth and yield data available only for the most commercialized species while many other species have had little direct sampling (ex. Honer 1983; Plonski 1974). However, large databases are available from wide-scale growth and yield data collection using provincial permanent sample plot (PSP) networks throughout the AFR (NSDNR 2004; Porter et al. 2001). These PSP networks represent a significant

investment and effort in data collection and are indispensable for many aspects of growth and yield and forest health monitoring. Unfortunately, the representation of many species and stand types is still low, remeasurement represents a relatively short timeframe compared to the lifespan of many of the species, and there were concerns regarding the validity of some records with extremely large or small measurements in relation to recorded tree age that could not be verified. In addition, our method of initialization from bare ground results in very low variability between stands, which did not reflect the natural condition where legacy effects of establishment and unique forest communities create more variation within and between stands. These factors make formal statistical validation inappropriate for a generalized calibration across the entire AFR.

2.2.6 Permanent Sample Plot Data

Tree and stand information were obtained from the PSP networks of NS, NB, and PEI (NSDNR 2004, Porter et al. 2001). The NS PSP network was initially established in 1965 with 1765 plots located randomly throughout the province in all forest types including disturbed or harvested areas and silviculture treatments, as well as natural forest, on Crown and Private land, and in 1998 the network was expanded to include 2139 additional plots (NSDNR 2004). The NB PSP network was established in 1987 and includes 2499 PSPs distributed throughout the province, excluding private and industrial freehold land (Porter et al. 2001) with 532 additional plots established from 2000–2010. For both networks, the plots are remeasured every 5 years. The PEI PSP network was initially established in 1976 and includes 959 plots, 563 of which are considered active, with a 3-year remeasurement cycle (M. Angus, personal communication, Nov. 10, 2022).

The plots are located largely in softwood plantations on Crown land, with few distributed in natural forest on Crown or private land (M. Angus, personal communication, Nov. 10, 2022).

For species comparisons, the PSP datasets were filtered for live stems of the target species with observations of age, diameter at breast height (DBH, cm) and height (m). Volume per tree ($m^3 \cdot tree^{-1}$) was available only for NS. For mixed-species landscape comparisons, plot summary data was created for NS PSP plots containing tree ages. After filtering, there were 2983 remeasured plots available totaling 4982 observations. Each plot was then filtered for live trees of the 18 target species and the individual ages were averaged to represent stand age. Stand densities were obtained from the NS PSP dataset for both mature stems and saplings by filtering for plots with > 75% basal area ($m^2 \cdot ha^{-1}$) contributed by the target species. Average DBH and average height were summarized; volume per hectare ($m^3 \cdot ha^{-1}$), and stem and sapling density ($stems \cdot ha^{-1}$) were calculated using the fixed-plot radius (NSDNR 2004).

A discrepancy exists in the definition of saplings and trees between iLand and PSP inventory protocols. iLand moves stems from the sapling to tree stage at >4m height, regardless of their DBH. This results in many very small stems (minimum ~3 cm DBH) present in the tree output. The NB dataset defines trees as DBH > 5.1cm and does not record saplings, PEI measures trees > 7cm and does not record saplings, while Nova Scotia defines trees as DBH > 9.0cm and records saplings by count per species in 4, 6, and 8 cm DBH classes. To account for this difference in tree and stand dynamic calculations in the evaluation, the “trees” output and the NB and PEI PSP data were filtered to remove stems < 9.1 cm to match the sampling design of the NS PSP plots.

Once removed as trees, the stems < 9.1cm were added directly to the sapling counts in both the individual species and stand calibrations.

2.2.7 Population Dynamics

For the individual species calibration process, 1-ha monospecific stands × 3 soil conditions (3 stands) were initiated from bare ground using the provided species parameters for a period relative to the maximum age of the species under consideration. Simulations of individual species were run using *torus* mode activated in iLand which allows multiple discrete stands to be run in parallel while remaining self-contained. The full simulation output was then reviewed, particularly to ensure species were reaching the appropriate maximum age and size. For direct assessment against the PSP observations, only 0 to 200 years of each simulation were used due the low representation of old individuals in the PSP datasets. The 200-year results were compared visually and numerically with the individual tree data taken from observed data.

Growth measurements were averaged over time, along with maximum DBH, height, volume per tree, and stand and sapling density. Adjustments to various parameter values were made based on visual comparisons of predicted and observed values over time, until model outputs conformed sufficiently with species-specific empirical observations. A final monospecific model run of 200 years was then created and compared quantitatively to the full NS, NB, and PEI datasets by calculating the average and maximum DBH, height, volume per tree, and age. Available literature describing species life history characteristics such as Burns and Honkala (1990), Farrar (1995), and Honer et al. (1983) were also consulted throughout the process.

2.2.8 Stand Dynamics

To assess stand dynamics, 100 1-ha stands were established for each of the three soil conditions using the adjusted species parameters running the simulations for 200 years. The output data was then compared visually to NS plot data. Measures that were assessed for stand dynamics include average DBH, height, volume per hectare, as well as density of all stems and stems > 9.0 cm only, and sapling density over stand age. To assess succession patterns, relative abundance by species and shade tolerance class (Table 2.2) were calculated for the combined 300 simulated stands and NS observational data and compared between early, mid, and late successional stages. Shade tolerance class was assigned based on the light response parameter value (Table A1) with 1-2.75 as low, 2.76-3.75 as moderate, and 3.76-5 as high tolerance while successional stages were divided by stand age with 0–40 years, 41–100 years, and 100+ years representing early, mid, and late succession, respectively. Once again, adjustments to various parameter values were made based on the results until model outputs conformed sufficiently with observations.

2.3 Results

2.3.1 Population Dynamics

For each species, select parameters (Table A1) were adjusted as necessary with the goal of producing simulation results that approximately overlaid the distribution of empirical observations. iLand was able to sufficiently simulate the growth and yield of all species across the environmental gradient and study period being modeled. Initially, species growth patterns were assessed by plotting simulated mean DBH, height, and

volume by soil nitrogen class alongside observed data from NB, NS, and PEI (i.e., sample trees) over tree age. The model correctly simulated a rapid increase in height (Fig. 2.2), diameter (Fig. 2.3), and volume (Fig 2.4) early during the simulation, conforming to the observed data, with a decreased growth rate in the mid- to late term. Growth responses to increasing nitrogen levels were species-specific, but displayed a common positive, initial response which declines under increasing N.

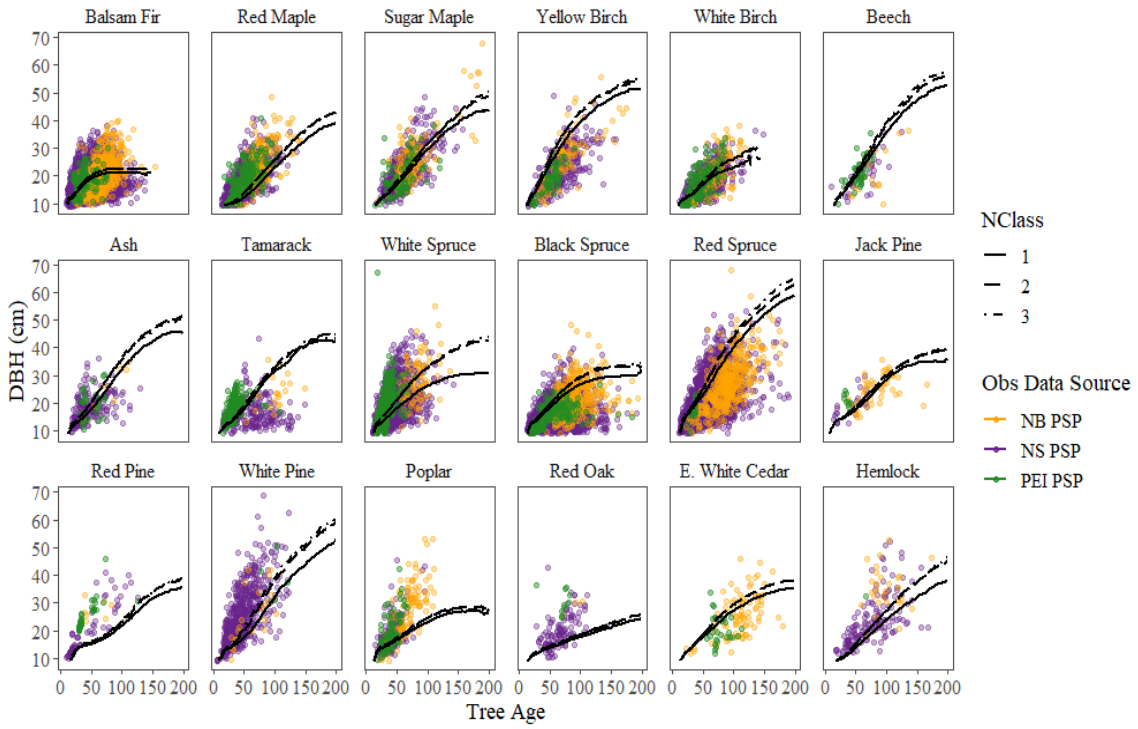

Fig. 2.2. Simulated iLand average diameter at breast height (DBH; cm) by nitrogen class and species at tree age over observed data from the New Brunswick (NB), Nova Scotia (NS), and Prince Edward Island (PEI) permanent sample plot (PSP) networks.

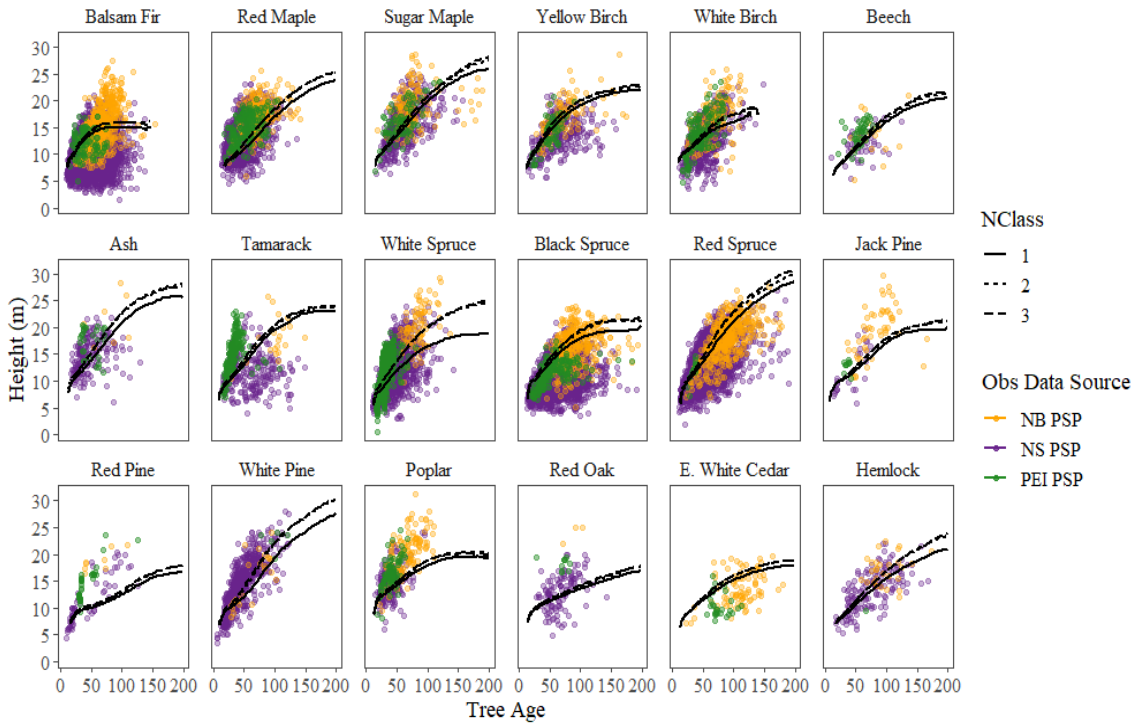

Fig 2.3. Simulated iLand average height (m) by nitrogen class and species at tree age over observed data from the New Brunswick (NB), Nova Scotia (NS), and Prince Edward Island (PEI) permanent sample plot (PSP) networks.

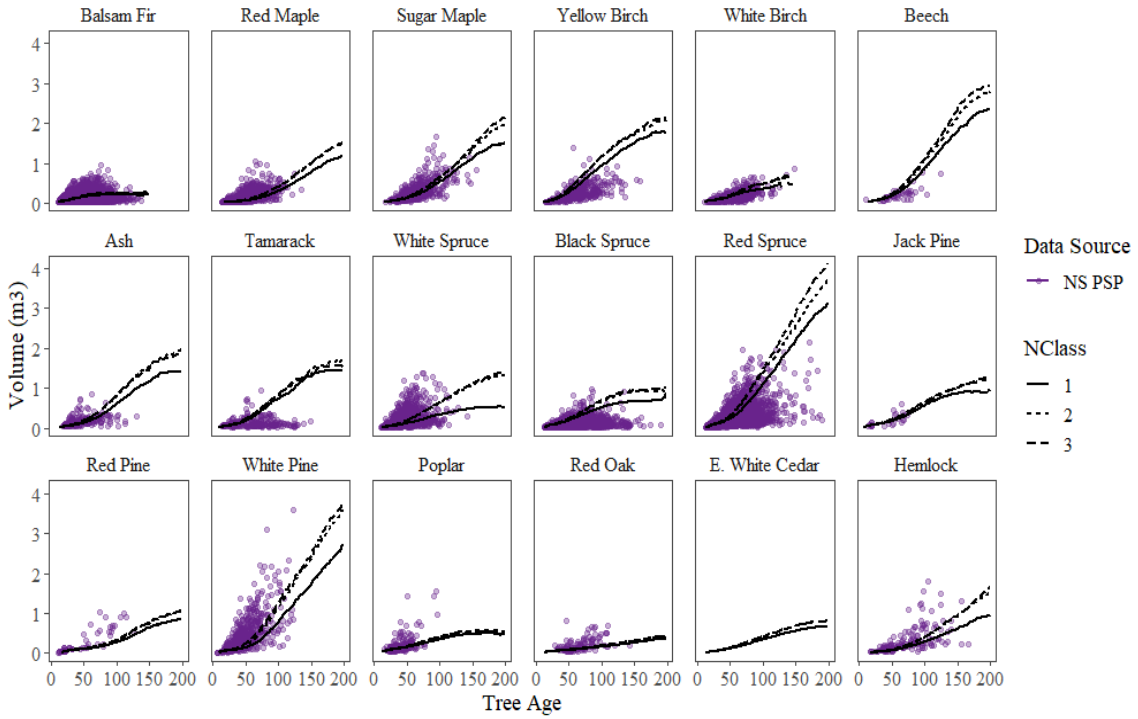

Fig. 2.4. Simulated iLand average volume per tree ($m^3 \cdot ha^{-1}$) by nitrogen class at tree age over observed data from the Nova Scotia permanent sample plot (PSP) network.

Stem and sapling density from the simulations were also assessed visually over stand age against the NS observed data. For all species, stand densities peaked significantly early in the simulations as stands colonized rapidly, followed by a decline and subsequent plateau in the mid- to late term (Fig. 2.5). Sapling densities followed a similar pattern, with an early peak with densities dropping to near zero before starting to increase as tree mortality occurred and secondary regeneration began (Fig. 2.6). Observed data was not available or plentiful for all species and understory regeneration is highly variable and dependent on many factors (Paluch 2004); therefore, in addition to direct comparison with observed data, the pattern we were expecting to observe in the simulated data was a secondary increase in sapling density beginning between 50 and 100 years and

reaching 500–3000 saplings/ha which was represented in all species (Brisette 1996; Angers et al. 2005; Leak 2006).

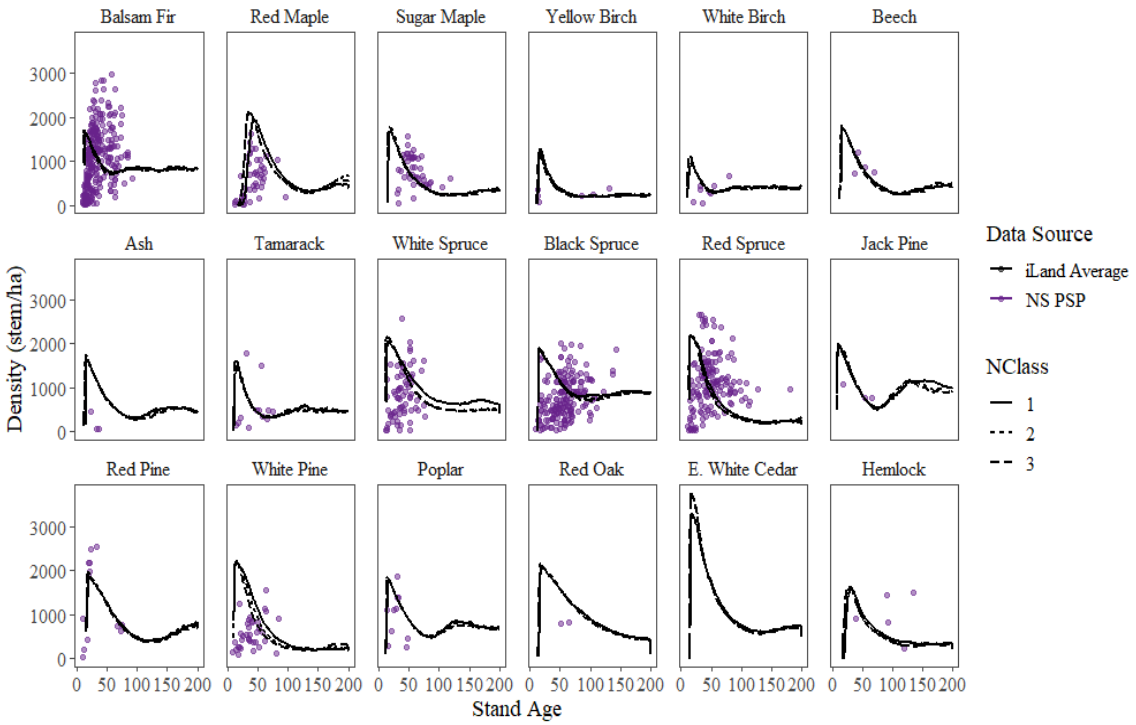

Fig. 2.5. Simulated iLand stem density (stems·ha^{-1}) including only stems > 9.1cm DBH by nitrogen class at stand age over observed data from the Nova Scotia permanent sample plot (PSP) network.

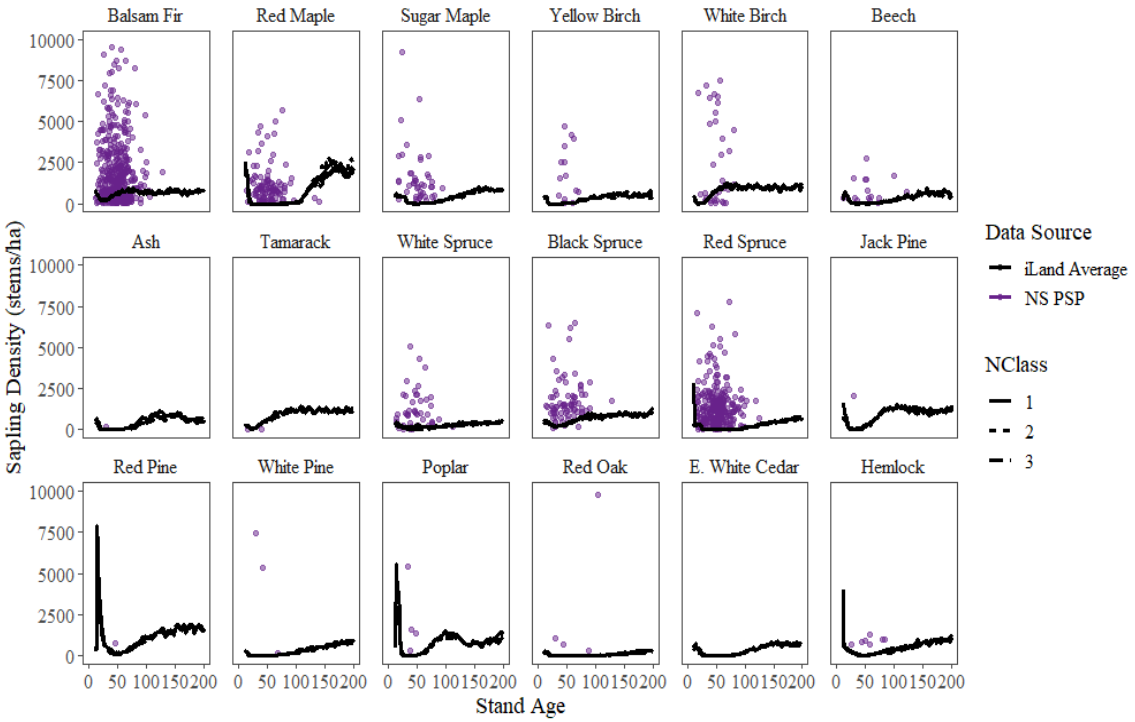

Fig. 2.6. Simulated iLand sapling density (stems·ha^{-1}) including stems < 4m height by nitrogen class at stand age over observed data from the Nova Scotia permanent sample plot (PSP) network.

After completing parameter adjustments, each species was again compared to the empirical observations by averaging DBH, height, volume, and age for the 200-year simulation data and NB, NS, and PEI datasets (Table 2.3). In the observed data, the NB average values were higher than the NS and PEI values in nearly species, except white pine and beech, for both DBH and height measures. Overall, the DBH and height averages in the iLand simulations were closer to the NS averages but fell within the interquartile ranges (i.e., between the 25th and 75th percentile) of all observed data, with few exceptions. The simulated DBH and height results for red pine, red oak, and hemlock were close to the NS observations, but much lower than the NB and PEI averages.

Volume comparisons between the iLand results and NS averages across species are congruous with the DBH and height comparisons, suggesting that the height to diameter ratios and volume calculation parameters in iLand are appropriate.

Maximum individual measurements simulated in iLand over the 200-year simulation period were compared with the NB, NS, and PEI observations, where available. The largest and oldest simulated individuals were generally represented in the empirical observations, and all were within species maxima documented in the literature (Table 2.4, Burns and Honkala 1990, Farrar 1995, Honer et al.1983). The largest difference in DBH growth was seen in American beech (+28.5 cm) and white ash (+23.0 cm). White ash showed the largest difference in maximum height growth at +7.3 m. The "aging" parameter, which is used to calculate a decline in gross primary production with age relative to a maximum age and height, was adjusted so that approximately 7–10 stems per ha would reach the maximum species age on long simulations which is not able to be observed on the 200-year simulation for long-lived species but was tested throughout the process with longer simulations. For example, red spruce has a lifespan of 400+ years (Burns and Honkala 1990) and had a maximum of 13 individuals per ha > 400 years of age over an 800-year simulation, with a maximum age of 502 years. Some typically short-lived, intolerant species, such as jack pine, were observed to live longer than expected in the monospecific simulations, but where their overall growth was as expected, no further adjustments were made and in later simulations, with mixed species competition, their life span was shorter, within normal range.

2.3.2 Stand Dynamics

Stand Structure

Stand dynamics were well represented in the multi-species simulations when compared to the NS observational data. Stand dynamics were assessed visually by comparing the average DBH (Fig. 2.7), height (Fig. 2.8), volume (Fig. 2.9), density of stems > 9.1cm (Fig. 2.10), and sapling density (Fig. 2.11) of each simulated stand at 10-year increments to plot averages from the NS observations. The 300 simulated stands displayed less variation in growth than the observed stands, with simulated DBH (Fig. 2.7) and height (Fig. 2.8) trending in the mid-to-high range of the observed data. This fits expectations as the simulated stands do not include disturbance or exceptionally low productivity sites such as bogs (e.g., observed plots > 130 years of age with average DBH < 15cm of pure black spruce (Fig. 2.6)). Average density of stems (DBH < 9.1 cm) showed a similar pattern as in the monospecific stands where the initial density peaked high, but the stands quickly thinned to an expected tree number (Fig. 2.10). Density trended low in the observed data which is not unexpected considering the moderate–to-high diameter range recorded (Fig. 2.10; Westoby 1984). Sapling densities were variable between stands, but conformed well to the observed data, averaging 1742 stems/ha to the observed 1844 stems/ha (Fig. 2.11).

Table 2.3 Average diameter at breast height (DBH, cm), height (m), volume per tree (m^3/tree), Age (years), and total stem count over by species for 200-year iLand simulation data and all trees with a counted age in the Nova Scotia (NS), New Brunswick (NB), and Prince Edward Island (PEI) permanent sample plot (PSP) networks.

	Diameter at Breast Height (cm)				Height (m)				Volume (m^3)		Age (years)				Count			
Species	**iLand**	**NS**	**NB**	**PEI**	**iLand**	**NS**	**NB**	**PEI**	**iLand**	**NS**	**iLand**	**NS**	**NB**	**PEI**	**iLand**	**NS**	**NB**	**PEI**
Balsam Fir	17.2 (4.1)	16.5 (3.9)	20.7 (6.0)	18.5 (4.0)	12.7 (2.5)	10.2 (2.7)	15.4 (3.8)	12.2 (2.1)	0.13 (0.32)	0.12 (0.09)	44 (24)	45(20)	67(19)	40 (14)	497,634	5,665	510	128
Red Maple	17.3 (8.0)	17.7 (4.7)	22.8 (7.1)	19.2 (5.2)	13.6 (4.1)	13.5 (3.0)	17.1 (3.0)	14.7 (2.5)	0.21 (0.29)	0.21 (0.14)	67 (36)	51 (17)	73 (20)	52 (17)	388,402	1,640	235	205
Sugar Maple	18.9 (8.9)	21.2 (6.3)	26.3 (9.5)	19.7 (6.0)	14.2 (4.6)	15.5 (3.2)	19.1 (3.5)	15.9 (3.2)	0.25 (0.36)	0.26 (0.22)	55 (36)	60 (21)	79 (35)	57 (21)	278,063	635	142	85
Yellow Birch	23.9 (12.4)	21.6 (6.9)	26.4 (9.5)	18.5 (4.9)	13.7 (4.2)	13.8 (2.9)	17.1 (3.4)	13.8 (2.9)	0.40 (0.50)	0.26 (0.19)	51 (37)	64 (26)	75 (32)	50 (14)	178,472	347	93	63
White Birch	15.7 (5.5)	17.1 (4.4)	20.6 (6.9)	17.5 (5.5)	12.4 (2.7)	12.8 (3.4)	16.5 (4.1)	13.8 (3.4)	0.15 (0.15)	0.15 (0.11)	42 (22)	55 (20)	67 (22)	46 (16)	244,385	675	133	159
Beech	21.5 (10.9)	20.7 (5.5)	21.3 (7.8)	21.7 (4.8)	11.2 (3.5)	11.9 (2.5)	13.4 (3.7)	13.7 (2.1)	0.36 (0.54)	0.22 (0.16)	52 (35)	62 (22)	76 (25)	56 (11)	320,997	42	18	44
White Ash	20.5 (9.6)	18.5 (4.9)	25.6 (7.9)	19.7 (5.1)	14.9 (4.7)	14.8 (3.1)	21.3 (4.6)	17.2 (2.7)	0.26 (0.36)	0.19 (0.13)	52 (32)	81 (27)	49 (22)	49 (14)	334,096	178	7	29
Tamarack	18.0 (8.8)	16.1 (4.7)	23.2 (6.1)	17.8 (3.6)	12.8 (4.3)	11.5 (3.4)	17.9 (3.7)	15.0 (3)	0.24 (0.34)	0.13 (0.12)	45 (29)	63 (30)	98 (26)	32 (10)	312,889	228	21	247
White Spruce	21.6 (8.6)	19.7 (5.9)	28.3 (7.7)	15.1 (5.3)	13.6 (4.8)	12.1 (3.5)	19.8 (3.9)	8.8 (3.6)	0.28 (0.32)	0.20 (0.18)	62 (44)	46 (17)	83 (18)	26 (7)	482,790	1,561	90	1428
Black Spruce	20.2 (6.6)	15.3 (4.0)	22.1 (6.0)	16.0 (3.5)	14.2 (3.7)	10.2 (2.7)	16.4 (3.3)	11.4 (2.2)	0.30 (0.25)	0.10 (0.09)	59 (36)	92 (27)	58 (24)	52 (23)	546,998	2,636	361	223
Red Spruce	26.4 (13.4)	19.4 (6.3)	27.4 (8.4)	17.3 (3.4)	14.6 (6.0)	12.7 (3.3)	18.0 (3.6)	12 (1.8)	0.65 (0.91)	0.41 (0.37)	59 (43)	53 (23)	90 (27)	34 (4)	334,030	4,063	444	16
Jack Pine	18.8 (7.8)	19.2 (4.8)	25.1 (5.2)	20.9 (2.3)	12.4 (3.8)	11.9 (4.1)	19.6 (4.5)	12.8 (1)	0.24 (0.26)	0.19 (0.15)	50 (31)	43 (22)	84 (28)	36 (3)	580,029	24	51	10
Red Pine	18.1 (7.9)	19.9 (8.9)	27.1 (3.3)	24.7 (4.9)	11.0 (2.7)	11.2 (4.3)	18.7 (1.9)	14.2 (3)	0.20 (0.26)	0.25 (0.29)	64 (38)	44 (32)	63 (26)	41 (17)	435,368	64	8	43
White Pine	21.0 (12.2)	24.8 (9.5)	25.1 (9.5)	38.3 (8.0)	13.5 (5.7)	14.2 (4.3)	15.1 (4.6)	22.5 (1.9)	0.41 (0.77)	0.42 (0.44)	52 (40)	47 (25)	62 (26)	99 (15)	331,800	631	24	5
Poplar	17.8 (5.3)	17.9 (5.9)	27.0 (9.3)	19.2 (5.9)	14.8 (3.0)	14.7 (2.9)	20.1 (3.8)	16.2 (2.7)	0.20 (0.15)	0.20 (0.22)	56 (32)	39 (15)	66 (21)	40 (10)	451,046	194	119	96
Red Oak	16.2 (5.1)	19.8 (5.8)	28.7 (3.1)	30.4 (4.2)	12.6 (2.8)	12.9 (3.2)	23.9 (1.6)	18.2 (1)	0.14 (0.13)	0.21 (0.16)	78 (49)	67 (22)	88 (16)	69 (15)	544,778	113	3	10
E. White Cedar	20.5 (8.4)	-	25.8 (7.6)	20.4 (5.1)	12.3 (3.3)	-	13.7 (3.0)	10.5 (2.1)	0.22 (0.22)	-	65 (45)	110 (29)	110 (29)	77 (14)	635,514	89	-	28
Eastern Hemlock	18.8 (9.0)	23.9 (9.0)	35.1 (7.8)	32.4 (-)	12.7 (4.1)	13.5 (3.7)	17.1 (2.7)	9.5 (-)	0.23 (0.31)	0.36 (0.38)	69 (42)	82 (44)	99 (25)	66 (-)	304,912	153	28	1

[1]Mean(SD)

Table 2.4 Maximum diameter at breast height (DBH, cm), height (m), volume per tree (m^3/tree), Age (years) by species for 200-year iLand simulation data and the all trees with a counted age in the Nova Scotia (NS), New Brunswick (NB), and Prince Edward Island (PEI) permanent sample plot (PSP) networks.

	Diameter at Breast Height (cm)				Height (m)				Volume (m^3)		Age			
Species	**iLand**	**NS**	**NB**	**PEI**	**iLand**	**NS**	**NB**	**PEI**	**iLand**	**NS**	**iLand**	**NS**	**NB**	**PEI**
Balsam Fir	25.3	22.0	39.8	30.5	16.5	13.5	27.5	17.0	0.32	0.23	149	138	153	77
Red Maple	51.2	41.0	48.4	41.0	26.5	23.1	25.5	20.3	2.24	1.06	200	135	142	104
Sugar Maple	54.8	48.4	67.8	38.2	29.1	25.1	28.7	23.5	2.61	1.66	200	156	216	120
Yellow Birch	61.9	48.9	55.6	30.0	23.6	21.5	28.7	20.8	2.77	1.37	200	158	174	90
White Birch	36.4	36.4	38.2	33.4	20.5	23.0	25.8	23.6	1.04	0.85	145	220	118	86
Beech	64.9	35.7	36.4	35.2	21.9	16.9	20.9	17.3	3.82	0.77	200	124	135	77
White Ash	59.0	36.0	36.0	30.2	29.1	21.9	21.8	20.5	2.67	0.85	200	130	110	72
Tamarack	53.4	43.4	35.8	27.6	24.5	22.5	25.8	23.0	2.40	0.93	200	149	149	107
White Spruce	51.5	46.1	55.1	67.0	27.1	24.0	29.3	19.0	2.06	1.39	200	141	137	80
Black Spruce	37.7	39.8	48.2	26.7	22.8	20.9	24.0	17.4	1.25	0.98	200	191	204	183
Red Spruce	68.4	53.0	68.0	23.1	31.2	27.0	27.6	14.8	5.20	2.15	200	219	200	38
Jack Pine	43.3	29.8	35.7	24.7	21.9	19.5	29.6	14.0	1.53	0.61	200	74	165	42
Red Pine	50.9	40.9	32.7	46.0	20.8	20.4	21.8	23.5	1.84	1.02	200	125	109	125
White Pine	76.1	68.8	42.1	50.4	34.5	28.0	24.0	24.0	6.55	3.60	200	330	102	120
Poplar	34.0	45.3	53.1	42.4	21.2	24.0	31.2	24.6	0.82	1.56	200	95	110	66
Red Oak	38.8	43.0	29.5	36.5	22.1	20.0	24.9	19.5	1.11	0.81	200	143	102	83
Eastern White Cedar	47.2	-	46.1	33.6	19.9	-	19.6	16.0	1.26	-	200	-	180	113
Eastern Hemlock	53.3	55.3	52.6	32.4	25.2	27.5	22.5	9.5	2.23	2.65	200	255	173	66

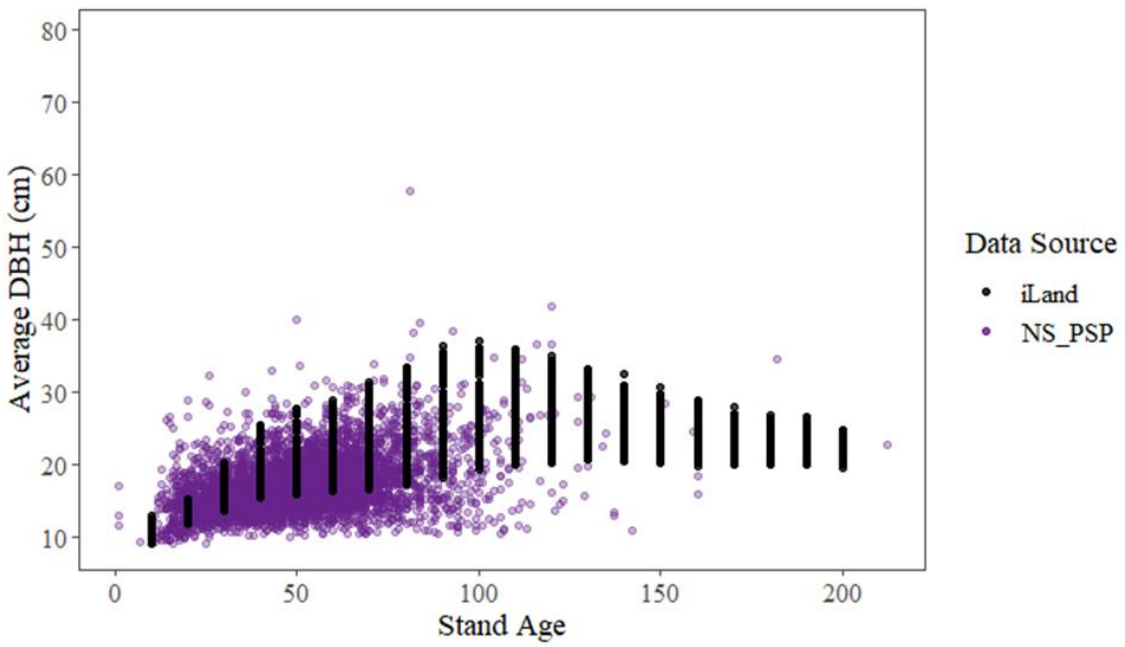

Fig. 2.7. Simulated iLand average diameter at breast height (DBH; cm) for each of the 300 simulated stands at 10-year increments over observed data from the Nova Scotia (NS) permanent sample plot (PSP) network.

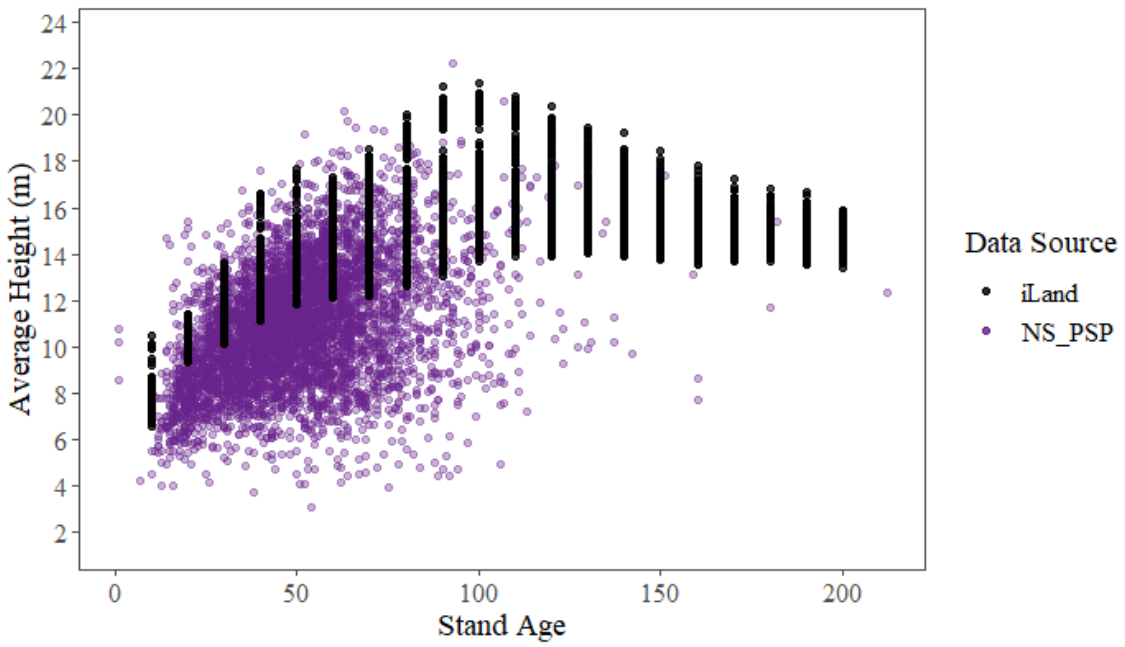

Fig. 2.8. Simulated iLand height (m) for each of the 300 simulated stands at 10-year increments over observed data from the Nova Scotia (NS) permanent sample plot (PSP) network.

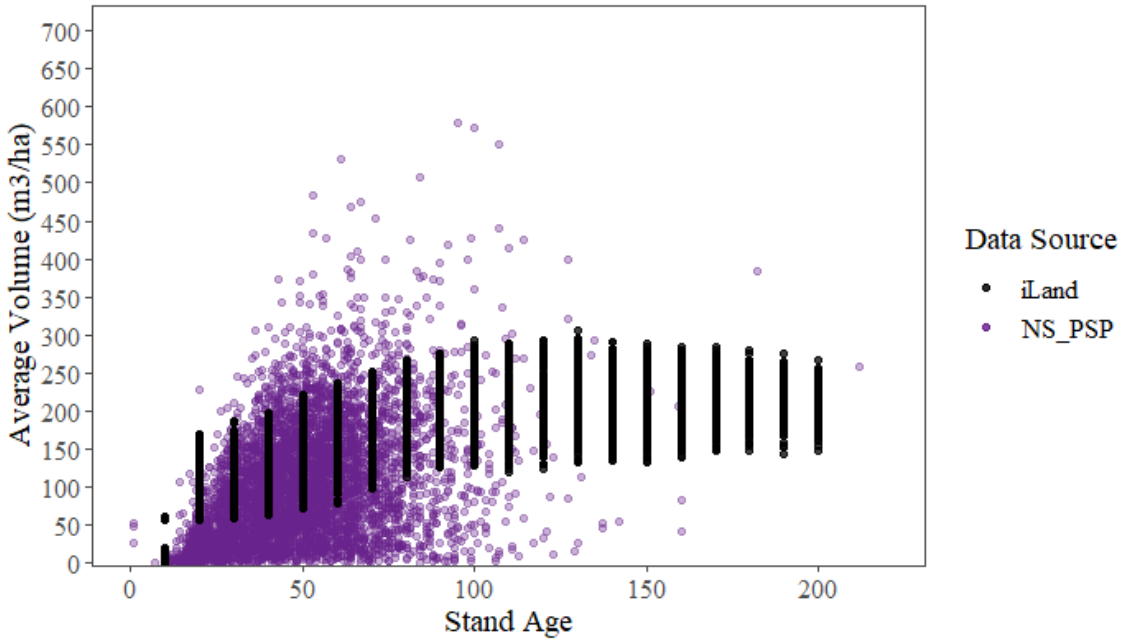

Fig. 2.9. Simulated iLand average volume per hectare ($m^3 \cdot ha^{-1}$) for each of the 300 simulated stands at 10-year increments over observed data from the Nova Scotia (NS) permanent sample plot (PSP) network.

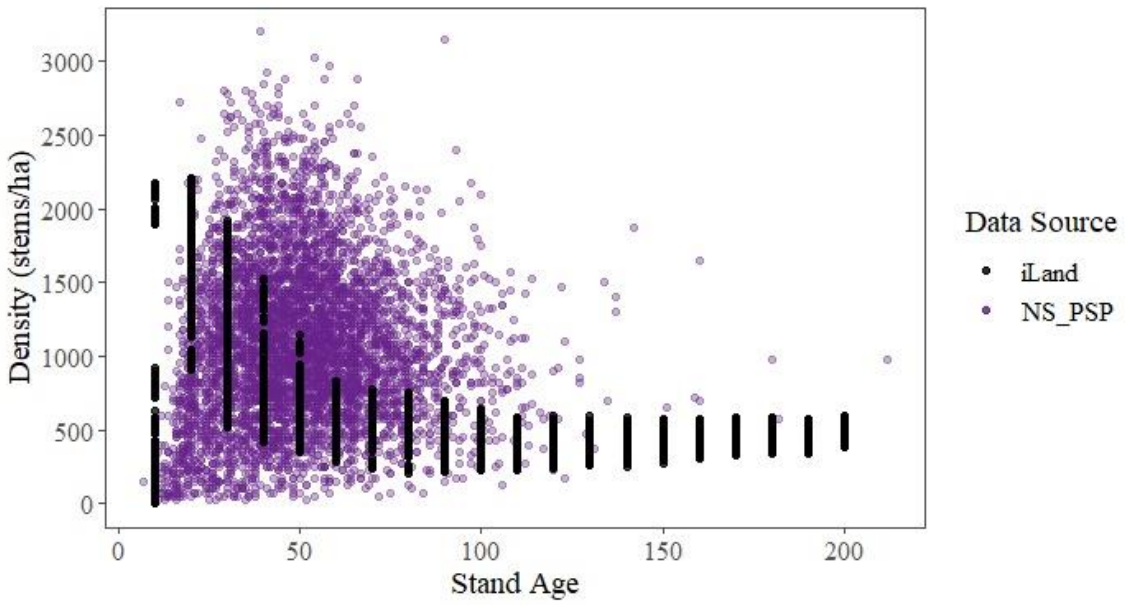

Fig. 2.10 Simulated iLand density (stems·ha^{-1}) for each of the 300 simulated stands at 10-year increments over observed data from the Nova Scotia (NS) permanent sample plot (PSP) network.

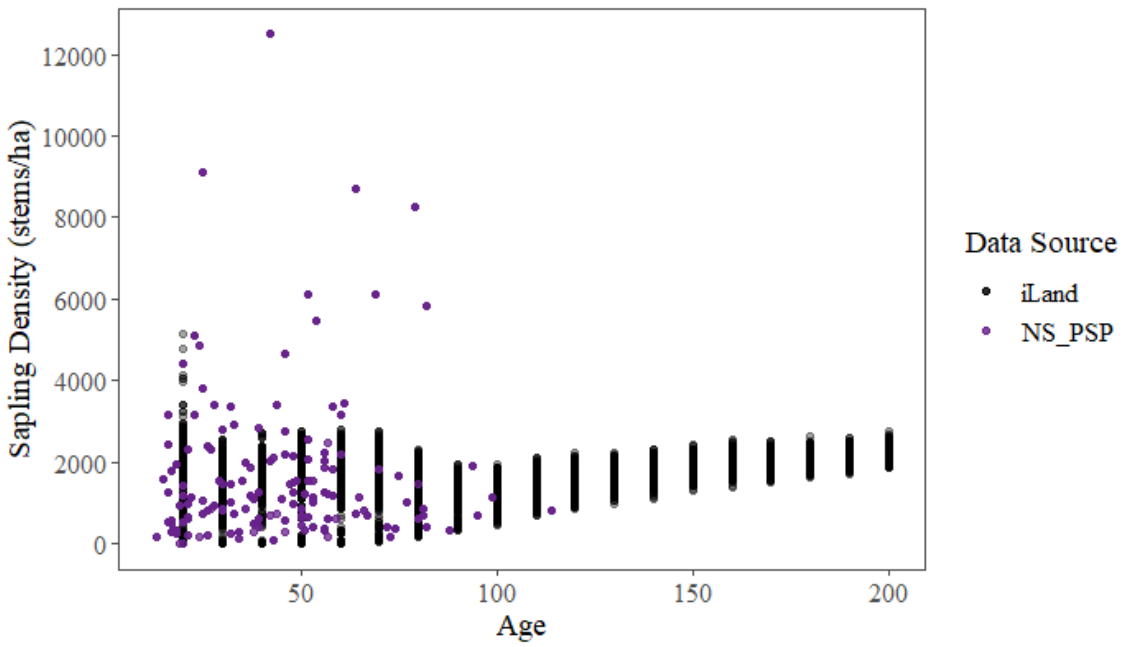

Fig. 2.11 Simulated iLand sapling density (stems·ha^{-1}) for each of the 300 simulated stands at 10-year increments over observed data from the Nova Scotia (NS) permanent sample plot (PSP) network.

Succession

During early succession (0–40 years), the simulation was comprised of 59.4% relative abundance of low shade-tolerance, pioneer species such as white birch, tamarack, and jack pine. In comparison, young stands in the NS observational data were dominated by 63.5% high shade-tolerance species, made up largely of balsam fir and white, black, and red spruce (Fig. 2.6). During mid-succession (41–100 years), the simulations showed a dramatic reduction in low shade-tolerance species to 3.9%, a 14.3% increase in moderate shade-tolerance, and a 41.4% increase in high shade-tolerance species, bringing it closer in line to the NS data which included 9.2% low, 29.8% moderate, and 60.9% high shade-tolerance species by volume (Fig. 2.6). In late-stage succession (101+ years),

the model closely matched observations. The relative abundance of both moderate and high shade-tolerance species closely matched with that of the observed data (Fig. 2.6). A larger difference was seen in the relative abundance of low shade-tolerance species in late succession, which was 0.04% in iLand, but was substantially higher in the NS data at 8.4%, made up of 5.2% tamarack and 2% or less white ash, white birch, red pine, and poplar

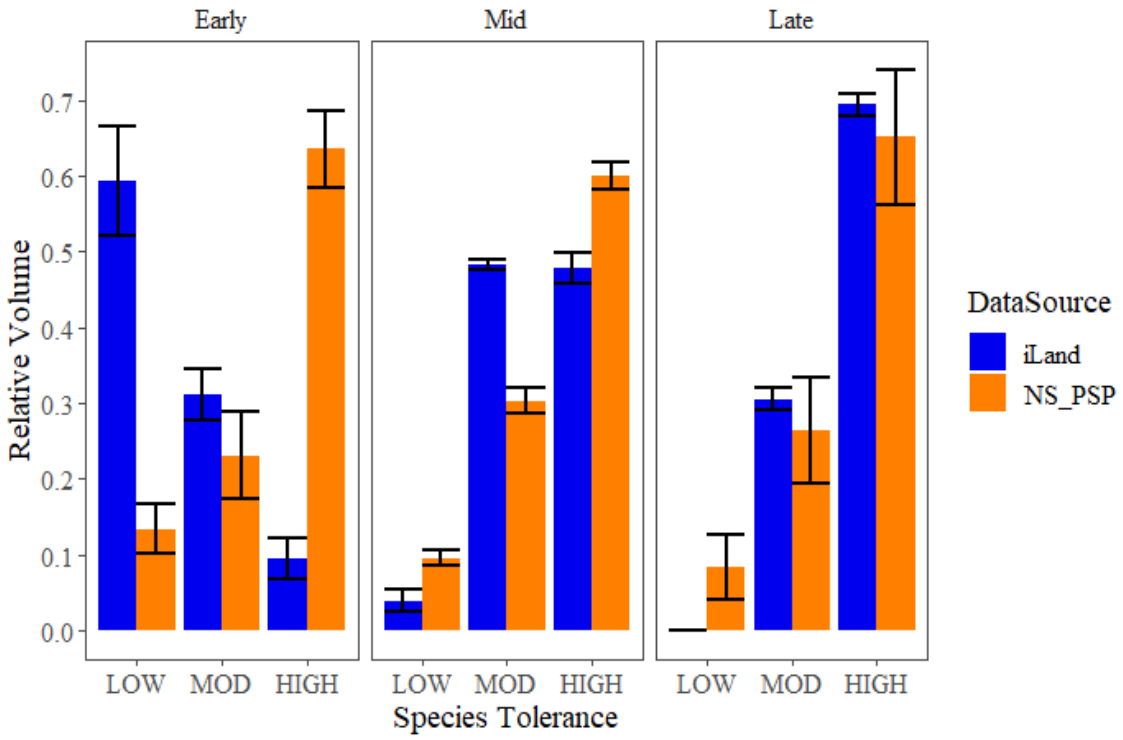

Fig. 2.12. Relative abundance by species shade tolerance the combined 300 simulated stands and NS permanent sample plot data compared between early, mid, and late successional stages. Successional stages were divided by stand age with 0–40 years, 41–100 years, and 100+ years representing early, mid, and late succession, respectively.

2.4 Discussion

It is imperative for forest managers to integrate process-based modelling into their decision-making toolkit in the face of rising uncertainty due to climate change (Cuddington et al. 2013). Complex process-based models are becoming increasingly accessible and have been used in a variety of climate sensitive landscape projections, the results of which can be used to inform decision making (e.g., Taylor et la. 2017; Ashraf et al. 2012; Boulanger et al. 2018; Dobor et al. 2018; Rammer and Seidl 2015; Seidl et al. 2017; Steenburg et al. 2013). Although the data requirements for initialization and calibration still present a challenge, increasing data availability along with tools for remote data collection and interpolation will continue to improve ease of use and the opportunity for application in long-term management planning (Ruiz-Benito et al. 2020; LaDeau et al. 2017).

The model iLand provides a unique combination of dynamic interactions between individual trees and their environment across the simulated landscape, at high spatial and temporal climate resolution, as well as dynamically simulated disturbances and options for including forest management making it well suited for investigating the impacts of climate change on forest dynamics and disturbance regimes (Thom et al. 2017b; Seidl 2014a; Rammer and Seidl 2015). Although the model is very complex in detail and requires many species and environmental parameters variables, necessitating thorough data collection and calibration, it has a user-friendly graphical user interface, uses open-source software, and has extensive online-resources, making it accessible for experienced forest professionals with adequate resources and good understanding of modelling concepts.

Population Dynamics

In this study, we successfully calibrated iLand, closely approximating observed patterns for both individual species and stand dynamics in the AFR. Simulated diameter, height, and volume growth for all species fell within the ranges of observed natural variation. Increased N levels between the low and moderate produced a noticeable increase in growth, but only a slight further increase was observed from moderate to high N levels, reflecting known soil N saturation trends (Aber et al. 1989). Tree ages were also well represented, although for many long-lived species there were limited observations in the upper ages; simulated averages remained within known species maxima (Burns and Honkala 1990; Farrar 1995). However, certain differences were noted between the observed data and simulated results, relating to model function, characteristics of the observational data sets, and project design.

In some cases, differences identified between simulated and observed species average growth were influenced by factors not accounted for in the model. For example, simulated American beech was able to obtain larger maximum diameters and longer life spans than observed, possibly due to the influence of beech bark disease in the AFR which is currently unaccounted for in the model (Le Guerrier et al. 2003). Adjustments were made to decrease the productivity of beech to reflect the impact of beech bark disease, however, large individuals were still able to occur with a frequency that is now rarely observed in the AFR (Taylor et al. 2013). Awareness and special considerations need to be made in the application of iLand and analysis of results for biotic disturbance agents that are having a significant impact on species in the area of interest. There are several methods that can be used to replicate the impact of disturbance agents including

the bark beetle module (Dobor et al. 2018) and biotic disturbance engine (BITE; Honkaniemi et al. 2021).

Comparisons were also impacted by low representation of some species in the observational data. Observational averages for DBH and height were much higher for white ash, red pine, and red oak in NB, and white pine, red oak, and hemlock in PEI. The NB observations for those three species were limited to 39 records in total, none of which contained stems younger than 50 years, while the PEI observations totaled only five, ten, and one, older stems for each of the three species, respectively, which may have inflated the observational average values. The quality and quantity of forest inventory data will vary depending on the scale, jurisdiction, and heterogeneity of the area of interest but should be cleaned and assessed critically when being used in model validation or initialization to evaluate characteristics of the data that may not be reflective of the true on-the-ground conditions. Models are a representation, not a replication of a landscape and comparison with biological realism should be considered in addition to direct comparison to existing inventory data (Vanclay and Skovsgaard 1997).

Stand Structure

Establishment and regeneration patterns were reflective of natural patterns, with simulated densities over time displaying the expected pattern of high stand initiation density, followed by self-thinning as age and average DBH increased (Westoby 1984). Sapling density remained steady throughout the simulation, which is to be expected when modeling without disturbance. Despite reflecting the natural pattern of establishment, the simulated stand densities were significantly lower than the observed values from NS.

This can be attributed to the establishment routine used in the model and the exclusion of forest disturbances from the initial calibration (Valle et la. 2009). Using the bare ground establishment routine, the model showed consistently high establishment densities both in the individual and multi-species testing scenarios, characteristic of natural establishment patterns following stand replacing disturbance (Bartels et al. 2016). However, large-scale stand replacing disturbances are not widespread in the AFR, with return intervals for high severity fires and hurricanes estimated at 250–600 years and 1,250 years, respectively (Taylor et al. 2020). These high initial densities reflect on the growth patterns of the stands and species densities for up to 200+ years, depending on the species composition, with stands eventually converging towards a mean condition (Braziunas et al. 2018). The AFR has many disturbance agents that interact to create canopy gaps, allowing for continuous regeneration throughout stand development (Amos-Binks and MacLean, 2016), whereas without the inclusion of disturbance in the model of any type, regeneration is reduced as the forest develops and competition for light precludes the establishment of new cohorts. In addition, the bare ground establishment routine used had external seed input from all 18 parameterized species simultaneously, which continued throughout the simulation, in addition to dynamic seed rain from the forest as it developed. This creates a more consistently heterogenous environment across the simulated landscape with stand types and species mixtures that would not typically develop in a natural forest. With these considerations, the emergence of natural patterns of stand structure supports the validation of the model calibration. When applying the model in a new forest, typically forest inventory data is used to inform stand delineation, species composition, size, and density, along with a spinup routine (i.e., a process of

combining multiple model initializations to reduce idiosyncrasies associated with the random element of initialization to create a more stable environment) to better characterize natural conditions (Thom et al. 2016) and mitigate the impacts of initialization on the simulated future conditions (Temperli et al. 2013).

Succession

The simulation results showed marked difference from the NS PSP results for composition by species and tolerance level in the early and into mid-successional stages. Early successional species dominated in the model at stand initialization and then experienced a sharp decline in the mid-successional period up to 100 years, having been overtaken by more tolerant species. By the late successional stages, the intolerant species were essentially non-existent and the division between moderate and high shade tolerance species was reflected in the observed data, a well-documented successional pattern (Fraver et al. 2009; Gauthier et al. 2010; Basquill and Baldwin 2020). That pathway is not reflected in the NS observations, which showed a consistent division of relative tolerance across successional stages. The disproportionate presence of high-shade-tolerance species such as balsam fir and white spruce can be attributed to the "borealization" impact of previous land clearing for settlement, timber exploitation, and agriculture, and more recent industrial forest management (Noseworthy and Beckley 2020).

In addition, the NS observations showed a higher prevalence of low-shade-tolerance species in the late successional stage, made up largely of tamarack. Tamarack is highly intolerant of shade and cannot reproduce under a full canopy; it must establish

early and become dominant to survive in the canopy of a stand (Burns and Honkala 1990). Due to the prevalence of shade-tolerant species in all stands and lack of disturbances in the iLand simulations, tamarack was unable to compete on the landscape. However, when assessed with fewer species, it was able to persist. For initial calibration purposes, the increasing trend in agreement over time and the representation of the simulation data by the observed data for species and tolerance composition in the late successional stage are considered successful because the replication of the current state of NS forests was not the overarching goal and would require the more specific stand initiation techniques to replicate mentioned previously.

2.5 Conclusion

By providing this case study of the calibration and validation of a novel process-based model we hope to contribute to the increased use of modelling in the forest management context. The complexity of process-based models creates challenges for users; however, it is also their greatest asset, allowing a properly calibrated model to be invaluable for applications such as assessment of adaptive forest management, projecting changes in forest growth and composition, ecosystem services, biodiversity, and disturbance regimes, and predicting the spread of invasive pests and diseases.

Using iLand as a case study, we have demonstrated a robust methodology for the parameterization, calibration, and validation of a process-based model for the AFR. Based on our results, this calibration of the iLand model is currently suitable for application in most of the AFR. In the most northern regions where the forest has a distinctly more boreal characteristic further testing should be done with a subset of

growth and yield data. The model is calibrated only for general landscape characteristics and is not currently verified to represent specific stand types that represent a smaller proportion of the forest, such as bogs or coastal krummholz stands. At this stage, iLand is ready to be used in general modelling projects throughout the AFR and to undergo more region-specific evaluation.

2.6 References

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Chapter 3 – PROJECTING FOREST SUCCESSIONAL AND STRUCTURAL DYNAMICS FOR PRINCE EDWARD ISLAND NATIONAL PARK UNDER CLIMATE CHANGE

Willis, S.; Taylor, A.R.; Thom, D.; D'Orangeville, L.; Bourque, C.P.-A.

3.1 Introduction

Based on current projections, global average temperatures are expected to rise 3–7°C by 2100 (IPCC 2018, Peters et al. 2020). Climatic changes will expose global forests to novel conditions, driving shifts in forest structure and function, and influencing the provision of goods and services we derive from our forestlands (Hoegh-Guldberg et al. 2019).

The forest of Prince Edward Island National Park (PEINP; Fig. 3.1) is part of the Acadian Forest Region (AFR) of eastern Canada (Rowe 1972) and may be especially impacted by climate change, as the AFR is an ecological transition zone between the boreal and temperate forest biomes with many of its tree species being at their extreme northern or southern range limits (Little, 1971). The AFR, including the provinces of PEI, New Brunswick (NB), and Nova Scotia (NS), has already seen a rise in annual average temperature of 0.7°C from 1948 to 2016 (Zhang et al. 2019). An additional warming of 1.5°C to 5.2°C is expected by 2100 under the moderate and high radiative climate forcing scenarios (Zhang et al. 2019) defined by Representative Concentration Pathways 4.5 and 8.5 (RCP; van Vuuren et al. 2011), respectively. Precipitation averages in the region have also increased by approximately 11% during the same period with a further increase of 3–12% possible (Zhang et al. 2019). Along with shifting climatic conditions, more frequent severe weather events such as extreme hot or cold periods

(Zhang et al. 2019), heavy rain and wind (Zhang and Colle 2017; Li et al. 2019), and increased frequency of spring and summer drought (Yang et al. 2020) are expected. Compared to Canada's mainland, small islands such as PEI and their forests may be more at risk of compounded effects of climate change due to their reduced ability to buffer climatic or biological change, limited fresh water supply, coastal exposure to severe maritime weather, and dramatic erosion (IPCC 2014; PEI 2018).

Over the past several centuries, the AFR has undergone dramatic changes in forest structure and composition from the anthropogenic impact of settlement, timber harvesting, the removal of forest for agriculture, and the increase of disturbances such as invasive insects, disease, and human-caused forest fires (Loo and Ives 2003). This anthropogenic impact was especially severe on PEI due to its small landmass (5,600 km^2), high private land ownership, prime agricultural conditions, and few topographical limitations to inhibit development (McFadyen 2016). As a result, the forest of PEI (and throughout much of the AFR) has shifted from a predominantly mixedwood forest conditions, dominated by long-lived, shade tolerant species, to a younger, fragmented forest comprised of more boreal conifers and early successional hardwood species (Sobey and Glen, 2004; Noseworthy and Beckley 2020).

Studies of many types including paleobotany (Overpeck et al. 1991), biogeoclimatic envelope modelling (McKenney et al. 2007; Glen 2008), and forest modelling (Bourque and Hassan 2010; Steenberg et al. 2013; Taylor et al. 2017; D'Orangeville et al. 2018) agree regarding the further impact climate change will have on the AFR and adjacent boreal-temperate areas. Specifically, these studies consistently

predict a decline of boreal tree species such a balsam fir (*Abies balsamea* L.), black (*Picea mariana* (Mill.) BSP) and white spruce (*Picea glauca* (Moench) Voss), and trembling aspen (*Populus tremuloides* Michx.), with a concurrent increase in temperate species such a red maple (*Acer rubrum* L.) and American beech (*Fagus grandifolia* Ehrh.). Due to their prevalence in most areas, a decline in boreal tree species will likely translate to a period of overall decline in forest productivity as the natural transition to temperate species lags in comparison to the speed of climate change (Taylor et al. 2017).

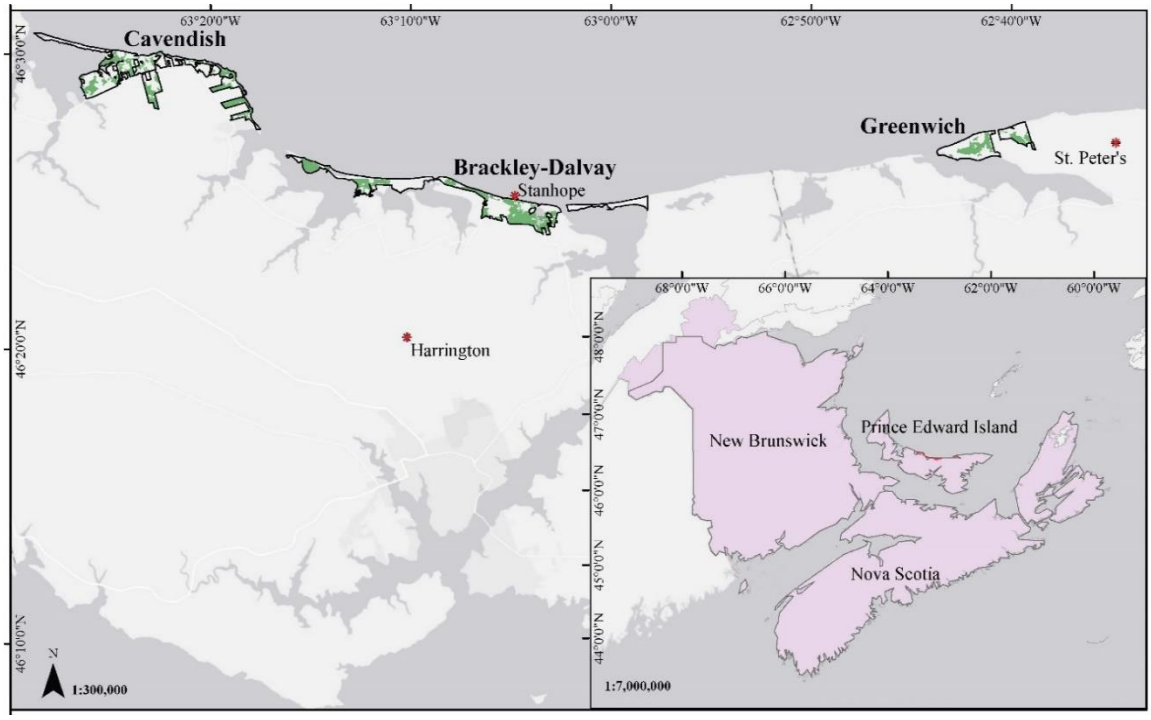

Fig. 3. 1. PEINP (delineated in black) with the 2015 Forest Management Plan (Amero et al. 2015) in green. Red asterisks indicate wind stations used in creation of the wind event timelines. The inset map shows the extent of the AFR in purple over the provinces of PEI, NB, and NS with the PEINP shown in red along the northern coast of PEI.

Climate change will impact forest composition not only through temperature and precipitation changes but also through changes to the natural disturbance regime (Dale et al. 2001). Gap disturbances of small, infrequent fires, windthrow events, and endemic insect damage are most frequent in the AFR (Basquill and Baldwin 2020), however larger wind events, fires, and insect outbreaks also occur throughout the region and are expected to increase in frequency and severity (Taylor et al. 2020). For PEINP, wind disturbance is of particular concern due to its coastal exposure and stand conditions (Taylor et al. 2019). Although there is large uncertainty around projections of future storm activity, currently no significant increase in the number of hurricanes or tropical storms is expected, but an increase in the severity of storms, including stronger peak wind speeds and increased rainfall, is projected (NOAA 2021) which can lead to increased rates of forest disturbance (Taylor et al. 2020; Thom et al. 2017a). An example of the swift and dramatic impact of severe wind damage was seen in PEINP in 2019 because of Hurricane Dorian with the loss or significant damage of 80–90% of the trees on the Cavendish campsite and in the surrounding forest (NOAA 2020; CBC 2019). Very recently, Hurricane Fiona caused unprecedented devastation across PEI on September 24th, 2022. PEINP experienced severe damage to the forest, coastline, and infrastructure throughout all sections of the park. Due to the extent of the damage, forest losses have yet to be quantified at this time, but it is known that they are widespread and severe, particularly impacting old-field white spruce (OFWS) stands in various stages of collapse.

As a result of the legacy impacts of past agricultural land use, the forest of PEINP currently has a young forest with low species diversity and a high percentage of stands that are in danger of collapse (Amero et al. 2015). Management programs need to

advance quickly to feasibly manage the transition of these stands while maintaining the overall ecosystem services of the forest. Management objectives for PEINP include conservation and restoration of ecological integrity, alongside public access, and recreation opportunities (Overton 2003). PEINP joined the Parks Canada *Conservation and Restoration* (CoRe) program in 2008 and Acadian Forest Restoration has been one of their longest running projects (Parks Canada 2018). Projects have included development of a forest inventory and management plan, increased forest monitoring, and planting of native species (Amero et al. 2015). However, considering the current condition of the forest and the potential impacts of climate change, using historical forest conditions as a restoration goal may no longer be relevant (Seastedt et al 2008; Taylor et al. 2017; Boulanger et al. 2019). Looking forward, focusing on increasing resiliency (i.e., the ability for a forest to resist or recover from disturbances) may be what is required to best balance the ecological function and societal needs within the PEINP (Millar et al. 2007; Messier et al. 2019).

Projecting the long-term effects of management efforts and climate change is vital to gauging the potential success of the Acadian Forest Restoration Program at PEINP and comparing future management scenarios. Process-based forest ecosystem simulation models offer advantages for assessing novel scenarios because they use a dynamic response-based approach grounded in first principles (Marquet et al. 2014) to reproduce interactions of ecosystem processes and environmental conditions (Battaglia and Sands 1998). This is contrary to empirical models, also known as pattern-based or phenomenological models, which model the resulting change based on past observation, rather than the process. This difference allows for the use of process-based models to

increase understanding of potential outcomes when extrapolating forest response to novel environmental conditions (Cuddington et al. 2013).

In this project, we will be using the individual-based forest landscape and disturbance model, iLand (v1.1.1). iLand has been calibrated and validated for 18 of the most common species in the AFR (Willis et al. 2022). It was shown effective in simulating landscape level dynamics as well as the individual species growth patterns under the same climatic and environmental conditions present at PEINP. The wind module was parameterized and validated for this project and was found effective in simulating low–moderate disturbance (i.e., 5–60% stand mortality).

The objective of this chapter was to initialize the model for the PEINP using the 2015 Management Plan inventory and to simulate the park landscape over 100 years under baseline (historical), RCP 4.5, and 8.5 climate forcing scenarios. The simulations were completed without and with wind disturbance. The results were analyzed to describe the impact of climate change and low to moderate severity disturbance on (i) landscape level forest structure and productivity, and (ii) species population dynamics. The expected benefits of this project are twofold: (1) provision of a ready to use forest model for PEINP to provide a basis for ongoing investigation by Park Management; and (2) provide specific results that can be used immediately by PEINP to help inform forest management decisions going forward.

3.2 Methods

3.2.1 Study Area

Prince Edward Island National Park (PEINP; Fig. 3.1), a long, narrow stretch of land along the north shore of Prince Edward Island (PEI), Canada, encompasses a total area of 2,220 ha (approximately 50% forested) varying in width from 200 m of sandspit to a maximum of 3.5 km. The PEINP region is characterized by low-lying, gently rolling terrain with a maximum elevation of 62 m and features over 40 km of coastline. The soils are largely well-drained, sandy loams of glaciofluvial origin over bedrock of red sandstone with moderate to high fertility in most areas, although historical forest depletion and agricultural use has impacted the soil (Anderson 1980; MacDougall et al. 1988; Keenlyside and Kristmanson 2016). The climate is cool and humid due to the moderating effect of the Gulf of St. Lawrence with summer averages of 17–19°C and winter averages of -6°C. PEI receives an average of 1200 mm of precipitation per year, distributed equally across the island due the narrow landmass and low relief (ECCC 2022). Prevailing winds are westerly through most of the year with an average speed of 18 $km \cdot hr^{-1}$ and eight days per year with gusts > 50 $km \cdot hr^{-1}$ occurring most frequently in the winter months (ECCC 2022).

Established in 1937 to provide tourist access to the beautiful coastal sand dunes of the area, PEINP consists of three main sections at Cavendish, Brackley-Dalvay, and Greenwich (Fig. 3.1; Parks Canada 2017). Settlement in these areas began in the mid-18th century, followed by establishment of a significant shipbuilding industry (de Jong and Moore 1994) and clearance for agricultural communities (McFadyen 2016). PEINP

originated from the expropriation of well-established farmland that had been largely cleared in the preceding ~200 years (McFadyen 2016). Following creation of the PEINP, much of the farmland was left to reforest naturally, and developed to old-field white spruce (OFWS) forests. This occurs due to a lack of seed sources for other native species and the ability of white spruce to colonize quickly on the disturbed soils of cultivated lands and in full light conditions, unlike many of the shade-tolerant Acadian species (Glen 2013).

These forests exhibit physiological differences from typical white spruce including shorter life span, shallower rooting, maintenance of a larger crown, and larger branching (Drinkwater 1957; NSDNR 2011). There has not been a lot of study into the cause of the differences the OFWS exhibit (Drinkwater 1957; Salonius et al. 1988), however, the phenomenon is widely observed throughout the AFR (Basquill and Baldwin 2020; Loos and Ives 2003). These even-aged stands tend to "collapse," i.e., experience widespread mortality, between 35–70 years of age and most do not have a significant amount of established regeneration or nearby seed sources to maintain closed-crown forest characteristics (Glen 2013). Today, 51% of the operable forest (i.e., forest which can be managed using harvest-based silvicultural techniques; not including areas within campgrounds, surrounding facilities, or ornamental plantings) of PEINP is composed of stands of OFWS > 40 years of age (Fig. 3.2; Amero et al. 2015). In addition to white spruce, other species commonly found within the park include black spruce, red spruce (*Picea rubens* Sarg.), balsam fir, red maple, trembling aspen, and white birch (*Betula papyrifera* Marshall). Less prevalent species include Eastern white pine (*Pinus strobus* L.), tamarack (*Larix laricina* ((Du Roi) K. Koch), sugar maple (*Acer saccharum*

Marshall), yellow birch (*Betula alleghaniensis* (Britt), large-toothed aspen (*Populus grandidentata* Michaux), and red oak (*Quercus rubra* L.).

The 2015 forest inventory of PEINP identified ~1250 ha of PEINP as forested (Amero et al. 2015; Fig. 3.1). Of that area, 95% is considered operable, with the remaining 5% in treed swamps (Fig. 3.2). The softwood leading stands are usually dominated by OFWS, with components of aspen, white birch and/or red maple, however, there are instances of stands dominated by black spruce and balsam fir. Additionally, the "krummholz" forest type, common along maritime coasts, is observed in PEINP. It is characterized by tightly grown and severely stunted white spruce forests that have a very distinctive growth pattern caused by strong winds, salt spray, and poor soil (NSDNR, 2011, p. 39–40).

Most hardwood leading stands within PEINP are dominated by trembling aspen, white birch, and red maple, with scattered large-tooth aspen, white spruce, and balsam fir. In the Cavendish portion of PEINP (Fig. 3.1), nine stands were identified as containing shade-tolerant hardwoods including sugar maple, yellow birch, and red oak; however, the area dominated by these tolerant hardwood species is < 8 ha. Throughout the forest there are also many mixedwood stands that are a combination to varying degrees of the common softwood and intolerant hardwood species, with a minimal presence of tolerant hardwoods. There are also plantations of native and non-native species, silvicultural trials, and ornamental species found throughout PEINP.

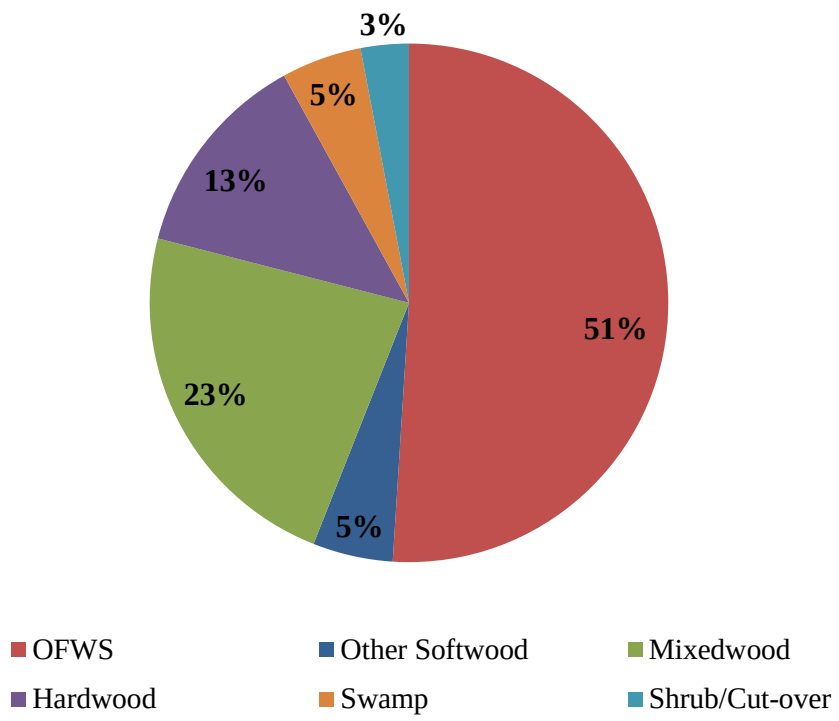

Fig. 3.2 Division of PEINP forested area by forest type

3.2.2 Description of Forest Model: iLand

iLand was released in 2012 and offers a novel approach for simulating the interaction between individual trees (demographic processes) and their environment (ecosystem processes, climate, and disturbance) in a scalable manner (Seidl et al. 2012a). It operates at the individual-tree level while simultaneously modelling dynamic ecosystem processes at the landscape scale, allowing for explicit spatial monitoring of forest succession and disturbances. iLand uses a novel, multi-hierarchical scaling approach based in ecological field theory to simulate the demographic processes (growth, mortality, regeneration) at the individual tree level.

The development of iLand was not focused on increasing the complexity of the individual tree processes, but on overcoming previous limitations of computational demand in integrating true feedbacks between individuals on a fine spatial scale and the changing climatic conditions on a landscape scale (Seidl et al. 2012a). iLand was initially shown effective in replicating multiple current landscapes: the unique forest conditions of an old-growth forest in the Cascades of Oregon, along an elevational gradient transect in Oregon, USA, and along a second transect in the east Austrian Alps (Seidl et al. 2012a). Since then, iLand has been used to model forest growth and the impact of climate change and disturbance in the temperate forests of central Europe and the western USA (e.g., Old Growth Dynamics – Seidl et al. 2012b; Climate Change and Disturbance – Thom et al. 2017b; Wildfire – Seidl et al. 2014a; Wind disturbance – Seidl et al. 2014b, Bark Beetle – Dobor et al. 2018; Wildfire – Braziunas et al. 2018; Other Biotic Disturbance – Honkaniemi et al. 2021).

Growth and competition are simulated based on light use efficiency and environmental performance modifiers. Light, water availability, and climate are considered on a daily timestep, while nutrient availability and atmospheric CO_2 are used monthly, to calculate annual tree growth and/or mortality. The default spatial units are 2x2m for individual tree locations and competition for resources, 10x10m for stand initialization, and 100x100m grids for resource units (RU; soil and climate). More than 60 individual species-specific parameters are used to calculate these interactions and determine allocation of carbon (C) within the tree. A descriptive list of parameters is available in Appendix A and at the online resource (iland-model.org/species+parameter). Tree mortality occurs intrinsically from age-related decline, through C starvation due to

stress, or from disturbance. Growth and mortality outputs are recorded on an annual timestep. Regeneration is impacted by seed-source availability, spatially explicit seed distribution defined via species-specific kernel functions, resprouting, environmental constraints, and light availability. Figure 3.3 represents the flow of interactions within the stand: the climate inputs from the top include temperature, precipitation, vapor pressure deficit (VPD), and radiation; the individual processes affecting growth and allocation are indicated in the center; and soil inputs from the bottom (Seidl et al. 2012a).

To initialize iLand to simulate a forest landscape, it requires tree vegetation, climate, and soil data. Climate data is required at a daily time scale and includes minimum and maximum temperature (°C), precipitation (mm), solar radiation, and vapor pressure deficit (VPD). Basic soil data required includes available nitrogen, effective soil depth, and soil texture for each resource unit. A complex carbon and nitrogen soil cycling sub-model is available, however it requires extensive parameterization and calibration, and will not be used here as it is outside of the scope of this study.

For this study, the wind disturbance module was used with the goal of emulating low to moderate disturbance regimes typical for the landscape. A temporal distribution for wind events is applied in the model, indicating year and day of year, created from either empirically observed data or climate projections with wind speed, direction, and duration. The events are applied across the landscape by identifying “edges” (i.e., 10m cells with height >10m above a neighbouring cell) and calculating wind throw potential for the dominant stem on that edge cell. This is done iteratively with new edge cells being detected after each iteration until the wind event duration is complete or no new edges are detected. Topography modifies wind speed and direction. Wind impact on a tree

individual is calculated through the combined consideration of edge effect, vertical wind profile (i.e., calculation of canopy top wind speed), species-specific turning coefficients, gaps and neighboring shelter trees, soil temperature, and critical wind speed. Greater detail regarding the function of iLand and the wind module can be found in Seidl et. al (2012a), Seidl et al. (2014), and on the comprehensive online resource (iland-model.org).

3.2.3 Simulated Landscape and Drivers

Forest Stands

The delineation of forest stands in PEINP was previously completed for the 2010 Provincial inventory using aerial imagery (PEI 2010). The predetermined stands from this inventory were maintained during the development of the updated inventory for the 2015 Management Plan and in our model initialization work. During the management plan inventory, a prism point tally sample method was used in each stand to obtain basal area by species, average DBH, and height (Amero et al. 2015). Additional qualitative stand attributes such as development stage, regeneration, and shrub cover were also recorded (Amero et al. 2015). This inventory data was then summarized to inform the iLand initialization, specifically to populate trees and saplings within the model for each stand using species, stand density, DBH minimum and maximum, height-to-diameter ratio, and age in a pseudo-random manner.

iLand was not able to accurately represent the earlier age-related decline of OFWS relative to “natural” white spruce (PIGL) at PEINP as species parameters were derived natural forest conditions. Instead, a separate “species” was created for OFWS where the maximum age and aging parameters were manipulated to match the observed

earlier decline on OFWS. Adjustments were not made to biomass partitioning, height/diameter ratio, etc. due to the lack of stand specific measurements available for comparison. All stands that were identified in the inventory as “old field white spruce” were input as OFWS while white spruce occurring in a mixed stand was input as PIGL.

Table 3.1 List of species common name, scientific name, four letter iLand code, and shade tolerance class

Common Name	Latin	iLand Code	Shade Tolerance
Balsam Fir	*Abies balsamea*	abba	high
Red Maple	*Acer rubrum*	acru	mod
Sugar Maple	*Acer saccharum*	acsa	high
Yellow Birch	*Betula alleghaniensis*	beal	mod
White Birch	*Betula papyrifera*	bepa	low
Beech	*Fagus grandifolia*	fagr	high
White Ash	*Fraxinus americana*	fram	low
Tamarack	*Larix laricina*	lala	low
White Spruce	*Picea glauca*	pigl	high
Old Field White Spruce	*Picea glauca*	ofws	high
Black Spruce	*Picea mariana*	pima	high
Red Spruce	*Picea rubens*	piru	high
Jack Pine	*Pinus banksiana*	piba	low
Red Pine	*Pinus resinosa*	pire	low
White Pine	*Pinus strobus*	pist	mod
Trembling Aspen	*Populus tremuloides*	potr	low
Red Oak	*Quercus rubra*	quru	mod

During the inventory, the only other species of spruce identified was black spruce, however it is known that red spruce is found within PEINP (Cavallin and Vasseur 2008), and it was noted in the Management Plan that the black spruce growing in upland conditions showed red spruce characteristics (Amero et al. 2015, p. 34). For initialization,

black spruce (PIMA) occurring in upland, mixed stands were input as red spruce (PIRU) while stands of > 80% black spruce or described as low-lying were input as PIMA.

Soil Data

Soil texture layers acquired from the PEI Provincial GIS Database were compiled from the Soil Survey of PEI completed across the island between 1970 and 1978 (PEI 1994). The 1-ha resource unit grid was used to clip the soil survey polygons and then the Zonal Statistics tool in ArcMap (ESRI 2018) was used to determine the leading soil type for each resource unit and assign soil texture. An average soil depth of 1 m was used for all resource units based on assessment of combined horizon thickness. Available nitrogen (kg/ha) was derived using total nitrogen and bulk density from Mansuy et al. (2014) and an available nitrogen ratio of 2%.

Climate and Wind

The three different scenarios used to drive the behavior of the model were: baseline climate conditions representing observed conditions from 1981–2010, and projected climate conditions under RCP 4.5 and 8.5 from 2022–2100. RCP 4.5 is an intermediate forcing scenario, where emissions peak around the year 2040 and then decline as global climate mitigation goals are met. RCP 8.5 represents a much more severe scenario where emissions continue to increase throughout the 21st century and beyond. Monthly historic and projected climate data were obtained from high-resolution interpolated climate data provided by Natural Resources Canada (McKenney et al. 2011). To provide daily estimates, an imputation routine was run using observed data from Environment and Climate Change Canada weather stations on PEI. For the baseline

climate scenario, the model uses random sampling of years from the observed data to extend through the simulation extent required. For the projected climate to complete a 100-year simulation (2022–2122), the last 21 years of the projected timelines (i.e., 2079–2100) were repeated in order as 2101–2122.

The climate projections show an increase in mean annual temperature from 5.7°C through the baseline scenario to 9.0±0.6°C and 11.5±0.6°C by 2080–2100 under RCP 4.5 and 8.5, respectively (Fig. 3.4). The trends for RCP 4.5 and 8.5 were similar for the first ~40 years, with RCP 8.5 increasing more dramatically later in the time series (Fig. 3.4). Seasonal increases were similar between summer and winter for both RCP 4.5 and 8.5. The peak annual average reached in the baseline scenario is 7.6°C, whereas RCP 4.5 and 8.5 reached 10.5 and 13.6°C, respectively. Precipitation amounts are similar between the three series with annual averages of 1262 (±438), 1245 (±136), and 1265 (±124) mm for baseline conditions, RCP 4.5 and 8.5 climate scenarios, respectively.

Daily and hourly observed data for mean hourly wind speed ($m \cdot s^{-1}$), maximum daily gust ($m \cdot s^{-1}$), and wind direction were available between 2003 and 2021 for St. Peters, Stanhope, and Harrington Environment Canada weather monitoring stations located within and around PEINP (Environment Canada 2022; Fig. 3.1). The wind timelines containing day of the year, wind speed (m/s), wind direction (degrees from true north), and duration (hours) of a single potential event (i.e., windstorm) per year were developed by sampling the observed data. Mean hourly wind speeds > 13.8 m/s (50 $km \cdot h^{-1}$) were used to define the observed events (Taylor 2020) that were sampled to assign the month, duration, and direction of the timeline events. The day of occurrence was randomly assigned within the selected month which was then converted to the day of

year (DOY, 1–365). A Gumbel distribution of the maximum daily gust values was used to assign the wind speed to the timeline events. For computational efficiency, wind timeline events were reduced to those with wind speeds > 22.2 $m \cdot s^{-1}$ (80 $km \cdot h^{-1}$) as most likely to cause windthrow (Taylor et al. 2019). The average number of events per simulation was 30 (minimum of 22, maximum of 41) with a range of speeds from 22.2 to 29.4 $m \cdot s^{-1}$ (or 80–106 $km \cdot h^{-1}$). Many of the events occurred during the winter, with events occurring most frequently in December, followed by January, and November.

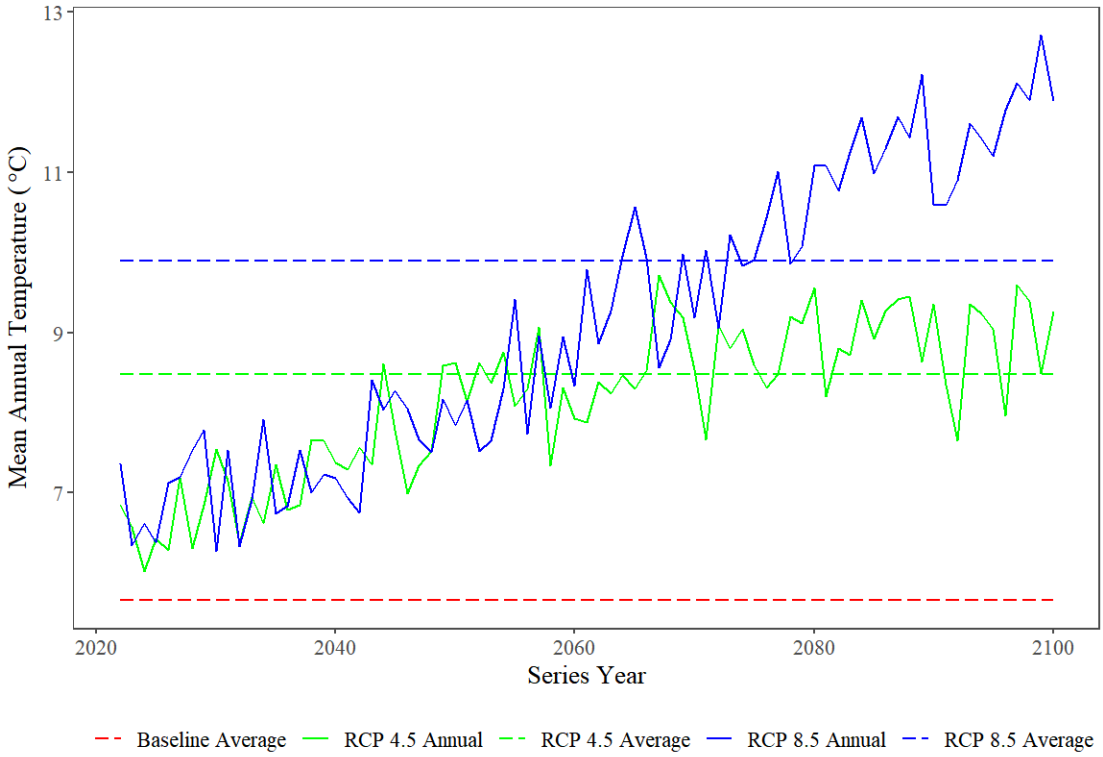

Fig. 3.3. Average mean annual temperature for observed baseline data (1981-2010) and for RCP 4.5 and 8.5 projected data over the period of 2080–2100 and mean annual temperatures for the projected data.

Despite evidence that climate change will affect disturbance frequency in the region (NOAA 2021), wind event timelines were not modified with climate change. Wind speed and direction is varied within the module, temporally by a gust modifier of ±5% and direction modifier of ±20° on each iteration, and spatially throughout the simulation using TOPEX values, which indicate the exposure of a particular cell due to elevation and aspect. The TOPEX values were calculated in QGIS (3.24.1) using the Topographic Position Index (TPI) tool. The wind regime was developed to approximate low (5–29% stand mortality) to moderate (30–60% stand mortality) severity disturbance, with a landscape mean annual disturbance rate (MADR) of 1.2–7% as observed for different forest types throughout the AFR (Taylor 2020; MacLean 2022).

Landscape Initialization

Process-based models are often unstable at initialization due to model idiosyncrasies that lead to trees establishing in locations where they cannot persist (e.g., insufficient light) resulting in high mortality in the first few years of simulation. A "spinup" process is generally used to correct this issue by running the model over a long period of time, until a steady state is reached. The disadvantage of a spinup is that the outcome often diverges from empirical observations. Thus, future simulations based on a spinup initialization of vegetation might not well reflect the true ecosystem dynamics. Here, it was found on several 100-yr test simulations of the PEINP landscape that initial basal area reduction was only ~10% of total basal area ($m \cdot ha^{-1}$) followed by a rebound within the first 10 years, with no discernable impacts to species composition or stand characteristics. The landscape was determined to be sufficiently stable because the

mortality did not disproportionately impact one area or species and did not decrease the overall productivity below an acceptable range of the inventory data. Therefore, a pseudo spinup process was used by running the model from the initialized state for 8 years to derive the current vegetation state and avoid early mortality in subsequent model runs. A "snapshot" (i.e., a full representation of the vegetation state including trees, saplings, and snags) was taken to be used as the starting point for the study simulations. The snapshot landscape was then compared graphically with the 2015 inventory data by park area to assess average basal area ($m^2 \cdot ha^{-1}$; Fig. B1), DBH (cm; Fig. B2), height (m; Fig. B3), and stem and sapling density (Fig. B4; $stems \cdot ha^{-1}$), along with species composition (Fig. B5).

3.2.4 Study Simulation Design

The snapshot of the simulation was used to initiate each of the three scenarios under investigation: baseline, RCP 4.5, and RCP 8.5. Each scenario was run for 100 years and replicated 20 times, without and with wind disturbance, for a total of 120 simulations across six scenarios. In the disturbance scenarios, a unique wind event timeline was used for each of the 20 replicate simulations to account for natural variation in wind patterns.

3.2.5 Data Analysis

Analyses of model results were conducted through a combination of visual assessment and descriptive statistics, assessing the magnitude and direction of change. For our first objective of determining the landscape level impact of climate change on the PEINP forest, we assessed change in average basal area over time ($m^2 \cdot ha^{-1}$), species composition through relative abundance (RA), and forest structure, including variation in: average DBH (cm), height (m), density ($stems \cdot ha^{-1}$), and regeneration ($stems \cdot ha^{-1}$). RA

was calculated as the percentage of total basal area represented by each species on the landscape as:

$$(1)\ RA_{iy} = 100\left(\frac{BA_{iy}}{\sum BA_y}\right),$$

where RA_{iy} is the relative abundance of species i in year y, BA_{iy} is the basal area ($m^2 \cdot ha^{-1}$) of species i in year y, and BA_y is the total basal area ($m^2 \cdot ha^{-1}$) in year y (Ricklefs 2006). Total basal area in iLand includes all stems > 4 m in height. The interaction between the climate forcing scenarios and the amount of disturbed area across the landscape was also assessed by calculating the mean and total disturbance areas (ha).

To meet the second objective of evaluating the impact of climate change on individual tree species population dynamics, we assessed changes in species growth and regeneration through average DBH, height, density, and sapling density. We also calculated the annual departure (i.e., the fractional difference) between the relative abundance of species under the baseline scenario compared with each of the RCP scenarios over the duration of the simulation period. Using 'departure from baseline' in addition to relative abundance offers several advantages for identifying trends in species responses, primarily because it corrects for the influence of model idiosyncrasies, allowing the assessment to focus on divergence caused by the climate forcings. As well, departure from baseline provides a clearer assessment of individual species response, particularly for those with very low relative abundance (e.g., red oak <1%). A species with low relative abundance may experience an important growth increase under climate change but it may not be noticeable due to their initially small presence. By using departure from baseline, their growth increase relative to their baseline condition can be

clearly identified and may have important management implications. Departure from baseline was calculated as:

$$(2)\Delta RA_{iy} = \frac{rcp\_RA_{iy} - baseline\_RA_{iy}}{baseline\_RA_{iy}}$$

where ΔRA_{iy} is the annual departure (expressed as a ratio) in the relative abundance of species *i* in year *y* between the RCP (rcp_RA_{iy}) and baseline scenario ($baseline\_RA_{iy}$; Taylor 2017).

3.3 Results

3.3.1 Landscape Response

Forest Growth and Composition

The PEINP forest exhibited a variable response to climate forcing, particularly with disturbance, exhibiting changes to forest structure and species composition. Under the baseline scenario without wind disturbance, a steady increase in basal area was observed over the 100-year simulation period from 23.5 to 28.9 $m^2 \cdot ha^{-1}$ (Fig. 3.4a). OFWS remained the dominant species, while the basal area increase was largely due to red spruce growth (Fig. 3.4a). Several of the intolerant species, such as trembling aspen and white birch, declined, following natural succession patterns of the AFR without disturbance (Gauthier et al. 2010; Fig. 3.4a). In RCP 4.5 and 8.5 scenarios without wind, forests experienced more overall growth, with both scenarios increasing to 33.1 $m^2 \cdot ha^{-1}$ at 2122 (Fig. 3.4c and e). Although, RCP 8.5 showed a higher peak basal area at 39.7 $m^2 \cdot ha^{-1}$ in 2078 (Fig. 3.4e) compared to 35.8 $m^2 \cdot ha^{-1}$ in 2080 for RCP 4.5 (Fig. 3.4c). The trends

in species composition were similar between RCP 4.5 and baseline with OFWS (Fig. 3.4a and c). However, RCP 8.5 differed with OFWS experiencing an increase in the first half of the simulation, followed by a significant decrease in the second half, ending the simulation at only 32.2% RA (Fig. 3.4e). The overall basal area increase for RCP 8.5 was largely made up of red spruce and red maple which increased to 37.1 and 13.2% RA (Fig. 3.4e), respectively, compared with 26.7% RA for red spruce and 6.1% RA for red maple at the end of the baseline simulation (Fig. 3.4a).

Under baseline climate with wind disturbance, the landscape fluctuated over time between 18.5 and 23.9 $m^2 \cdot ha^{-1}$. However, no overall change in total basal area was seen by the end of the simulation (Fig. 3.4b) and species distribution trends were similar to scenarios without disturbance (Fig. 3.4a and b). With wind disturbance, red maple maintained a more substantial presence and increased slightly from 12.6% RA in 2022 to 13.9% RA in 2122 (Fig 3.4b). Red spruce and OFWS did not experience the same increase in abundance with disturbance as without but remained a significant part of the landscape at 18.4 and 42.7% RA, respectively. Under RCP 4.5 with wind disturbance, the landscape responded similarly to baseline conditions, with slightly larger fluctuations in basal area (range = 20.2-26.2 $m^2 \cdot ha^{-1}$), and a decrease in OFWS from 49.5 to 26.1% RA and concurrent increase in red maple from 12.6 to 34% RA. However, dramatic changes were seen under RCP 8.5 with wind disturbance, showing in an overall decrease in basal area and a strong shift in species composition. Basal area fluctuated throughout the simulation (minimum 18.8, maximum 24.4 $m^2 \cdot ha^{-1}$), ending at 19.8 $m^2 \cdot ha^{-1}$. OFWS exhibited a dramatic decline, particularly after ca. 2080, to 3.2% RA by the end of the

simulation allowing for an overall shift in dominance to red maple, which increased to 73.4% (Fig. 3.4f). Red spruce ended the simulation as the second most abundant species at 17.2% RA while all other species were ≤1% RA.

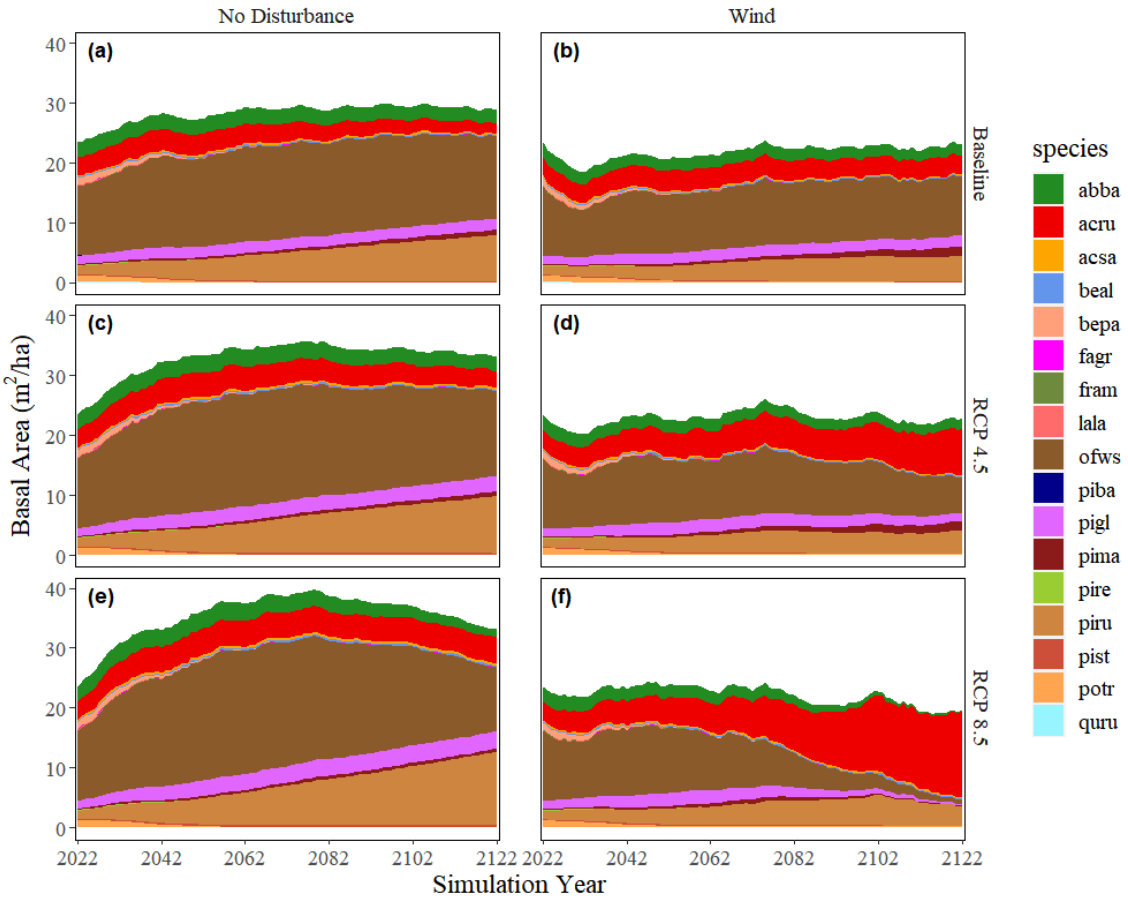

Fig. 3.4. Total basal area ($m^2 \cdot ha^{-1}$) over the 100-yr simulation period (2022–2122) by species under a) baseline climate – no wind, b) baseline climate – with wind, c) RCP 4.5 – no wind, d) RCP 4.5 – with wind, e) RCP 8.5 – no wind, f) RCP 8.5 – with wind

Changes in Forest Structure

Shifts in overall basal area and species composition were also accompanied by important changes in forest structure across all scenarios. Under baseline climate with no

disturbance, the structure remained stable in average DBH and height, with an increase in density over the first 20 years (Fig. 3.5a–c). Sapling density decreased throughout the simulation (Fig. 3.5d). Under the climate forcing scenarios without disturbance, the trend was reversed with increases in average DBH and height, combined with smaller density peaks in the first 20 years, followed by large decreases in density (Fig. 3.5a—c). For all measures, the effects are more severe under RCP 8.5 forcing than under RCP 4.5. The decrease in sapling density was moderate from baseline to RCP 4.5, but was extreme under RCP 8.5, decreasing from approximately 1200 in 2022 to < 300 stems·ha^{-1} by 2122 (Fig. 3.5d).

For baseline climate under wind disturbance, the average DBH and height decreased slightly over time, while the stem density increased to a peak value around 1100 stems·ha^{-1} (Fig. 3.5a—c). The baseline sapling density with disturbance was slightly higher than without disturbance, but the same pattern of steady decrease followed by stability was observed (Fig. 3.5d). These conditions are indicative of a landscape remaining in a younger, more disturbed state with ample regeneration. The wind disturbance scenarios for RCP 4.5 and 8.5 showed a sigmoidal trend in average DBH and height with decreases in the near term (i.e., first 30 years), followed by a partial recovery through the mid-term (i.e.,30–60 years), and a second decline in the late term (i.e., 60–100 years) (Fig. 3.5a–b). Density showed a steady increase in the near term under both RCP 4.5 and 8.5 but remained consistent at ca. 800 stems·ha^{-1} under RCP 4.5, while RCP 8.5 decreased through mid- to late term to ca. 500 stems·ha^{-1} (Fig. 3.5c). Sapling density remained relatively stable under RCP 4.5 slightly below baseline levels but decreased dramatically under RCP 8.5 (Fig. 3.5d). Therefore, the similar total basal areas are

maintained across the disturbance scenarios by increasing growth, despite decreasing densities, with climate forcing although the impact is less dramatic that in the scenarios without disturbance.

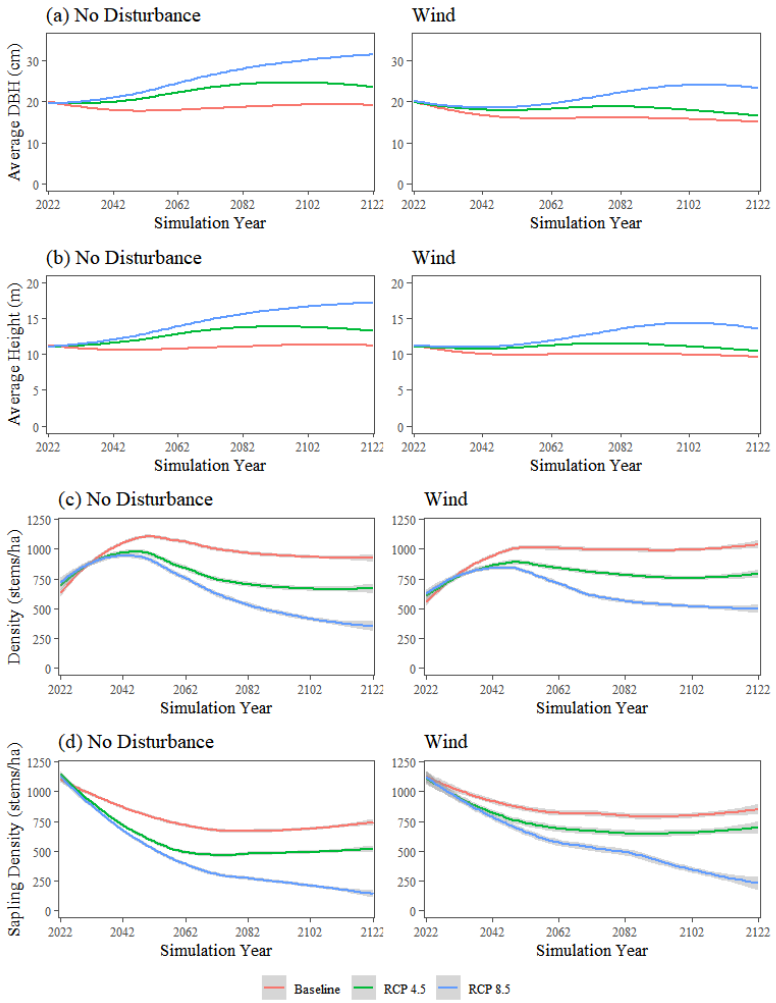

Fig. 3.5. Landscape (a) average DBH (cm), (b) average height (m), (c) average density (stems·ha^{-1}), and (d) average sapling density (stems·ha^{-1}), by climate change scenario without and with wind disturbance

Disturbance Impacts

Despite holding the wind timelines constant, our results showed disturbance area increased with climate forcing. In the baseline climate scenario, the average area disturbed per event was 75.5±30.6 ha, equaling a MADR of 6.4%, consistent with disturbances levels that have been observed for coastal softwood and hardwood stands in the AFR (MacLean 2022). Average area disturbed and therefore MADR increased substantially under both RCP 4.5 and 8.5 to 94.5±30.6 and 101.9±30.4 ha, respectively, resulting in a MADR of 8.0% for RCP 4.5 and 8.7% for RCP 8.5.

3.3.2 Species Response

Growth and Regeneration Responses

The reported increase in landscape-level DBH and height growth with decreasing density under warming without disturbance is generally reflected in the species-level growth trends. However, there were notable differences in the magnitude of response between the boreal adapted conifers (i.e., balsam fir, white spruce, black spruce, and tamarack), where a small increase was observed under RCP 4.5 but a significant continuous increase was observed under RCP 8.5 for DBH (Fig. 3.6a) and height (Fig. 3.7a), and many of the other species (i.e., red maple, sugar maple, yellow birch, white birch, American beech, White ash, red spruce, trembling aspen, and red oak) which exhibited an equal moderate increase between RCP 4.5 and 8.5. White pine showed a larger increase under both RCP 4.5 and 8.5 for both DBH (Fig. 3.6a) and height (Fig. 3.7a). Jack pine and red pine both exhibited increased growth under climate forcing,

despite their overall decline. With wind disturbance, most species did not show increased average DBH (Fig. 3.6b) or height (Fig. 3.7b), except for the boreal conifers (i.e., balsam fir, white spruce, and black spruce) which without disturbance, experience a significant growth increase under RCP 8.5. Tamarack initially had a positive growth response to RCP 8.5 with wind as well but shows a dramatic decline in the late-term due to their removal from the landscape (Fig. 3.6b and 3.7b).

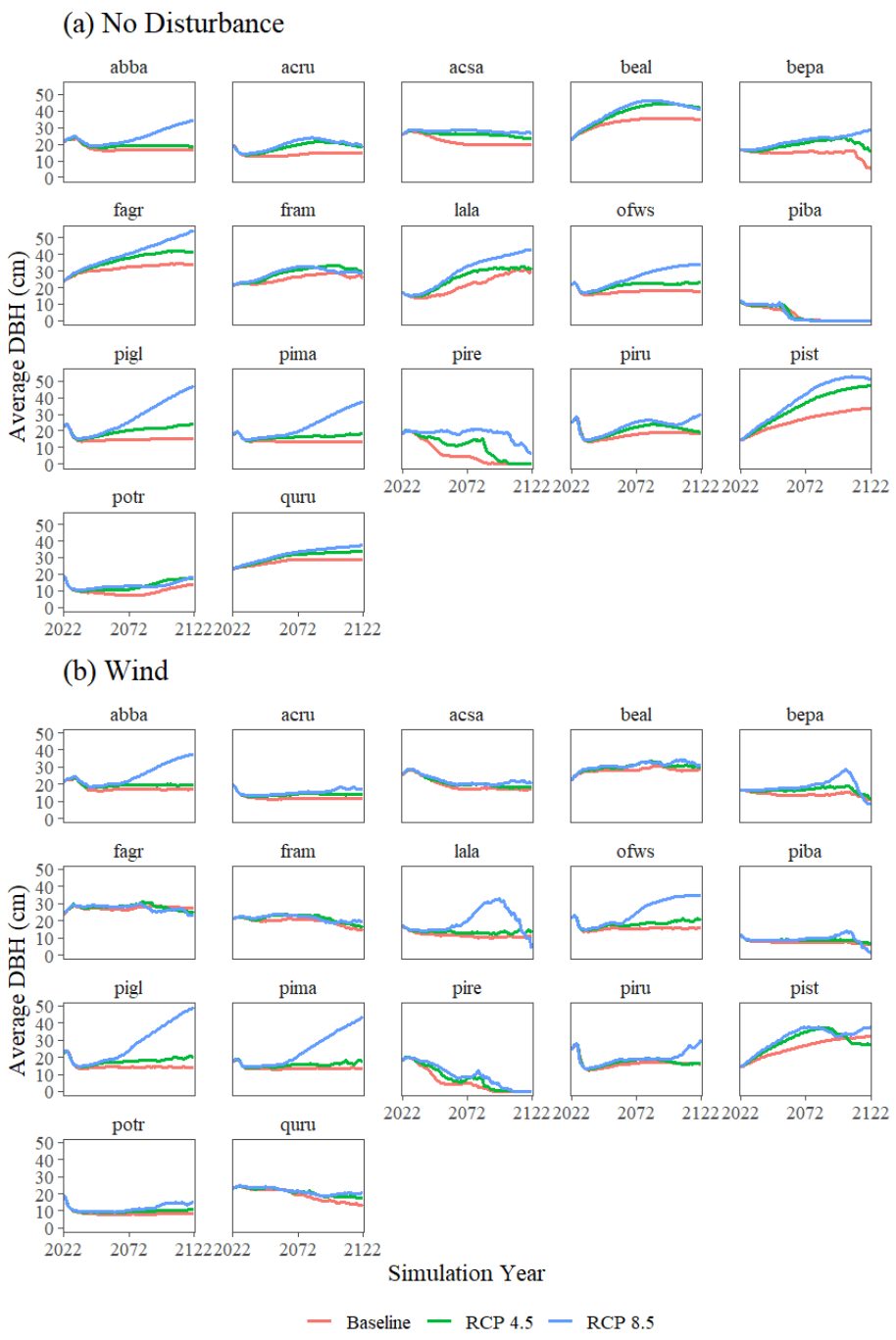

Fig. 3.6. Average diameter at breast height (cm) over time by species a) without and b) with disturbance

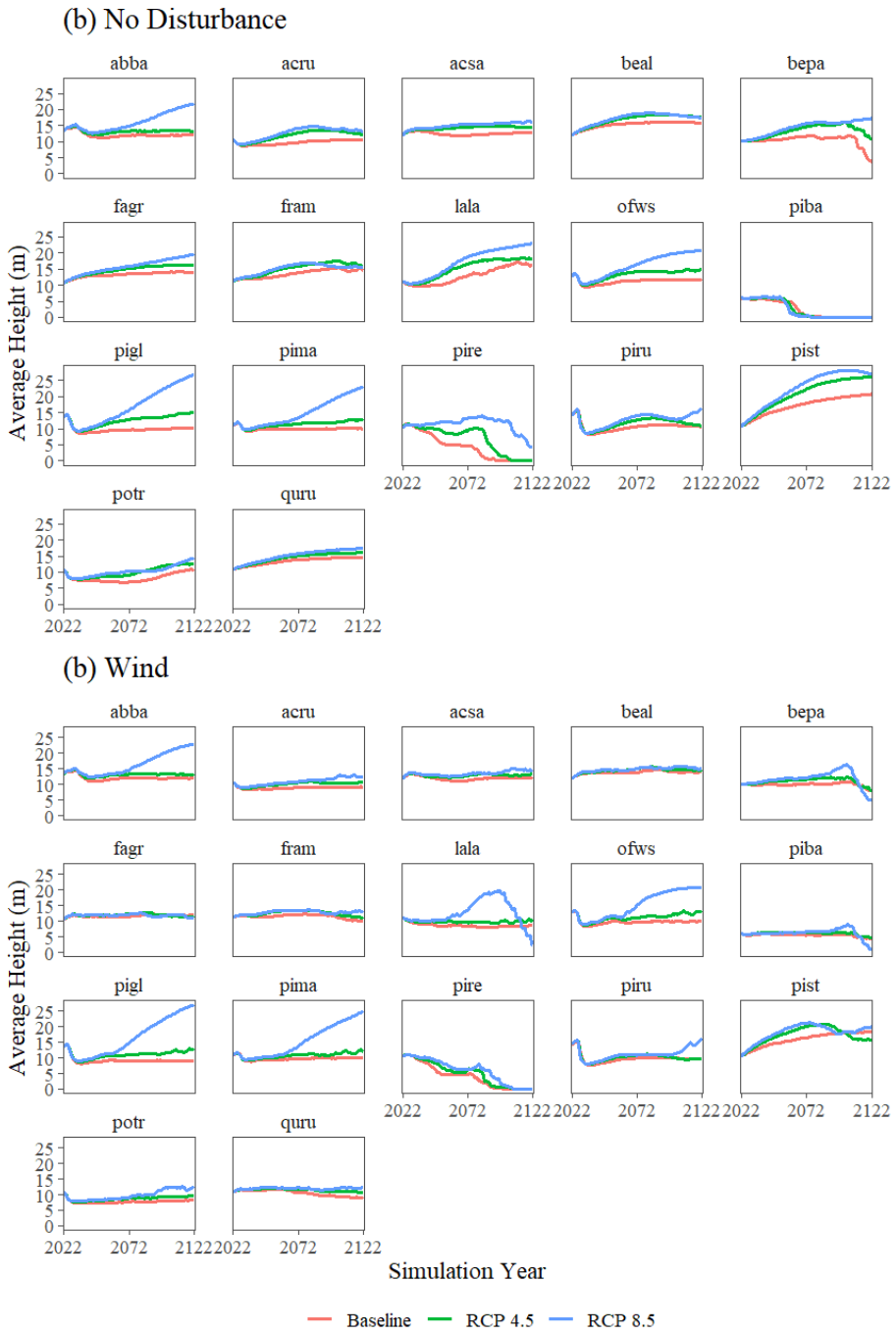

Fig. 3.7. Average height (m) over time by species a) without and b) with disturbance

Generally, the individual species densities were reflective of the overall landscape results of decreasing densities under all climates without wind disturbance, except for

black spruce and red spruce which increased under baseline and RCP 4.5 but had a more varied response to RCP 8.5 (Fig 3.8a). In addition, there are several species with very low prevalence on the landscape that showed equal severe decline across all climate forcing scenarios without wind (i.e., yellow birch, American beech, white ash, tamarack, jack pine, red pine, white pine, red oak; Fig. 3.8a). Sugar maple was the only species with very low prevalence (ca. 4 stems·ha^{-1}) that maintained density throughout the simulations (Fig. 3.8a). With wind disturbance, most species trends remained the same except for red and sugar maple (Fig. 3.8b). Red maple experienced a significant positive response to wind and climate with a maintenance of density through baseline conditions and a significant increase under both RCP 4.5 and 8.5 (Fig. 3.8b). Sugar maple maintained a very low prevalence on the landscape but experienced a small positive response to disturbance across all climates (Fig. 3.8b).

Sapling density was highly variable across all species and climate scenarios but in general exhibited a negative trend over time, particularly with warming (Fig. 3.9a). Several species, including white birch, tamarack, OFWS, white spruce, and black spruce had 0 saplings·ha^{-1} in the late-term under RCP 8.5 (Fig. 3.9a). Wind disturbance further increased the variability but had a positive influence on the overall number of saplings for several species including red maple, sugar maple, yellow birch, white pine, trembling aspen, and red oak (Fig. 3.9b).

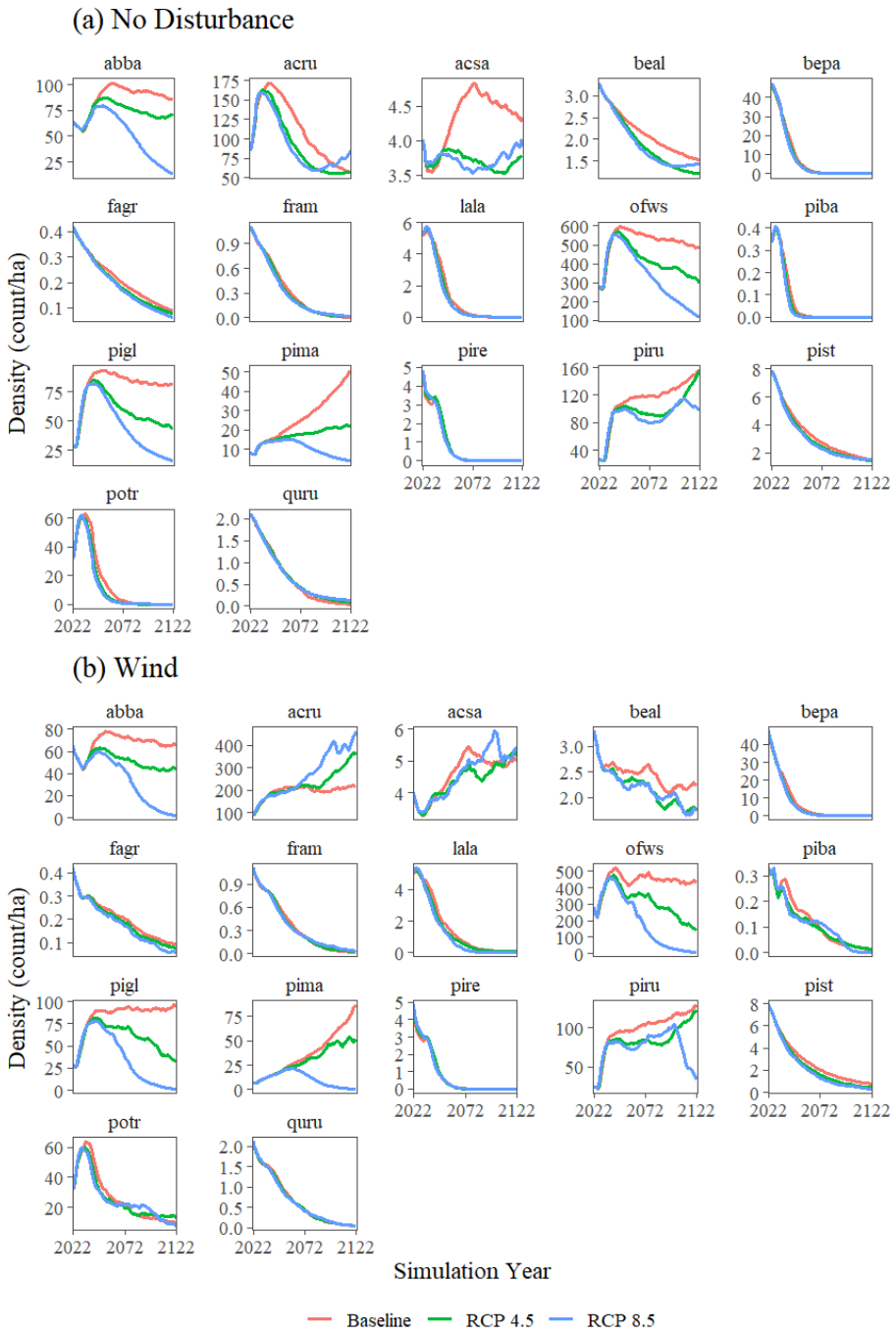

Fig. 3.8. Average density (stems·ha^{-1}) of stems > 4 m in height over time by species without and with disturbance.

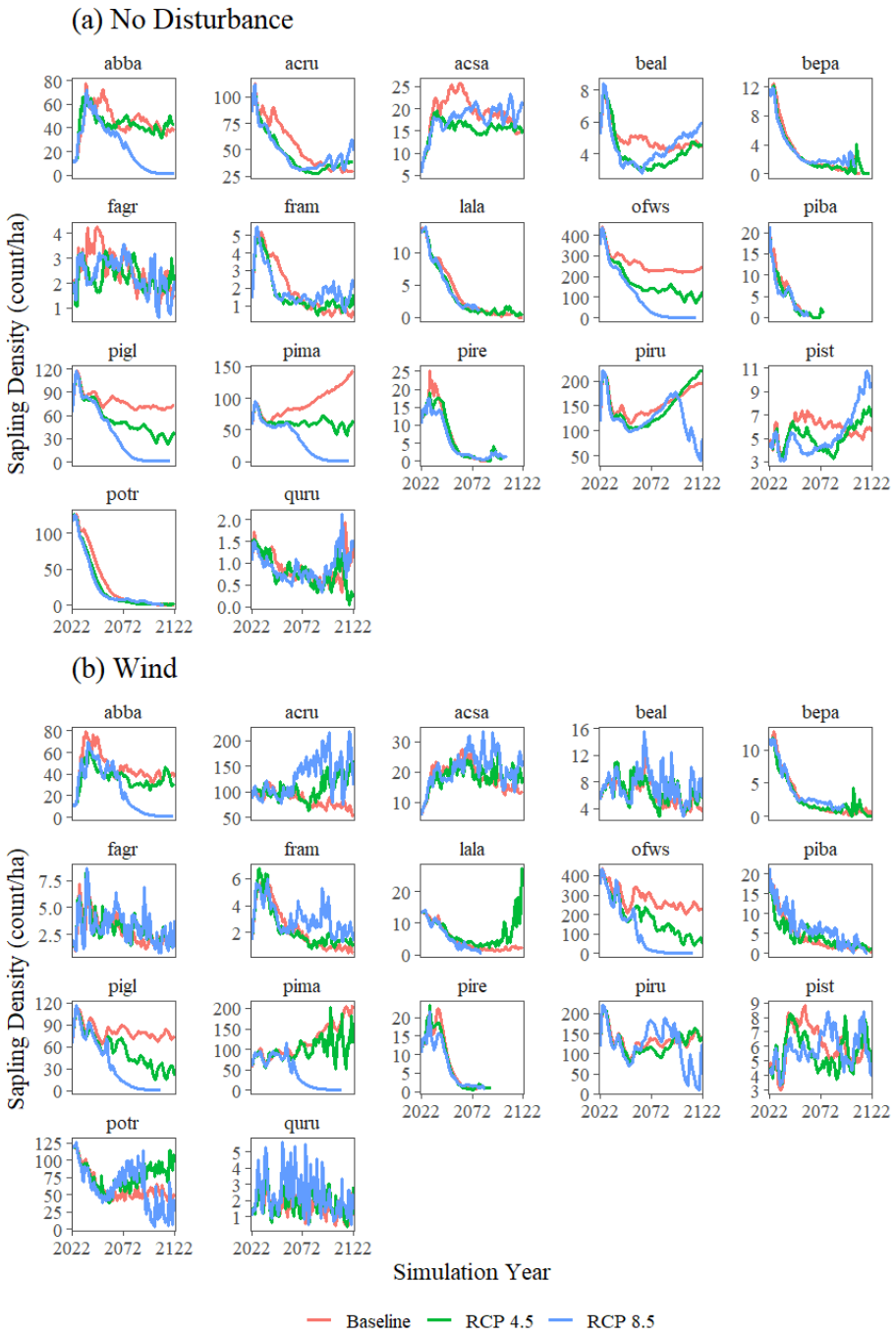

Fig. 3.9. Average sapling density (stems·ha^{-1}) of stems > 1.3m and < 4 m in height over time by species without and with disturbance.

Departure from Baseline

Individual species response was assessed through the calculation of departure from baseline, or the fractional change in relative abundance between the climate change scenarios and baseline for each year. Departure from baseline is most informative for species of low abundance (i.e., <5% RA) where trends can be difficult to identify visually and trend lines stop where a species was lost entirely from the landscape under the baseline scenario due to being undefined (i.e., division by zero). It was assumed that near-term declines of species with < 1% RA at initiation were related to competitive pressures, while rebounds in the mid- to late term were climate induced. Departure from baseline shows a 10 and 30% increase, respectively, for sugar maple under RCP 4.5 and 8.5 (Fig. 3.10) although there was no overall increase in relative abundance from 0.01%. Red oak (initial RA of 0.4%) showed little response to climate through the mid-term but experienced up to a 200% increase under RCP 8.5 in the late term (Fig. 3.10). To the contrary, both yellow birch (initial RA of 0.6%) and American beech (0.09%) showed near-term declines with a recovery trend in the late term, particularly under RCP 8.5 (Fig. 3.10). The intolerant species of white birch, white ash, and trembling aspen (initial RA < 5%) declined so low during the baseline scenarios due to competition that the climate forcing trend is skewed and difficult to establish (Fig. 3.10). Coniferous species had divergent results with a similar decline of 10–20% and 50% was seen for balsam and black spruce under RCP 4.5 and 8.5, respectively, while white spruce and white pine increased 40 to 100% (Fig. 3.10). Like the intolerant deciduous species, no trend was identified for tamarack, jack pine, and red pine due to RA of <0.001% (Fig. 3.10).

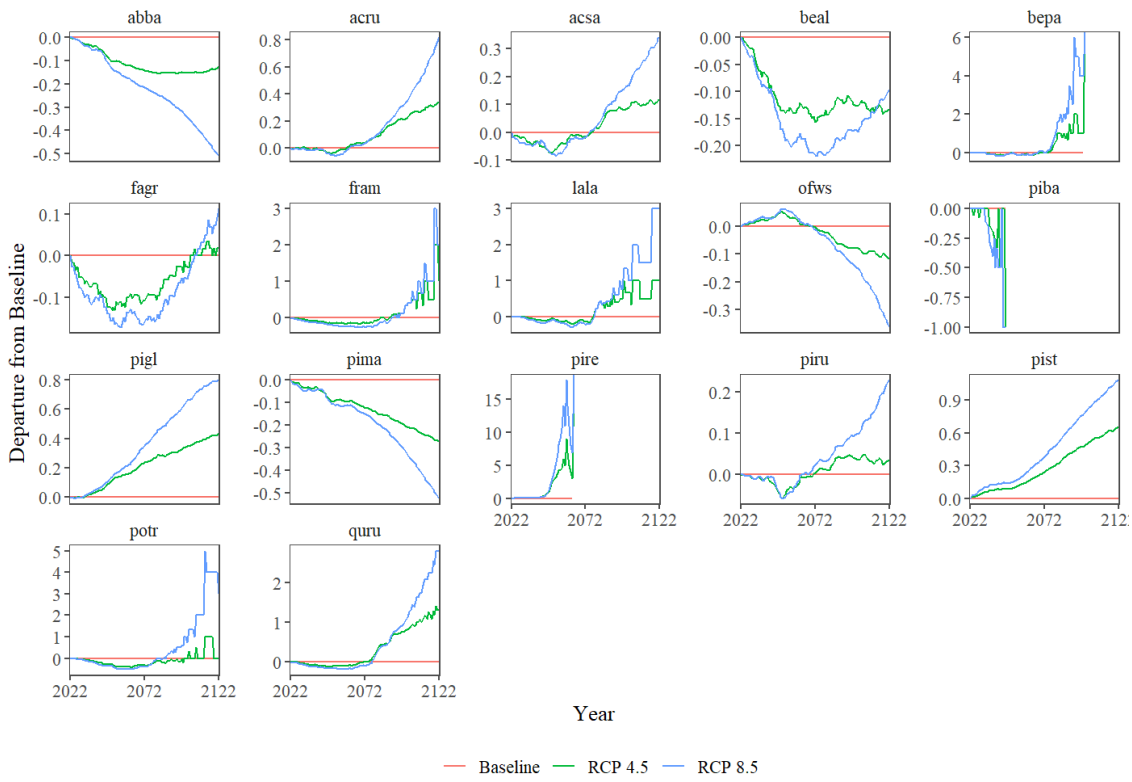

Fig. 3.10. Departure from baseline (fractional change in relative abundance) over time by species

3.4 Discussion

As the climate warms, forests everywhere will swiftly be facing novel environmental conditions that will drive shifts in their structure and function. Forest managers must use all the tools at their disposal to ensure their management decisions are as effective as possible, given the conflicting limits of time between the fast pace of climate change and the slow, natural adaptation of forests (Turner at al. 2020). The ability of process-based forest models to project forest outcomes under multiple scenarios can be a powerful asset as part of an integrated planning process, particularly because of the

logistical constraints on long-term empirical studies (Cuddington et al. 2013; Battaglia and Sands 1998).

The model iLand provides a unique combination of dynamic interactions between individual trees and their environment across the simulated landscape, at high spatial and temporal climate resolution, as well as dynamically simulated disturbances and options for including forest management making it well suited for investigating the impacts of climate change on forest dynamics and disturbance regimes (Thom et al. 2017b; Seidl 2014a; Rammer and Seidl 2015). Although application of the model is very resource intensive, its user-friendly graphical user interface, uses open-source software, and extensive online-resources help make it more accessible for experienced forest professionals with adequate means and good understanding of modelling concepts. The results obtained through the simulation of PEINP under climate change and wind disturbance provide important information to inform management decisions in the short to mid-term, as well as an opportunity for further investigation to enhance model performance and the application of other available modules.

Forest Growth

Our simulation results describe a significant impact of climate change on the forest PEINP, particularly when combined with disturbance. Under baseline conditions, average tree size did not change over time, while large increases in individual growth for both DBH and height was seen across all species with warming in scenarios, without and with disturbance. Increased growth in response to warming has been recorded in several studies (e.g., Pedlar & McKenney 2017; Boisvenue & Running 2006; Gamache &

Payette 2004), however there is evidence that temperature increases above a certain threshold may begin to have a negative impact on growth and survival (Crous et al. 2022; D'Orangeville et al. 2018). iLand modifies growth in response to temperature through a state acclimation approach, as presented by Mäkelä et al. (2004), based on the relationship between the effective temperature and species-specific maxima. Unlike the parabolic response functions commonly used in other models (Landsberg et al. 2003), which assume optimal growth is constrained when approaching either the minimum or maximum GDD limits, the state acclimation approach does not cause growth declines at high temperatures. Instead, the first order dynamic delay model of the state acclimation approach linearly increases gross primary production until a maximum effective temperature, beyond which temperature has no additional positive effect. While the use of the parabolic GDD functions has also been criticized (Schenk 1996; Reynolds 2001) there is evidence of physiological relationships to productivity declines during periods outside of thermal optimums (Berry and Bjorkman 1980; Way and Oren 2010) suggesting the linear increase model may not be appropriate for investigations outside of baseline climate conditions. In our study, the species that experienced the largest average DBH increase under RCP 8.5 included balsam fir, American beech, white spruce, black spruce, red spruce, and white pine. Particularly for cold-adapted species, such as balsam fir, white spruce, and black spruce, a negative response to increasing temperatures has been observed in some cases (Searls 2021; D'Orangeville 2018). Further investigation is required into the extremely complex interactions between temperature and growth, but it should be considered that the growth increases projected under warming without

disturbance maybe be larger than will be realized by the forest, although some level of increase is expected.

Forest Structure and Disturbance Response

Under warming without disturbance, total basal area increased under all climate scenarios. However, the mechanism for the observed increase differed between the baseline condition and warming scenarios. The increase in total basal area under baseline climate was due higher stem density with average stem size remaining approximately the same, while under climate forcing, the observed increases in basal area are attributed to increasing individual growth of a reduced number of trees. The large declines in stand and sapling densities that occurred are likely due to increased competition between the larger trees (Westoby 1984), as well as poor regeneration observed across the warming simulations (Wright et al. 2018). However, when including disturbances under climate change, higher individual growth with warming was negated by increasing disturbance rates leading to lower average DBH, height, and basal area, combined with a similar decline in density, leading to a significant reduction in basal area. These changes to forest structure have important implications for management as structure is closely linked with ecological services and landscape resilience (Bohn and Huth 2022; Felipe-Lucia et al. 2018).

Changes in forest structure are also related to forest vulnerability to changing natural disturbance regimes (Dale et al. 2001). Here, despite maintaining a constant frequency of disturbances, we report an increase in disturbed area and volume outside of

MADR levels that have been observed for any forest type or disturbance to date in the AFR (MacLean et al. 2022). As the wind event timelines applied were consistent between climate scenarios, the increase in disturbance response under climate change is likely caused by as the increase in larger, more widely dispersed trees which are more susceptible to wind throw, along with the decrease in frozen soil conditions associated with winter warming (Seidl et al. 2014). This observed trend is in line with earlier findings, as stand structural attributes like tree size have been linked to wind throw risk (e.g., Taylor et al. 2019; Rich et al. 2007; Canham et al. 2001). However, analyses revealed a high sensitivity of the wind module to DBH, which resulted in the over-estimation of mortality for some species known for wind firmness (e.g., white pine) and lack of empirical data for species-specific parameter estimation prevented further adjustment at this time. In the wind disturbance scenarios across all climate conditions, a noticeable decline occurred within the first 10 years of the simulation. This is attributable to the lack of wind inclusion in the spin-up process and is not directly reflective of the actual forest conditions. Therefore, while it is very likely that wind damage will increase over time, further calibration of the wind module to improve species specific response would be beneficial to better understand the potential interactions of species composition and forest structure with wind.

Regeneration Response and Composition

While most established trees displayed increased growth as a response to warming, several species failed to establish new individuals later in the simulation due to insufficient winter chilling or excess GDD. The early stages of species development,

from germination through establishment and seedling survival, are more sensitive to climatic variation than mature individuals (Johnstone et al. 2010). Temperature affects seed germination and establishment in many ways, including winter chilling requirements for dormancy release, temperature thresholds for germination, and cumulative GDD ranges (Zasada 1992). In the modelling of regeneration in iLand, failure to meet chilling requirements or GDD accumulation outside of the minimum or maximum species parameters are exclusionary limits resulting in failure to regenerate (Nitschke and Innes 2008). In iLand, winter chilling is calculated as the number of days with temperatures between +5˚C and -5˚C counted from the end of the previous growing season. Under baseline and RCP 4.5, only red pine and American beech were occasionally impacted by insufficient winter chilling (~10 years dispersed through simulations), while under RCP 8.5, chilling requirements were consistently not met for red pine and American beech after 2065, and frequently not met for red maple, sugar maple, white ash, tamarack, and trembling aspen after 2096. Chill requirement is listed between 90—52 days for the affected species. In empirical studies on reduced chilling due to climate warming for some Acadian species, divergent results have been seen with successful regeneration under warming (Vaughn et al. 2022) and increased regeneration failure under warming (Solarik et al. 2016; Wright et al. 2018) indicating a complex relationship between chilling and germination (Penfield and MacGregor 2016; Walck et al. 2011). GDD accumulation is calculated as a running sum of the mean daily temperature minus the GDD base temperature (5°C) for all days greater than base temperature during the growing season. As total GDD per year increased under climate change, the maximum GDD threshold was exceeded for OFWS/white spruce, black spruce, tamarack, and

balsam fir under RCP 4.5, and additionally for trembling aspen, white birch, jack pine, red spruce, and red pine under RCP 8.5 where the total GDD per year exceeded 3000 by ~2080 (Fig. B6). However, the use of GDD in relation to germination success is not fully supported by empirical evidence, and therefore it is likely to be overestimating the total regeneration failure of each species beyond the maximum GDD threshold. GDD maxima are parameterized based on species range limits, however, range determination is complex and related not only to direct impacts of temperature but also precipitation rates, site characteristics, competition, and other factors (Adler et al. 2012). Overall, further application of empirical evidence to improve species specific parameters, or the mechanism by which chill requirement and GDD accumulation is implemented would likely improve species composition predictions, however it is important to consider the implications of poor regeneration in the Park's most abundant species as empirical evidence does suggest a decline in regeneration for many cold-adapted species (e.g., Reich 2022; Boucher et al. 2020; Fischelli et al. 2014).

Individual Species and Departure from Baseline

Departure from baseline was used to identify trends in species response to climate change for species of low relative abundance. It is difficult to completely disentangle the compounding effects of competition and limited seed resources for species of low abundance (Miller and McGill 2018). However, our results are consistent with other empirical and modelling studies (e.g., Bourque and Hassan 2010; Steenberg et al. 2013; Taylor et al. 2017; D'Orangeville et al. 2018), with increased growth and survival under warming for several tolerant hardwood species including sugar maple, beech, and red

oak. White pine, an important and highly windfirm Acadian species, also experienced increased individual growth over baseline with warming. This provides key information for species selection in management, indicating that management favoring an increase in tolerant hardwood regeneration, along with white pine, may aid in the transition from a OFWS dominated forest and help avoid excessive abundance of red maple, while maintaining productivity and diversity under a future warmer climate.

Management Implications

Based on the results of the climate projections, forest management in PEINP should focus on the removal OFWS and increasing species diversity through planting due to lack of natural seed sources. Species selection should favour shade-tolerant hardwood species such as sugar maple and red oak and increased healthy white pine regeneration if possible. However, considerations must be for local impact of pathogens such as beech bark disease and white pine blister rust (*Cronartium ribicola* J.C. Fisch.). All management activities should be mindful of wind smart practices regarding harvest trail location and direction, stand densities, harvest adjacencies, etc. (Mason and Valinger 2013; Gardiner and Quine 2010). Salvage conditions post-Hurricane Fiona may also dictate some decisions – extreme devastation to stands may result in clear-cut like conditions precluding the artificial regeneration of hardwood species. Softwood plantings should be mixed favouring species that indicated a positive response to warming including white pine, red spruce, black spruce, and tamarack in addition to white spruce to increase diversity despite potential future issues with natural regeneration.

3.5 Conclusion

Process-based forest models, such as iLand, provide forest managers with the ability to investigate the potential impacts of climate change on their landscapes to inform decision making (Cuddington et al. 2013). This will be a vital tool as novel climatic conditions drive shifts in forest structure and function (Millar et al. 2007), while social, economic, and ecological demands on our forests increase. The forest of PEINP may be especially vulnerable to climate change due to its currently degraded condition (Sobey and Glen 2004; McFadyen 2016) and the compounding risk of its coastal location (IPCC 2014; PEI Climate Action Plan 2018). Our results indicate that the forest of the PEINP will undergo a dramatic shift in species composition and forest structure under high climate forcing. Near term applied management should focus on the transition of OFWS, leading stands to a more mixedwood characteristic, and the management of stand structure to reduce vulnerability to wind. To further inform management decisions, additional modelling with the inclusion of management strategies and improved regeneration and wind parameterization, can be undertaken using this the calibrated and initialized landscape for the PEINP.

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Chapter 4 – General Discussion

4.1 Summary of Results

The objectives of this thesis were to parameterize, calibrate and validate the iLand forest model and to apply the model to the forest of the PEINP to project forest outcomes under climate change. For the first objective, simulation outputs were assessed against empirical data using visual comparison and descriptive statistics. Satisfactory results were obtained for all levels of assessment including population dynamics (i.e., growth of individual species), stand dynamics (i.e., forest structure and succession). The model was well able to replicate average and maximum species growth for diameter at breast height (DBH; cm), height (m), volume per tree ($m^3 \cdot tree^{-1}$), density and sapling density ($stems \cdot ha^{-1}$). Stand dynamics were also comparable to the observed data for average DBH, height, and volume per ha but notable differences were observed for tree and sapling density. Simulations conformed with the well-known successional trajectory of the Acadian Forest Region (AFR) transitioning from shade-intolerant, early successional species early in the simulation (0–40 years) through the mid-term (41–100 years), to a dominant presence of shade-tolerant late successional species in the late-term (100+ years; Fraver et al. 2009; Gauthier et al. 2010; Basquill and Baldwin 2020

The simulation results for the PEINP indicated significant changes for the forest overall under climate change, particularly with disturbance due to changes in forest structure and species composition. Under warming, without disturbance, increased individual growth was seen in average DBH, height, and volume per hectare, however, this was accompanied by a concurrent decrease in density and sapling densities. A shift in species composition also occurred with a decrease in old-field white spruce (OFWS), and

an increase in red maple and red spruce. The positive growth response was seen under both RCP 4.5 and 8.5 with a much more pronounced effect under RCP 8.5, with a total basal area increase of 4.2 $m^2 \cdot ha^{-1}$ for RCP 8.5 over baseline at the end of the 100-year simulation.

With wind disturbance, the trends over increasing individual growth in forest structure were still observed, however they were less pronounced due to the removal of larger stems. Under baseline and RCP 4.5, basal area per hectare fluctuated throughout the simulation with no overall decrease at 100 years. Relative species composition remained more consistent throughout the simulation under baseline, while RCP 4.5 exhibited a noticeable decline is OFWS with an increase in red maple. However, dramatic changes were seen under RCP 8.5 with wind disturbance, showing in an overall decrease in basal area and a strong shift in species composition. Basal area fluctuated throughout the simulation with an overall decrease of 3.7 $m^2 \cdot ha^{-1}$ at 100-years. OFWS exhibited a dramatic decline, particularly after ca. 2080, nearly disappearing by the end of the simulation allowing for an overall shift in dominance to red maple.

Contrary to the growth response of mature individuals, several species experienced regeneration failure under warming. Several species experienced establishment failure due to the exclusionary limits of winter chilling minimum not being met or the growing degree day (GDD) maximum threshold being exceeding (Seidl et al. 2012a; Nitschke and Innes 2008). Under RCP 4.5, chilling requirements were not met for red pine or American beech, while the GDD maximum was exceeded for white spruce, OFWS, black spruce, tamarack, and fir. Additionally, under RCP 8.5, chilling

requirement was not met for red and sugar maple, white ash, tamarack, and trembling aspen in the late-term (ca. 2096), while the GDD maximum threshold was exceeded for trembling aspen, white birch, jack pine, red spruce, and red pine by 2080. The impact of regeneration failure was evident in the disturbance scenarios where the regeneration failure of prevalent species after disturbance contributed to the dramatic shift in species composition by the end of the simulation, particularly under RCP 8.5.

Despite holding the wind timelines constant, our results showed disturbance area increased with climate forcing. As the wind event timelines applied were consistent between climate scenarios, the increase in disturbance response under climate change is caused by changes in forest structure as larger, more widely dispersed trees are more susceptible to wind throw, and winter warming decreases frozen soil conditions (Seidl et al. 2014). This observed trend is in line with earlier findings, as stand structural attributes like tree size have been linked to wind throw risk (e.g., Taylor et al. 2019; Rich et al. 2007; Canham et al. 2001).

Individual species response was assessed as well using departure from baseline (i.e., the fractional difference) between the relative abundance of species under the baseline scenario compared with each of the RCP scenarios over the duration of the simulation period. Departure from baseline provides a clearer assessment of individual species response, particularly for those with very low relative abundance (e.g., red oak < 1%). A species with low relative abundance may experience an important growth increase under climate change but it may not be noticeable due to their initially small presence. It is difficult to completely disentangle the compounding effects of competition

and limited seed resources for species of low abundance (Miller and McGill 2018) however, our results are consistent with other empirical and modelling studies (e.g., Bourque and Hassan 2010; Steenberg et al. 2013; Taylor et al. 2017; D'Orangeville et al. 2018), with increased survival under warming for several tolerant hardwood species including sugar maple, beech, and red oak. White pine, an important and highly windfirm Acadian species, also experienced increased individual growth over baseline with warming.

4.2 Limitations and future research

Our calibration was intended to be generally applicable across the AFR. We used empirical data from New Brunswick (NB), Nova Scotia (NS), and Prince Edward Island (PEI) as comparative data and used visual assessment and descriptive statistics to characterize the ability of the model to represent the AFR. Though successful, this method does present some limitations to our species parameterization. No direct comparison was done for specific and relatively rare natural forest types such as bogs or krummholz forests, and additionally was not examined for softwood plantations which are common across the industrially managed forest landbase in the Maritimes. Further validation and perhaps parameter adjustments should be undertaken before the model is applied to landscapes containing a high proportion of such forest types. It may be necessary to separate a single species into multiple records, as we did for white spruce in to "forest" and "old-field", to represent highly divergent phenotypic responses to environmental conditions when the mechanism of the divergence is unknown or not accounted for in the model.

Review of the results from the simulation of PEINP suggested some potential areas for improvement in model application and areas where further empirical research would help to better inform the parameterization. The linear influence of temperature on growth does not reflect evidence suggesting productivity declines at temperatures outside of thermal optimums (Berry and Bjorkman 1980; Way and Oren 2010) suggesting the linear increase model may not be appropriate for investigations outside of baseline climate conditions. Another factor impacting growth that was not considered in this study is the effect of rising carbon dioxide (CO_2) levels. iLand is able to incorporate time series increases of CO_2 and applies the effect through an environmental modifier to radiation use efficiency. In future studies, this function should be utilized.

Additionally, the application chill requirement and GDD maxima as exclusionary limits in regeneration is not well supported by the literature. In empirical studies on reduced chilling due to climate warming for some Acadian species, divergent results have been seen with successful regeneration under warming (Vaughn et al. 2022) and increased regeneration failure under warming (Solarik et al. 2016; Wright et al. 2018) indicating a complex relationship between chilling and germination (Penfield and MacGregor 2016; Walck et al. 2011). Further investigation into the relationship between chill requirement and regeneration success would perhaps allow for more precise parameterization or the application of chill requirement as a gradient with increasing regeneration failure with increased warming, rather than complete exclusion. Similarly, GDD maxima are parameterized based on species range limits and is not indicated by empirical evidence to be an exclusionary limit to regeneration.

In addition, although the trend observed in our simulations of increasing disturbance with climate forcing is supported by empirical evidence (Taylor et al. 2019; Rich et al. 2007; Canham et al. 2001), in sensitivity analysis the wind module was found to be particularly sensitive to DBH, which resulted in the over-estimation of mortality for some species known for wind firmness (e.g., white pine) although landscape level MADR were appropriate for the AFR (Taylor et al. 2020, MacLean et al. 2022). Therefore, while it is likely that wind damage will increase over time, further calibration of the wind module to improve species specific response would be beneficial to better understand the potential interactions of species composition and forest structure with wind. Unfortunately, wind firmness parameter values are lacking in empirical studies, particularly for species of lower commercial value (i.e., red maple). There is also opportunity for further modeling of severe events using empirical evidence from recent storms such as Hurricanes Dorian and Fiona.

4.3 Management Implications

Our results indicate that the calibration of the iLand model is currently suitable for application in most of the AFR, with a parameter library available for 18 of the most common species. In the most northern regions where the forest has a distinctly more boreal characteristic, further testing should be done with a subset of growth and yield data. The model is calibrated for general landscape characteristics and is not currently verified to represent specific stand types that represent a smaller proportion of the forest, such as bogs or coastal krummholz stands. We have also provided a framework for the initialization and simulation of a local landscape to aid forest managers in the application

of iLand, or another complex forest landscape model. Also, while process-based models are an important tool for management planning, it should be noted that their intended use is not for short-term, operational planning, but rather projection of mid- to late-term trends and implications, as all models are a representation of their subject, not a replication.

Regarding the second objective of simulating and analyzing the development of the forest of PEINP under climate change, our results indicate that it will undergo a dramatic shift in species composition and forest structure under high climate forcing. Near term applied management should focus on the transition of OFWS, leading stands to a more mixedwood characteristic including sugar maple, red oak, red spruce, and white pine. Red maple should not be avoided as it is consistently projected as a clear “winner” under climate change. However, it is not likely to require any targeted silviculture and should be managed only in an effort to maintain species diversity and prevent red maple dominance. In addition, the management of stand structure to reduce vulnerability to wind is of utmost importance. To further inform management decisions, additional modelling with the inclusion of management strategies and improved regeneration and wind parameterization, can be undertaken using this the calibrated and initialized landscape for the PEINP.

4.4 References

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Appendix A – Model Parameters

Table A1. List of species-specific model parameters including units and brief description

Parameter Name	Unit	Description
Growth		
specificLeafArea	N/A	Factor to calculate leaf area from biomass
turnoverLeaf	N/A	Senescence factor of foliage (1 being complete turnover)
TurnoverRoot	N/A	Senescence factor for fine roots
HDLow	N/A	Expression of lower bound of height to diameter for open grown stands.
HDHigh	N/A	Expression of upper bound of height to diameter for high density stands
woodDensity	kg/m^3	Density of stemwood used in calculating volume (m^3)
formfactor	N/A	Taper factor of stem used for calculating volume (m^3)
Biomass Compartments		
bmWoody_a	N/A	Constant a in allometric equation of stem wood biomass
bmWoody_b	N/A	Constant b in allometric equation of stem wood biomass
bmFoliage_a	N/A	Constant a of the allometric equation for foliage biomass.
bmFoliage_b	N/A	Constant ab of the allometric equation for foliage biomass.

bmRoot_a	N/A	Constant a of the allometric equation for coarse root biomass.
bmRoot_b	N/A	Constant ab of the allometric equation for coarse root biomass.
bmBranch_a	N/A	Constant a of the allometric equation for branch biomass.
bmBranch_b	N/A	Constant ab of the allometric equation for branch biomass.
finerootFoliageRatio	N/A	Ratio of fine root pool relative to the size of the foliage pool
cnFoliage	N/A	Carbon to nitrogen ratio of foliage
cnFineroot	N/A	Carbon to nitrogen ratio of fine roots
cnWood	N/A	Carbon to nitrogen ratio of branches, stem, and coarse roots
barkThickness	N/A	Factor to calculate bark thickness
Mortality		
probIntrinsic	N/A	Probability of a tree to survive to maximum species age
probStress	N/A	Factor that determines the probability of death based on the stress index
Aging		
maximumAge	Years	Maximum age for a species (used in aging and mortality determination, not a deterministic cutoff)

maximumHeight	Meters	Maximum height (used in aging and mortality determination, not a deterministic cutoff)
Aging	N/A	Allometric equation used to calculate decline in efficiency with “age” (based on max height growth)
Environmental Response		
lightResponseClass	1-5	Determines light use efficiency in low light levels (i.e., shade tolerance)
respVpdExponent	N/A	Constant in the calculation of growth response to vapor pressure deficit
respTempMin	Celsius	Lower threshold temperature for tree growth
respTempMax	Celsius	Optimal maximum for tree growth
respNitrogenClass	1-3	1 = efficient with low nitrogen to 3 = high nitrogen demand
phenologyClass	0-2	0 = evergreen coniferous 1 = deciduous broadleaf 2 = deciduous conifer
maxCanopyConductance	$kg \cdot m^{-1} \cdot MPa^{-1} \cdot s^{-1}$	Maximum conductance of the canopy for water
psiMin	MPa	Maximum soil water potential that a species can access
Seed Production and Dispersal		
maturityYears	Years	Minimum age required for species to produce seeds
seedYearInterval	Years	Interval between seed years (probability of seed in a given year is 1/interval year)

nonSeedYearFraction	N/A	Fraction of the seed production in non-seed years
fecundity_m2	Count	Seedlings produced and surviving in the first weeks per m^2 canopy cover
seedKernal_as1	N/A	Dispersal kernel parameter
seedKernal_as2	N/A	Dispersal kernel parameter
seedKernal_ks0	N/A	Dispersal kernel parameter
Establishment		
estMinTemp	Celsius	Absolute minimum temperature for seedling survival
estChillRequirement	Count days	Number of days required since the end of the last growing season between -5°C and +5°C
estGDDMin	Count GDD	Minimum threshold of growing degree days for seedling establishment
estGDDMax	Count GDD	Maximum threshold of growing degree days for seedling establishment
estGDDBaseTemp	Celsius	Base temperature for growing degree day calculation
estBudBurstGDD	Count GDD	Required growing degree day accumulation before bud burst (reset by temperatures below 0°C)
estFrostFreeDays	Count	Required number of days without frost (>0°C) in the year
estFrostTolerance	N/A	Frost tolerance of seedlings for frost events after bud burst
estPsiMin	PSI	Minimum soil water potential for establishment

Sapling Growth		
sapHeightGrowthPotential	N/A	Expression to calculate maximum height growth of saplings
sapMaxStressYears	Years	Number of consecutive years a sapling can withstand stress
sapStressThreshold	N/A	Ratio of potential height growth to actual height growth to define stress
sapHDSapling	N/A	Fixed height to diameter ratio for saplings
sapReferenceRatio	N/A	Specifies constraint for optimal site
sapReinekesR	Count per cell	Stem count per regeneration cohort
sapSproutGrowth	N/A	Multiplier for acceleration growth for resprouted cohorts. If empty resprouting not possible for that species
Snags and Carbon Dynamics		
snagKSW	N/A	Snag decomposition rate at 10°C and optimal moisture
snagHalfLife	Years	Half-life in years used in calculation of transition from snag to down woody debris class
snagKYL	N/A	Litter decomposition rate at 10°C and optimal moisture
snagKYR	N/A	Downed woody debris decomposition rate at 10°C and optimal moisture
Browsingprobability	N/A	Annual probability that saplings up to 2m are browsed

Appendix B – Supplementary Figures

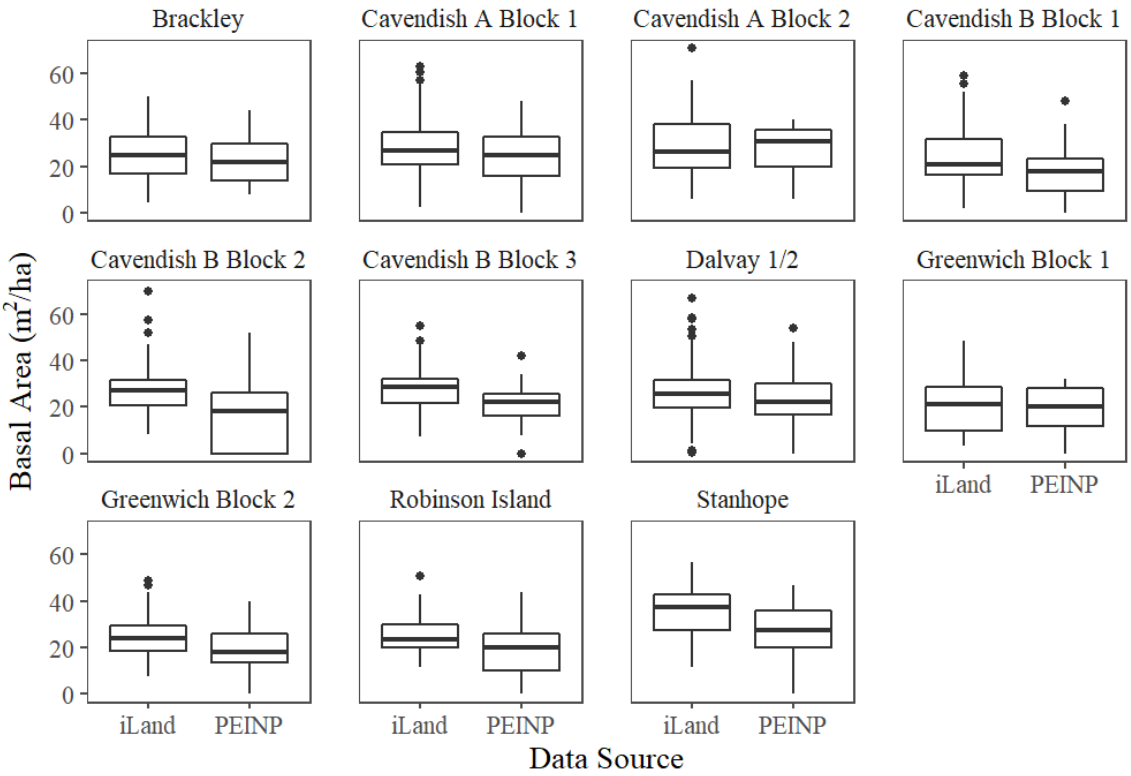

Fig. B1. Basal area per hectare ($m^2 \cdot ha^{-1}$) by park zone for iLand simulated landscape and Prince Edward Island National Park Management Plan (PEINP; Amero et al. 2015).

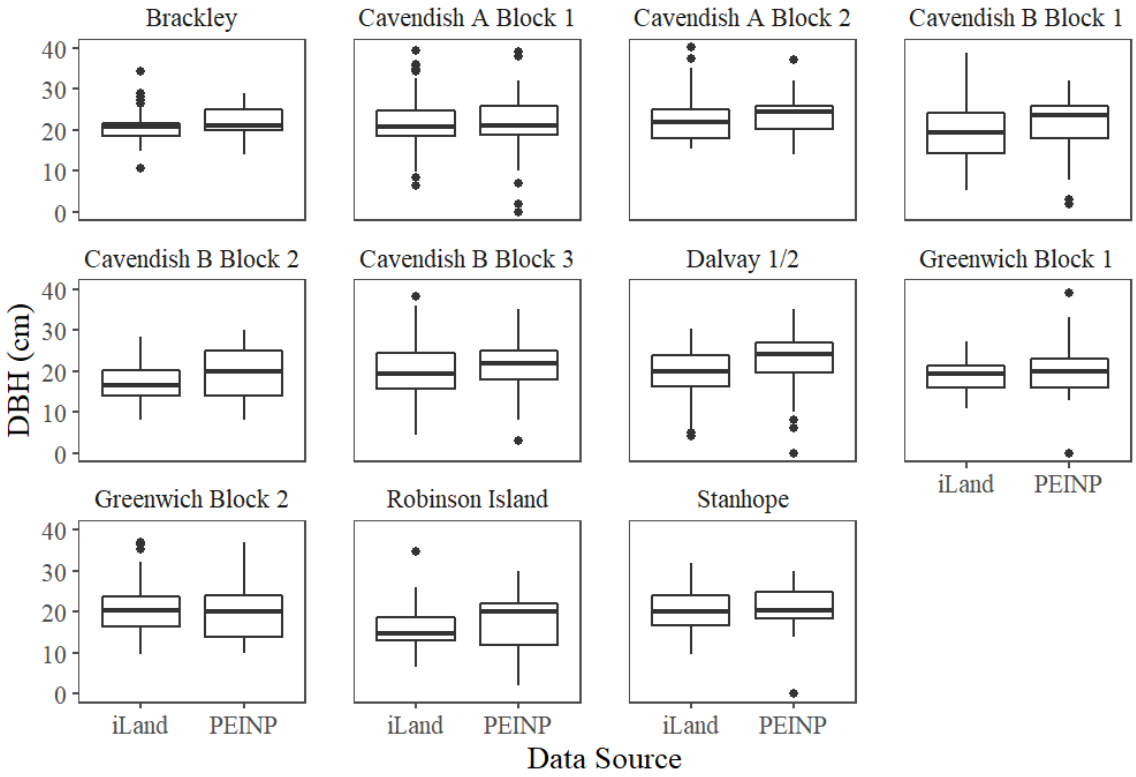

Fig. B2. Diameter at breast height (DBH; cm) by park zone for iLand simulated landscape and Prince Edward Island National Park Management Plan (PEINP; Amero et al. 2015)

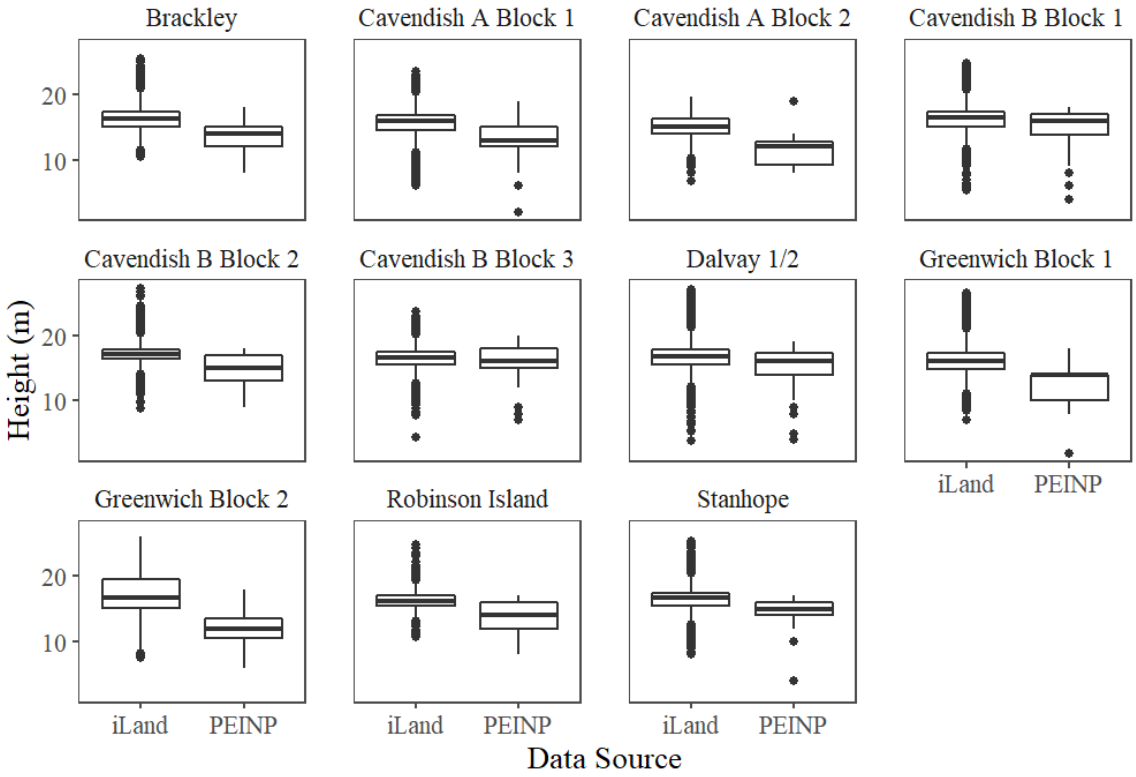

Fig. B3. Height (m; cm) by park zone for iLand simulated landscape and Prince Edward Island National Park Management Plan (PEINP; Amero et al. 2015)

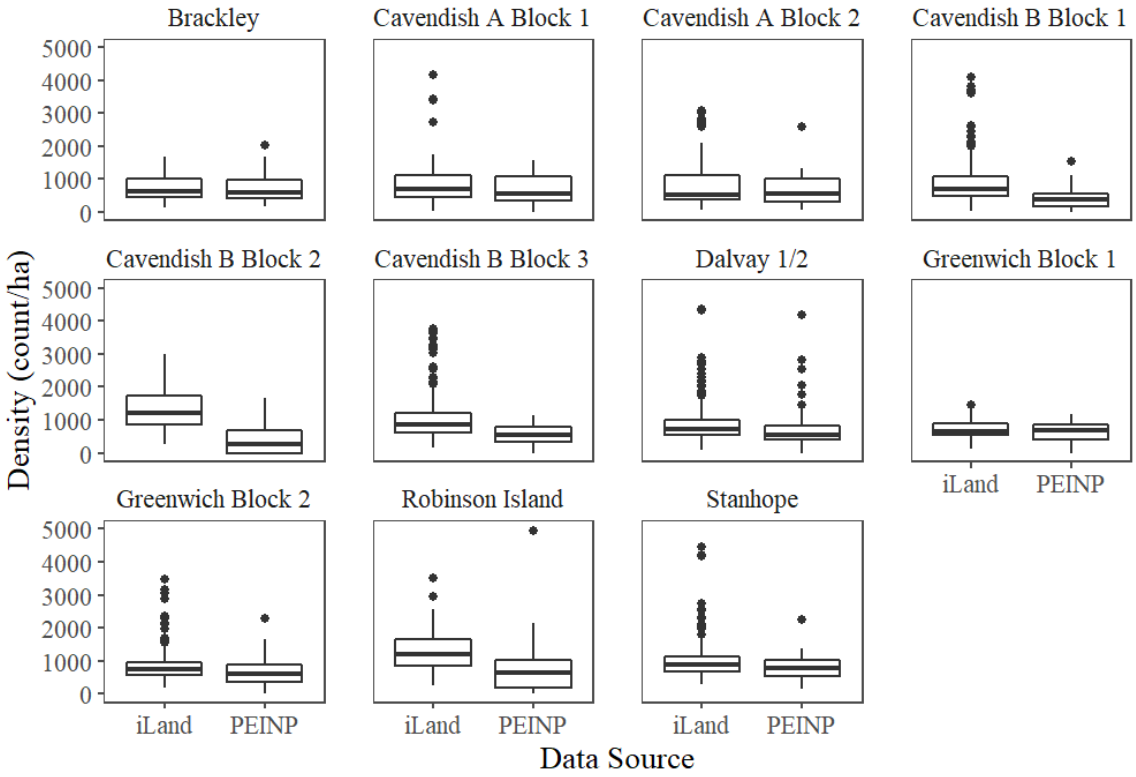

Fig. B4. Density (stems·ha^{-1}) by park zone for iLand simulated landscape and Prince Edward Island National Park Management Plan (PEINP; Amero et al. 2015).

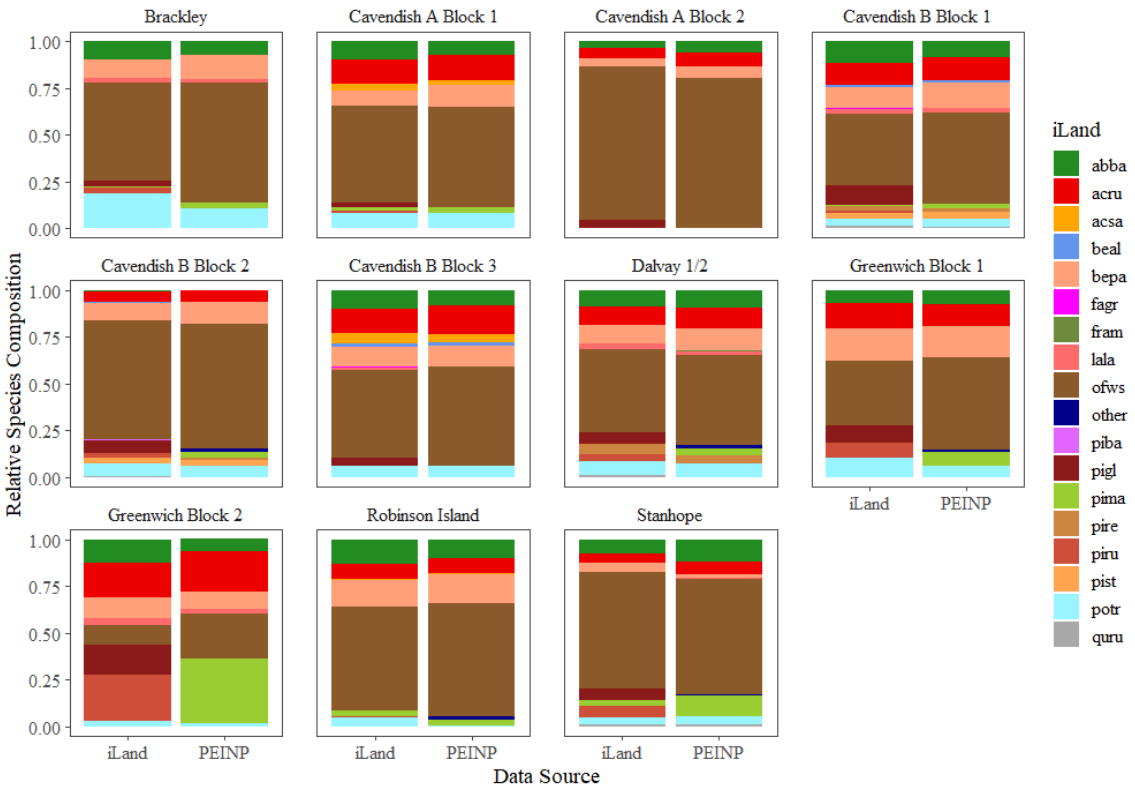

Fig. B5. Relative species composition by park zone for iLand simulated landscape and Prince Edward Island National Park Management Plan (PEINP; Amero et al. 2015). For initialization, black spruce (PIMA) occurring in upland, mixed stands were input as red spruce (PIRU) while stands of > 80% black spruce or described as low-lying were input as PIMA.

Fig. B6. Annual growing degree days (GDD; running sum of the mean daily temperature minus the GDD base temperature (5°C) for all days greater than 5°C during the growing season) under each climate scenario. Dashed lines indicate the GDDMax parameter for specified species.

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