

# Calibrating a process-based simulation model for the Acadian forest region

by Susan Willis,<sup>1,\*</sup> A. R. Taylor,<sup>2</sup> Dominik Thom,<sup>3,4</sup> and L. D'Orangeville<sup>1</sup>

## ABSTRACT

Climate change is projected to have profound impacts on Canada's Acadian Forest Region (AFR). However, large uncertainties arising from climate change and increasing disturbance activity pose challenges for forest management decisions. Process-based (mechanistic) simulation models offer a means by which vulnerabilities and different management strategies can be tested under multiple climate and disturbance regimes. However, applying these complex models can be daunting, especially for novice modelers and forest practitioners; nonetheless, this complexity is increasingly necessary to more realistically project changes in forest growth and composition, ecosystem services, biodiversity, disturbance regimes, and the spread of forest pests. Here, we present a methodology for calibrating and validating 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). For the first time, 18 tree species were parameterized and calibrated for the AFR and model performance was evaluated against independent field observations at the tree population and stand level. iLand was able to accurately emulate the dynamics of individual tree species populations as well as the succession of mixed-species forest stands across a range of soil conditions and is now ready to be used to simulate future forest dynamics of the AFR. We also discuss calibration method selection and the potential impacts of model and project structure in relation to our project. As the accessibility and usability of process-based forests models increases, our work provides a unique case study for forest managers looking to expand their toolbox.

**Keywords:** management, calibration, validation, climate change, temperate, boreal

## RÉSUMÉ

Les changements climatiques devraient avoir un large impact sur la forêt acadienne du Canada (FAC). Cependant, de larges incertitudes découlant des changements climatiques et des perturbations accrues posent des défis importants pour la prise de décision des gestionnaires forestiers. Les modèles de simulation basés sur les processus (mécanistiques) offrent un moyen de tester les vulnérabilités et les différentes stratégies de gestion selon différents régimes climatiques et de perturbations. Cependant, l'application de ces modèles complexes peut être intimidante, surtout pour les modélisateurs novices et les praticiens forestiers. Néanmoins, cette complexité est de plus en plus nécessaire pour projeter de manière plus réaliste les changements dans la croissance et la composition des forêts, les services écosystémiques, la biodiversité, les régimes de perturbations et la propagation des ravageurs forestiers. Dans cet article, nous présentons une méthodologie pour calibrer et valider iLand (v1.1.1), un modèle forestier basé sur les processus à l'échelle du paysage qui offre une approche novatrice pour évaluer les rétroactions entre les arbres individuels et leur environnement (processus écosystémiques, climat et perturbations). Pour la première fois, 18 espèces d'arbres ont été paramétrées et calibrées pour la FAC, et la performance du modèle a été évaluée par rapport à des observations indépendantes sur le terrain au niveau des populations d'arbres et des peuplements. iLand a pu reproduire avec précision les dynamiques des populations d'espèces d'arbres ainsi que la succession des peuplements forestiers mixtes dans une gamme de conditions de sol, et est maintenant prêt à être utilisé pour simuler les futures dynamiques forestières de la FAC. À mesure que l'accessibilité et l'utilisabilité des modèles forestiers basés sur les processus augmentent, notre travail constitue une étude de cas unique pour les gestionnaires forestiers qui cherchent à élargir leurs options.

**Mots clés :** aménagement, calibration, validation, changements climatiques, forêt tempérée, forêt boréale

<sup>1</sup>University of New Brunswick, Faculty of Forestry and Environmental Management, Fredericton, NB E3B 5A3

<sup>2</sup>Canadian Forest Service - Atlantic Forestry Centre, Natural Resources Canada, Fredericton, NB, E3B 5P7

<sup>3</sup>Ecosystem Dynamics and Forest Management Group, School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

<sup>4</sup>Gund Institute for Environment, University of Vermont, 617 Main Street, Burlington, VT 05405, USA



Susan Willis



A. R. Taylor



Dominik Thom



L. D'Orangeville

## 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 and simpler user interfaces, 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 the first principles of ecology (Marquet *et al.* 2014) to reproduce interactions of ecosystem processes and environmental conditions (Battaglia and Sands 1998). Contrary to pattern-based or so-called 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 (Gandhi and Herms 2010; Miller *et al.* 2021), and disturbance regimes (Dhar *et al.* 2016; Wang *et al.* 2017; Boucher *et al.* 2018a), 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; MacLean *et al.* 2022). Under these constraints, forest managers must divide limited forest resources for harvesting (McEwan *et al.* 2020), carbon storage and climate change mitigation (Anderegg *et al.* 2020; Zhao *et al.* 2022), 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 (Korzukhin *et al.* 1996; Gustafson 2013). However, climate change challenges the traditional empirical management approach based on the fundamental assumption that the past can inform the future (Millar *et al.* 2007; Achim *et al.* 2022). To better understand and predict the impacts of these stressors on forest management outcomes, it has become necessary 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 succession model, created to model the mixedwood forests of the northeastern United States (Botkin 1972, 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.

Process-based models of forest development have historically been divided by spatial scale, such as stand-level forest models (e.g., JABOWA-3, PICUS) and landscape-level forest models (e.g., LANDIS, LandClim). Stand-level models are further defined by their spatial resolution, that is individual tree-based or cells of varying sizes. In effect, stand models represent the forest at a higher resolution using more complex and detailed ecological processes than landscape models (Baker and Robinson 2010). Computational demand has traditionally limited the spatial extent to which these models can be applied to (e.g., < 100 hectares; Baker and Robinson 2010). In comparison, landscape models use a coarser representation of the forest—typically aggregating whole stand characteristics such as age class, species composition, or management technique. Thus, simulation of forest landscape dynamics relies more on abstract, empirical representation of whole stand dynamics rather than finer-scale interactions between individual trees, as typically found in stand-level forest models (Taylor *et al.* 2009). As a result, forest landscape models can emulate forest change and disturbance over much larger spatial and temporal scales but are limited in the representation of individual species or stand dynamics.

With many different models available, each with unique design and function, the task of selecting the appropriate model is a challenge for novice modelers and 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, or Keane *et al.* (2019),

which targets spatially explicit, process-based models, provide detailed insight on the model selection process. After a suitable model has been selected, a time and resource intensive process to parameterize, calibrate, and validate its functionality against observational data must be completed before the model may be applied. The process can be informationally and technically complex, is subject to disagreement, and is seldom described in detail in the literature (but see: Shifley *et al.* 2000; Forrester *et al.* 2021; Suárez-Muñoz *et al.* 2021). Nonetheless, growth in data availability for model calibration and improved complimentary software (e.g., spatial data management) has improved accessibility (Shifley *et al.* 2017) but, 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.

In this study, we calibrated iLand (v1.1.1), an individual-based forest landscape and disturbance model. Released in 2012, iLand 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 development and disturbance. 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 interactions (Thom *et al.* 2017b), wildfire (Braziunas *et al.* 2018), wind disturbance (Seidl *et al.* 2014b), bark beetle (Seidl and Rammer 2017), and other disturbances (Honkaniemi *et al.* 2021). 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](http://iland-model.org)).

Previous process-based modeling studies in the AFR have calibrated and used a variety of models such as PICUS (Taylor *et al.* 2017), LANDIS-II with PnET-II (Steenberg *et al.* 2013), JABOWA-3 (Ashraf *et al.* 2012), and LanDSET (Bourque *et al.* 2010), each with unique functions and applications. The addition of iLand is of interest 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 open-source and functions with the use of additional open-source software resources.

The objective of this study was to demonstrate a robust methodology for the parameterization, calibration, and validation of a process-based forest landscape model for the AFR. We parameterized 18 of the most common species of the AFR, many of which are also common throughout all eastern Canada and beyond. We then calibrated and verified the model performance in replicating (1) individual tree

species population dynamics, (2) stand level dynamics (growth and yield), and (3) forest landscape dynamics (succession). A manual multistep iterative process was used, comparing model outputs to empirical data from the AFR and repeatedly adjusting species parameters. The resulting parameter set is ready for initial application to modelling scenarios in the AFR and will provide a starting point for some species for further calibrations throughout Canada.

## Methods

### 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 (Fig. 1). 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 validation will refer to the overall evaluation of 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 model dynamics at each the tree population, 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). Although, development of publicly available databases, such as the TRY database (Kattge *et al.* 2020), has improved accessibility. 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). Environmental and forest data including climate, soil conditions, and empirical data from tree, stand, and landscape development over time are also required for model initialization to represent the simulated environment. The availability and format of these data can vary depending on the collection agency and scale of the data, for example, in Canada, climate data collected by federal government spans coast to coast with standardized formats, while forest inventory data is generally collected by the forest management branch of each province 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 spatial 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; Régnière *et al.* 2014) 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).

Empirical forest data is also utilized 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, 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.

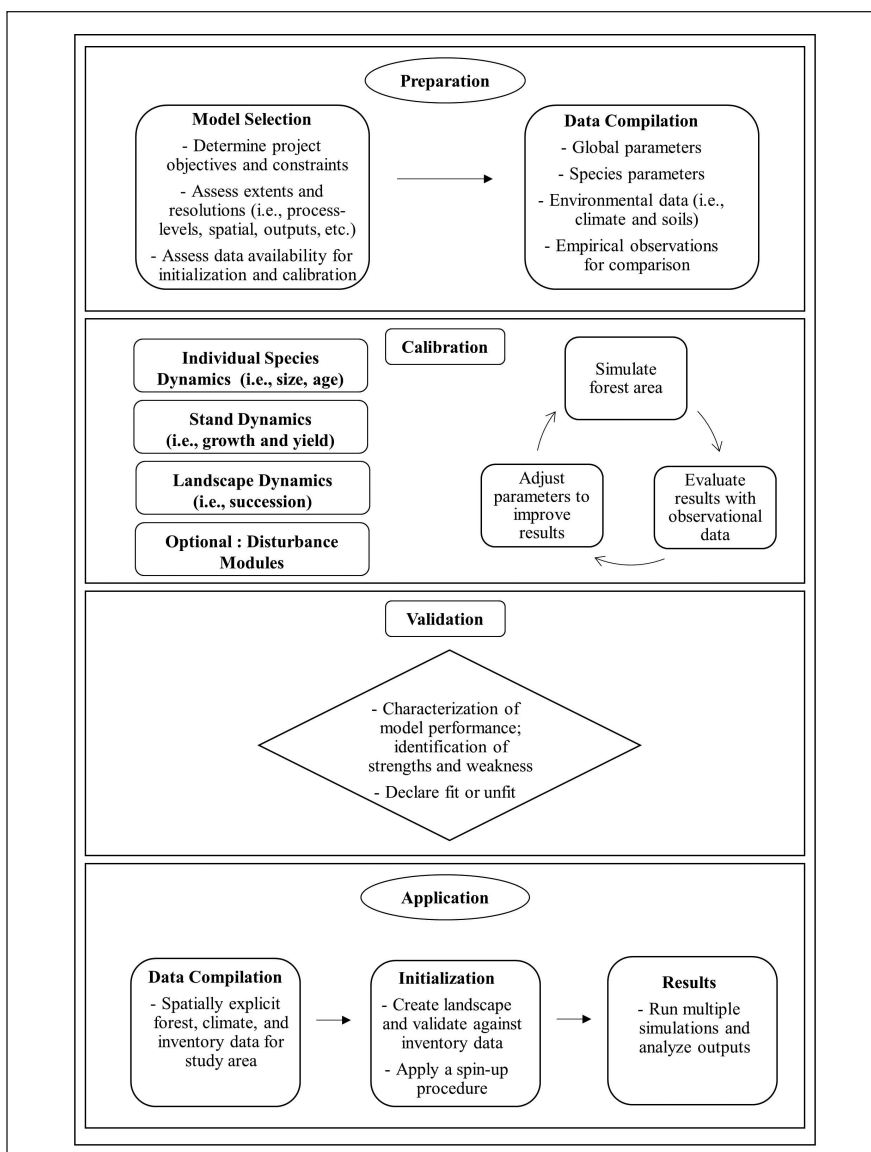
The calibration and validation of models can be a contentious topic due to subjectivity in the process depending on the assessment method used (Yang *et al.* 2004). It must be clarified for ecological models that valid does not equal a universal truth, but rather asserts acceptable model conformance 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.

Qualitative methods for validation include subjective assessments (e.g., face validity 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).

#### Case study model: iLand

iLand uses a novel, multi-hierarchical scaling approach based



**Fig. 1** Overview of the steps involved in the preparation, calibration, validation, and application of a process-based forest model.

in ecological field theory to simulate the demographic processes (growth, mortality, regeneration) at the individual tree level (Seidl *et al.* 2012a). 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 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 density. The tree's height and location within the LIF determines their Light Resource Index (LRI, i.e., potential to intercept radiation) and modifies their growth.

Light, water availability, and climate are considered on a daily timestep, while nutrient availability and atmospheric CO<sub>2</sub> are applied monthly, to calculate annual tree growth and mortality. Climate variables include 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 percent sand/silt/clay for each resource unit. Full carbon and nitrogen cycles can be simulated by iLand however these cycles require extensive parameterization and calibration and will not be used here as it is outside of the scope of this study. Atmospheric CO<sub>2</sub> can be held at a constant value or changed along a time series to represent the changing climate.

The default spatial units are 2x2m grid cells for individual tree location and competition for resources, nested within 10x10m cells for stand initialization, which are further nested within 100x100m cell resource units (homogeneous 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](http://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.

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. Throughout the simulation, regeneration arises from 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 a height of 1.3m; 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.

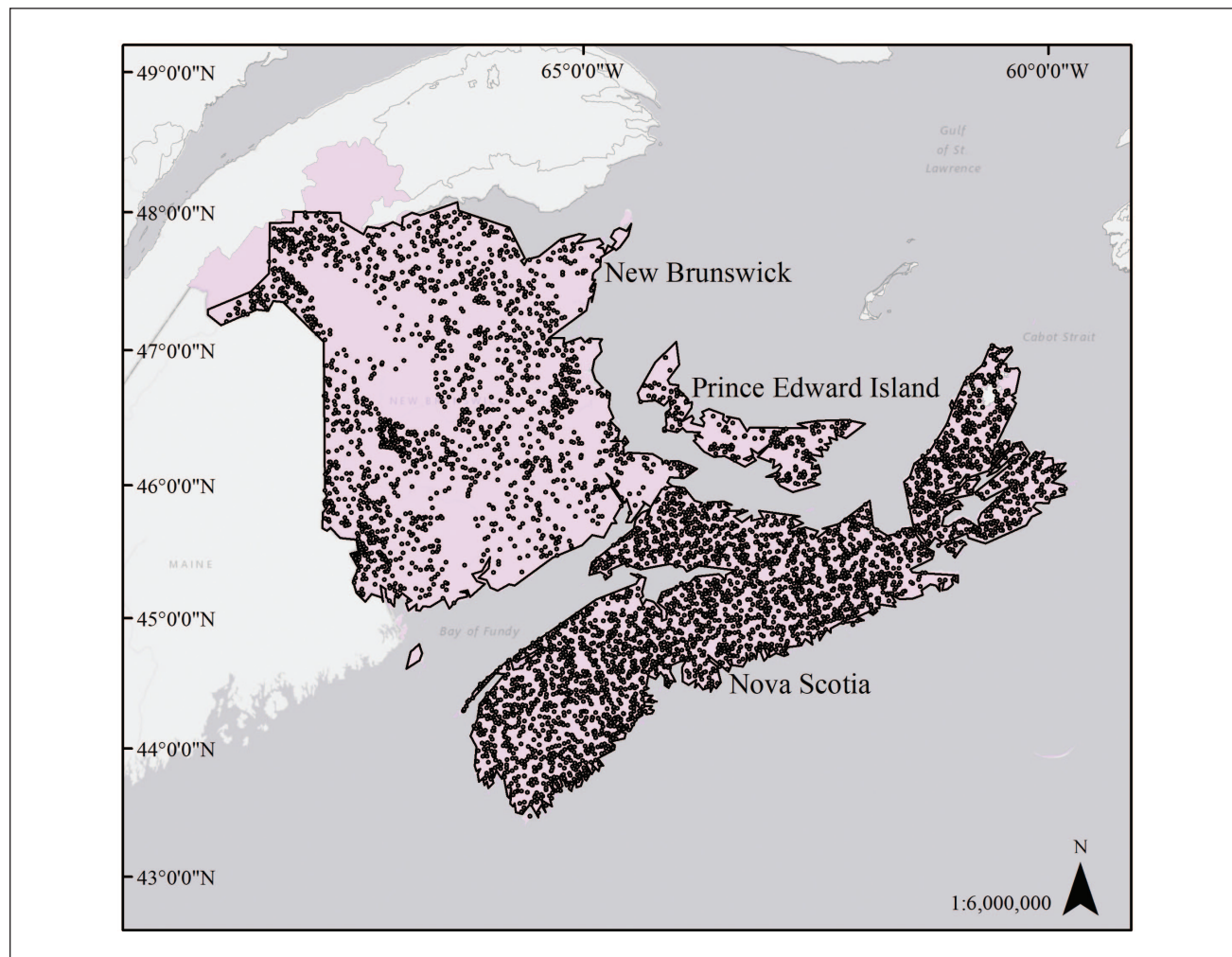
The model can also optionally simulate disturbances. Available modules include fire, wind, bark beetles, and other biotic disturbance agents including browsing, as well as generic user-defined "timed" disturbances allowing to control individual disturbance processes, such as disturbance size, frequency, and extent (Seidl *et al.* 2014a, 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 which will be considered in future studies of AFR.

Some additional software is required for the management of the input and output data of the model including a text editor (e.g., Notepad++; Ho 2023), an SQLite database manager (e.g., SQLiteStudio; Salawa 2020), and GIS software (e.g., ArcMap; ESRI 2018).

### Study area

The AFR extends through the maritime region of Canada encompassing the provinces of New Brunswick (NB), Nova Scotia (NS), and Prince Edward Island (PEI; Fig 2). The forest 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* Marsh.), 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 are 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 800–1500 mm with higher amounts falling along the coast and drier conditions inland (Environment Canada 2021). The cool climate and high rainfall lead to soil podsolization and nutrient-poor acidic soils in coastal areas, but soil quality varies with topography, resulting in well-drained and fertile upland ridges and river valleys. (Loo and Ives 2003). The large amount of coastline and general proximity to the Atlantic Ocean has 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).



**Fig. 2** Map of the study area indicating the extent of the Acadian Forest Region (AFR) in purple across the Canadian provinces of New Brunswick (NB), Nova Scotia (NS), and Prince Edward Island (PEI). The gray dots show the distribution of permanent sample plots (PSPs) across the region.

### Environment settings

iLand requires parameterization at the landscape, stand, and individual tree levels prior to model initialization. Landscape parameters include values such as CO<sub>2</sub> concentration, baseline temperature for growing degree days, and external seed input. These types of values are based on the geographic location of the landscape to be modelled and were determined based on literature review where information was available, or default values are available within the model. Site level parameters include climate and soil characteristics, as well as the establishment of the starting tree and sapling populations.

Throughout model calibration, the same representative climate and site condition inputs were used. Daily climate estimates were generated using historical monthly values 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. The dataset, representing 1970 to 2010, was randomly sampled by the model to extended over the simulation periods. Three stand soil conditions were used, based on Nova Scotia (NS) permanent sam-

ple plot (PSP) observations, with different soil composition and available nitrogen values (kg·ha<sup>-1</sup>·year<sup>-1</sup>) to represent low, moderate, and high productivity sites (Table S1). All simulations were initialized from bare ground conditions using seed from unlimited “outside” sources; seed remains available from outside sources throughout the simulation in addition to local seed rain as the forest develops.

The initial growth and life history parameters required by each of the 18 species (Table 1) were based on a previous calibration of the individual tree-based forest gap model PICUS by Taylor *et al.* (2017) for the AFR, the TRY database (Kattge *et al.* 2020), and an extensive literature review. A full list of the required parameters with descriptions can be found at <https://iland-model.org/species+parameter>. The final species parameter set is available in the supplementary material.

### Permanent sample plot data

Tree and stand information were obtained from the PSP networks of NS, PEI, and NB (Porter *et al.* 2001; NSDNR 2004). The NS PSP network was initially established in 1965 with 1765 plots located randomly throughout the province in all

**Table 1. Calibrated species common name, scientific name, four letter iLand code, and shade tolerance class**

Common Name	Latin	iLand Code	Shade Tolerance
balsam fir	<i>Abies balsamea</i>	abba	high
red maple	<i>Acer rubrum</i>	acru	mod
sugar maple	<i>Acer saccharum</i>	acsa	high
yellow birch	<i>Betula alleghaniensis</i>	beal	mod
white birch	<i>Betula papyrifera</i>	bepa	low
American beech	<i>Fagus grandifolia</i>	fagr	high
white ash	<i>Fraxinus americana</i>	fram	low
tamarack	<i>Larix laricina</i>	lala	low
white spruce	<i>Picea glauca</i>	pigl	high
black spruce	<i>Picea mariana</i>	pima	high
red spruce	<i>Picea rubens</i>	piru	high
jack pine	<i>Pinus banksiana</i>	piba	low
red pine	<i>Pinus resinosa</i>	pire	low
white pine	<i>Pinus strobus</i>	pist	mod
trembling aspen	<i>Populus tremuloides</i>	potr	low
red oak	<i>Quercus rubra</i>	quru	mod
eastern white cedar	<i>Thuja occidentalis</i>	thoc	high
eastern hemlock	<i>Tsuga canadensis</i>	tsca	high

forest types including disturbed and harvested areas, silviculture treatments, as well as natural forest, on Crown and Private land. 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 five 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, Forest Inventory Analyst, PEI Resource Inventory and Modelling, personal communication, November 2022). The plots are located largely in softwood plantations on Crown land, with a few distributed in natural forests on Crown or private lands (M. Angus, Forest Inventory Analyst, PEI Resource Inventory and Modelling, personal communication, November 2022).

For individual species comparisons, all 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) resulting in 85 to 6303 observations by species (Table S2). All three of the PSP datasets were used for the individual species calibration of growth measurements to ensure adequate representation of less common species and to capture the widest range of individual variability. However individual species density for mature stems and saplings was assessed using the NS PSP data only as the plots are consistently measured as 0.04 ha fixed-area plots allowing for the consistent calculation of density, while NB varies plot type and size by forest type, and plot specifications were not available for PEI. Stand densities were obtained from the NS PSP dataset by filtering for plots with > 75% basal area ( $m^2 \cdot ha^{-1}$ ) contributed by the target species and calculating density ( $stems \cdot ha^{-1}$ ) using the fixed-area expansion (NSDNR 2004).

For mixed-species landscape comparisons, plot summary data was created only for NS PSP plots containing tree ages,

as the NS dataset was the largest and most complete overall. In the NS dataset, there were 3259 plots available with tree ages, of which 3153 have been measured more than once, resulting in 20 487 observations. Each observation was then filtered for live trees of the 18 target species and the individual ages were averaged to represent stand age. Average DBH and 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-area expansion factor (NSDNR 2004).

A discrepancy exists in the definition of saplings and trees between iLand and the 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 NS defines trees as DBH > 9.1cm 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 iLand 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.

### Simulation analysis

Analyses of model results were conducted through a combination of visual assessment and descriptive statistics comparing simulated and empirical data available for the AFR. Tree population and stand dynamics were assessed visually using time series plots, overlaying model outputs with empirical data for individual species as well as stand values. The target for these plots was to ensure model results fell within the observational data ranges for all measures and represented well-known developmental patterns. Further qualitative assessment of individual species growth included comparison of average and maximum model results with observed values and available literature. Succession was assessed through the relative abundance (RA) of species by shade tolerance group. RA was calculated as the percentage of total volume represented by each species on the landscape as:

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

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

For the individual species calibration process, a single 1-ha monospecific stand was initiated for each of the three soil conditions from bare ground (i.e., three stands) 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 expected maximum age and size. For direct assessment against the PSP observations, only zero to 200 years of each simulation were used due to the low representation of very old trees in the PSP datasets. The 200-year results were compared visually by time-series with the indi-

vidual trees from the PSPs. Adjustments to various model parameter values were made based on these comparisons, until model outputs conformed sufficiently with species-specific empirical observations. Results were also compared quantitatively to the NS, NB, and PEI datasets by calculating the average and maximum DBH, height, volume per tree, and age over the 200-year simulation. Available literature describing species life history characteristics such as Honer *et al.* (1983), Burns and Honkala (1990) and Farrar (1995) were also consulted throughout the process to augment the observed data for less common species.

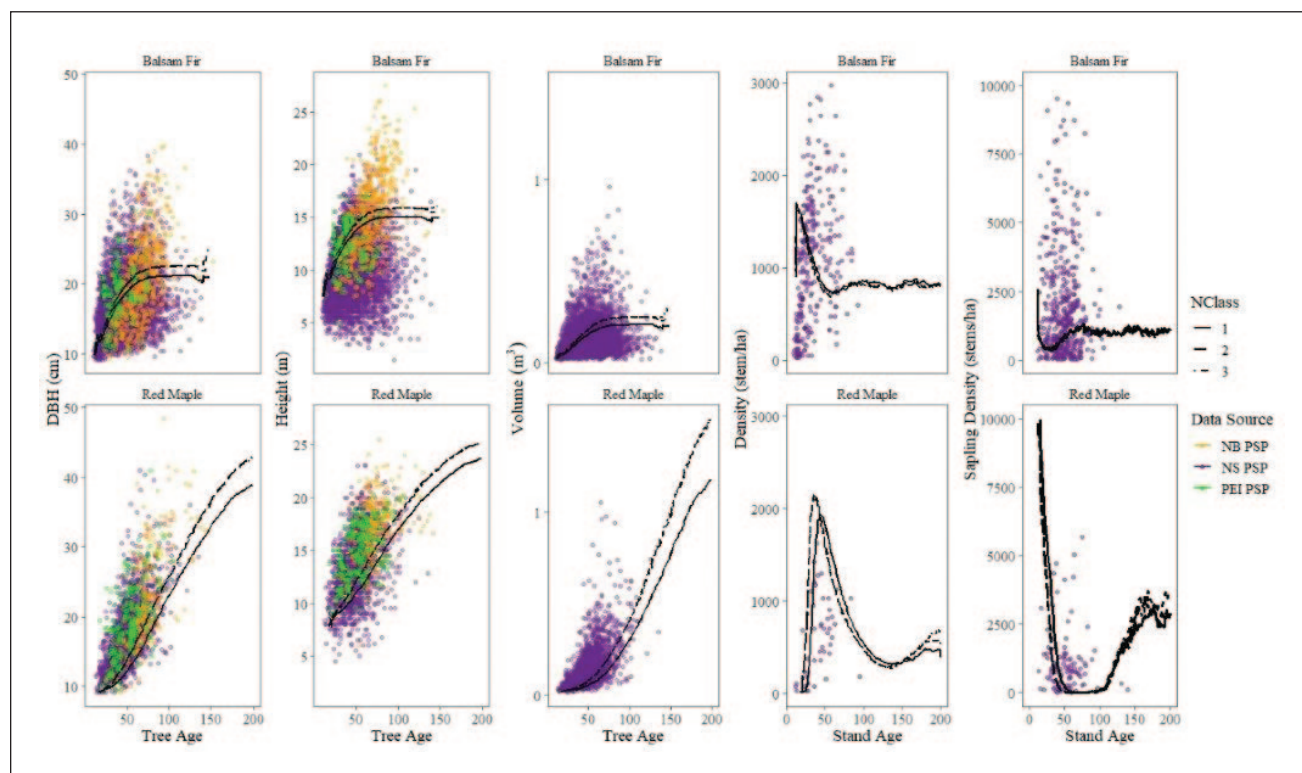
To assess stand dynamics, 100 1-ha stands were established for each of the three soil conditions using the adjusted species parameters running the simulations for 200 years (i.e., 300 stands). The output data was then compared visually to NS plot data. Measures that were assessed for stand dynamics included average DBH, height, volume per hectare, as well as density of all stems and stems > 9.1 cm only, and sapling density over stand age. To assess succession patterns, relative abundance by species and shade tolerance class (Table 1) were calculated for the combined 300 simulated stands and the NS observational data and compared by 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. Once again, adjustments to various parameter values were made based on the results of the comparisons until model outputs conformed sufficiently with observations of the evaluation dataset.

## Results

### Population dynamics

When visually assessing individual species' growth patterns over time, it was found that the model correctly reproduced the rapid increase in diameter, height, and volume (Fig. 3) early during the simulation. Results for all species are available in the supplementary material. Growth patterns conformed to the observed data of all species across the environmental gradient and study period, 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. For all species, stand densities peaked early in the simulations as stands colonized rapidly, followed by a decline and subsequent plateau in the mid- to late term (Fig. 3). 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. 3).

Each species was compared numerically against the empirical observations by averaging DBH, height, volume, and age for the complete 200-year simulation data and NB, NS, and PEI datasets (Table S2). In the observed data, the NB average values were higher than the NS and PEI values in nearly all species, except white pine and American 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 25<sup>th</sup> and 75<sup>th</sup> percentile) of all observed data, with few excep-



**Fig. 3** Simulated iLand average diameter at breast height (DBH; cm), height (m), volume ( $\text{m}^3 \cdot \text{ha}^{-1}$ ), density of stems > 9.1 cm ( $\text{stems} \cdot \text{ha}^{-1}$ ), and density of saplings < 4m in height ( $\text{stems} \cdot \text{ha}^{-1}$ ) by nitrogen class (NClass) and tree age over observed data from the New Brunswick (NB), Nova Scotia (NS), and Prince Edward Island (PEI) permanent sample plot (PSP) networks for balsam fir and red maple. Results for all 18 species available in the supplementary material Fig. S1-S5)



tions. 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 S3; Honer *et al.* 1983; Burns and Honkala 1990; Farrar 1995). 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, shade-intolerant species, such as jack pine, were observed to live longer than expected in the monospecific simulations, but as 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 (i.e., < 150 years of age).

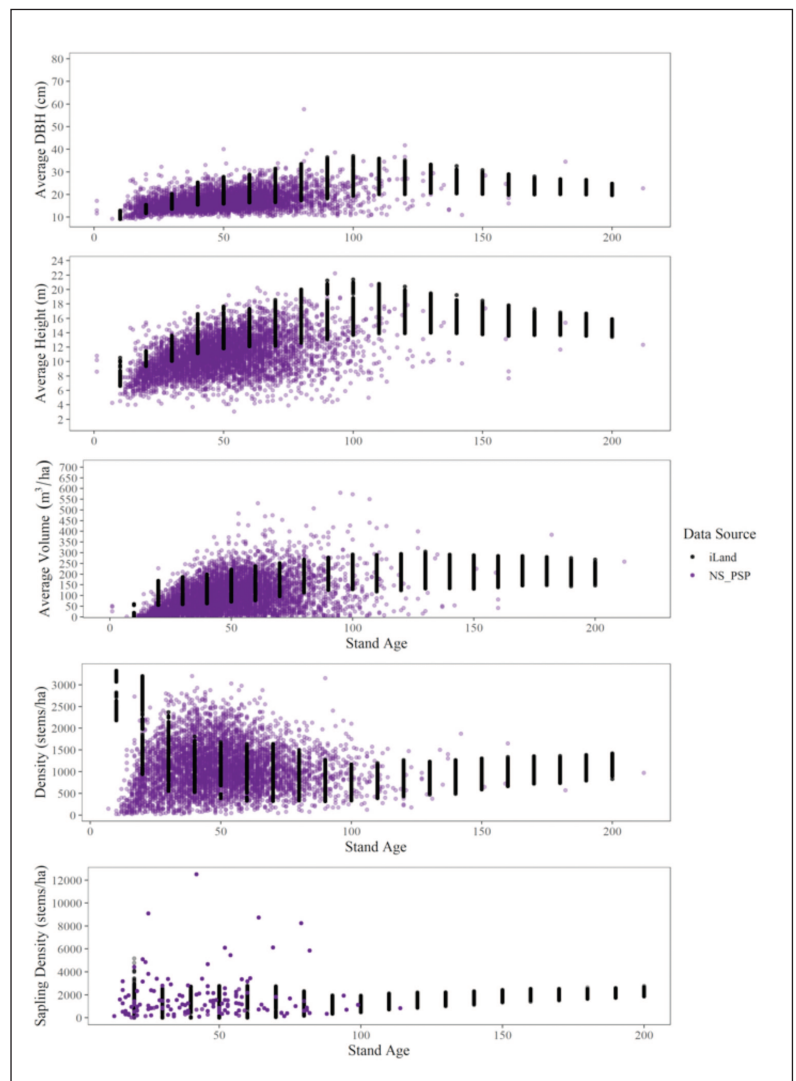
### Stand structure

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, height, volume, density of stems > 9.1cm, and sapling density (Fig. 4) of each simulated stand at 10-year increments against NS observations. The 300 simulated stands displayed less variation in growth than the observed stands, with simulated DBH and height (Fig. 4) trending in the mid-to-high range of the observed data. Average stand density (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. 4). Density trended low in the observed data which is not unexpected considering the moderate-to-high diameter range recorded (Fig. 4; Westoby 1984). Sapling densities were

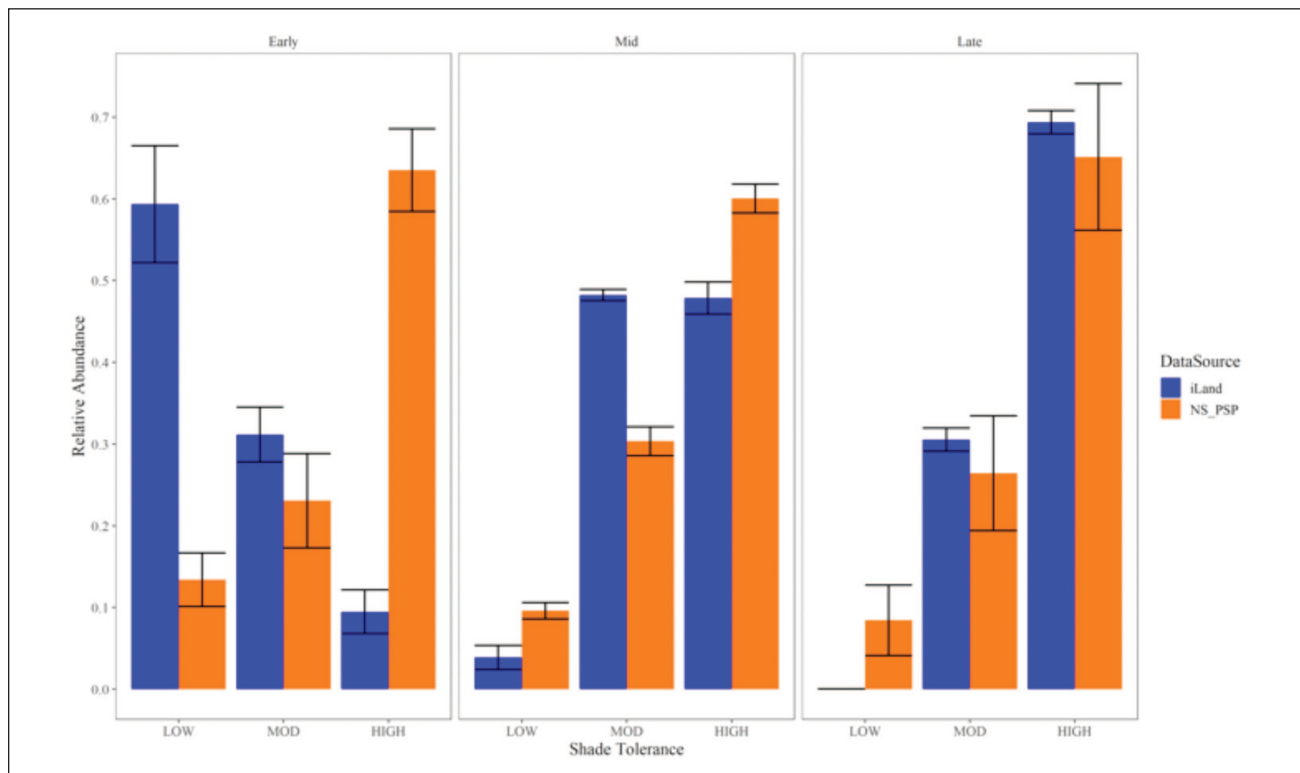
variable between stands, but conformed well to the observed data, averaging 1742 stems/ha to the observed 1844 stems/ha (Fig. 4).

### 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. 5). 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 (Fig. 5). In late-stage succession (101+ years), the



**Fig. 4** Simulated iLand average diameter at breast height (DBH; cm), height (m), volume ( $m^3 \cdot ha^{-1}$ ), density of stems > 9.1 cm ( $stems \cdot ha^{-1}$ ), and density of saplings < 4m in height ( $stems \cdot ha^{-1}$ ) for each of the 300 simulated stands at 10-year intervals over observed data from the Nova Scotia (NS) permanent sample plot (PSP) network.



**Fig. 5** Relative abundance by species shade tolerance for the combined 300 simulated stands and Nova Scotia (NS) permanent sample plot data (PSP) 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.

model closely matched observations of relative abundance for both moderate and high shade-tolerance species (Fig. 5). 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 trembling aspen.

## Discussion

Given the large challenges faced by forest managers today, such as global climate change and biodiversity loss, process-based modelling is becoming an increasingly valuable tool in the decision-making toolkit (Cuddington *et al.* 2013). Complex process-based models are also becoming increasingly accessible and have been used in a variety of climate sensitive landscape projections, the results of which have been used to inform policy and decision making (e.g., Ashraf *et al.* 2012; Steenberg *et al.* 2013; Rammer and Seidl 2015; Seidl *et al.* 2017; Taylor *et al.* 2017; Boulanger *et al.* 2018; Dobor *et al.* 2018). Despite improvements in data availability and complementary software, the task of calibrating and validating a process-based model remains unfamiliar to most forest professionals, necessitating the presentation of methodologies such as this one to facilitate the transition from theoretical research to general application.

iLand provides an excellent example of the power of process-based models and is well-suited to use in the AFR because of its suitability to heterogeneous environments –

both in species composition and environmental conditions – with its unique combination of dynamic interactions between individual trees and their environment across simulated landscapes. Although the model is very complex in detail and requires many species and environmental parameters variables, it has a user-friendly graphical 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.

As this was the first application of iLand in the AFR, calibration was required. There are many potential methods of calibration, including qualitative and quantitative options, and selecting the appropriate model is impacted by the quality and quantity of the empirical data available, as well as the format and function of the model in question. In this instance, formal statistical tests were not used after careful consideration of the observational data available for the AFR. The AFR and adjacent regions have been subject to timber exploitation and land clearing since the 17<sup>th</sup> 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 (e.g., Plonski 1974; Honer 1983). However, large databases are available from wide-scale growth and yield data collection using PSP networks throughout the AFR (e.g., Porter *et al.* 2001;

NSDNR 2004). 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, and remeasurement represents a relatively short timeframe compared to the lifespan of many of the species. Further, 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 but were not removed from the overall dataset. 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 actual stands. These combined factors make formal statistical validation inappropriate for a generalized calibration across the entire AFR.

Qualitative validation methods, including visual assessments, are sometimes discounted due to the subjectivity of the observer, however identifying natural patterns, and ensuring realism, are integral parts of model validation that is difficult to accomplish with statistical methods (Grimm *et al.* 2005). The large number of parameters results in complex interactions which may result in parameter trade-offs, where improving the fit of one variable may result in the poorer fit of another. Visual assessment allows for more nuanced understanding of these relationships, as patterns and trends can be observed and interpreted in context. Most importantly, calibrations and parameter values are not static and can continue to be improved as the model is applied to more specific regions, undergoes sensitivity analyses, and further empirical research becomes available for specific parameter values (McKenzie *et al.* 2019).

In the assessment of tree population dynamics, simulated diameter, height, and volume growth for all species fell within the ranges of observed natural variation. Increased N levels from low to 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 (Cale *et al.* 2017) 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 in iLand, including the bark beetle module (Seidl and Rammer 2017) and biotic disturbance engine (BITE; Honkaniemi *et al.* 2021).

Comparisons were also impacted by the uneven representation of 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 assessed critically when being used in model validation or initialization to evaluate characteristics of the data that may not be reflective of field conditions. Models are a representation, not a replication of ecosystems and comparison with biological realism should be considered in addition to direct comparison to existing inventory data (Vanclay and Skovsgaard 1997).

While modeled stand structure (i.e., DBH, height, volume) was generally reflective of the observed data, model results were limited to the mid- to high range of the observations with very little variation. This trend 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) which are the result of a great variation in natural establishment conditions. Simulated tree establishment and regeneration patterns were also reflective of natural trends, 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).

However, despite reflecting the natural pattern of establishment, overall, the simulated stand densities were substantially lower than the observed values from NS. This may be attributed to the establishment routine used in the model and the exclusion of forest disturbances from the initial calibration (Valle *et al.* 2009). Using the bare ground establishment routine, the model showed consistently high establishment densities both in the individual and multi-species testing scenarios, which were 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). 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 homogeneous 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, optionally 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.* 2018) and mitigate the impacts of initialization on the simulated future conditions (Temperli *et al.* 2013).

Sapling density remained steady throughout the simulation, which is to be expected when modeling without disturbance or ungulate browsing. 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).

The simulation results showed marked difference from the NS PSP results for composition by species and shade tolerance group in the early and into the mid-successional stages despite reflecting the well-documented successional pathway of early successional species dominating at establishment with a gradual transition favouring more shade-tolerant, late-successional species in the mid- to late-term (Fraver *et al.* 2009; Gauthier *et al.* 2010; Basquill and Baldwin 2020). This expected pathway is not reflected in the NS observations, which showed a consistent presence of high-tolerance species across successional stages.

However, the apparently disproportionate presence of high-shade-tolerance species such as balsam fir and white spruce in young PSP plots is not unexpected due to the complex interactions of disturbance size and severity, time since disturbance, and biological legacies in the long-term stand development. As extreme disturbances are rare, stands throughout the AFR are often regenerating on secondary successional pathways which are influenced greatly by biological legacies such as seed beds, stump sprouting, and advanced regeneration allowing the maintenance of consistent species composition, especially for shade tolerant species (Frelich and Reich 1995). In addition, the phenomenon of “borealization” that has been identified through the AFR as a result of the impact of previous land clearing for settlements, timber exploitation and agriculture, and more recent industrial forest management leading to an overall increase in the presence of conifers (Noseworthy and Beckley 2020).

The NS observations also 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 with other species. However, when assessed with fewer species, it was able to persist.

Overall, for initial calibration purposes, the representation of the well-known successional pathway by the model and the agreement between the simulation data and 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 more specific stand initiation techniques to replicate.

## Conclusion

In this study, we successfully calibrated iLand, closely approximating observed patterns for both individual species and stand dynamics in the AFR. By demonstrating a robust methodology 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. Based on our results, this calibration of the iLand model is currently suitable for application throughout the AFR and it is very likely that many species will provide a starting point for further calibrations throughout their Canadian range. However, in all cases when a model is applied to a new geographic range further testing should be done with local 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.

## Acknowledgements

We would like to thank the principal developers of iLand, Rupert Seidl and Werner Rammer, for providing open-access to the model, and Werner Rammer for technical support during the calibration process. We would also like to thank Dr. Charles Bourque for providing additional review and comments for this work. This study was funded by Natural Resources Canada and Prince Edward Island National Park.

## References

- Aber, J. D., K.J. Nadelhoffer, P. Steudler and J.M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. *BioScience* 39(6): 378–286.
- Achim, A., G. Moreau, N.C. Coops, J.N. Axelson, J. Barrette, S. Bédard, K.E. Byrne, J. Caspersen, A.R. Dick, L. D’Orangeville, G. Drolet, B.N.I. Eskelson, C.N. Filipescu, M. Flamand-Hubert, T.R.H. Goodbody, V.C. Griess, S.M. Hagerman, K. Keys, B. Lafleur, ... *et al.* 2021. The changing culture of silviculture. *Forestry: An International Journal of Forest Research* 95(2): 143–152. <https://doi.org/10.1093/forestry/cpab047>
- Amos-Binks, L. J. and D.A. MacLean. 2016. The influence of natural disturbances on developmental patterns in Acadian mixed-wood forests from 1946 to 2008. *Dendrochronologia*, 37: 9–16. <https://doi.org/10.1016/j.dendro.2015.11.002>
- Anderegg, W. R. L., A.T. Trugman, G. Badgley, C.M. Anderson, A. Bartuska, P. Ciais, D. Cullenward, C.B. Field, J. Freeman, S.J. Goetz, J. Hicke, D. Huntzinger, R.B. Jackson, J. Nickerson, S. Pacala and J.T. Randerson. 2020. Climate-driven risks to the climate mitigation potential of forests. *Science* 368: 6497. <https://doi.org/10.1126/science.aaz7005>

- Angers, V.A., C. Messier, M. Beaudet and A. Leduc. 2005.** Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *Forest Ecol. Manag.* 217(2-3): 275-293. <https://doi.org/10.1016/j.foreco.2005.06.008>
- Ashraf, M.I., C. P.-A. Bourque, D.A. MacLean, T. Erdle and F.-R. Meng. 2012.** Using JABOWA-3 for forest growth and yield predictions under diverse forest conditions of Nova Scotia, Canada. *For. Chron.* 88(06): 708-721. <https://doi.org/10.5558/tfc2012-137>
- Baker, P.J. and A. Robinson. 2010.** Review and comparison of tree- and stand-based forest growth models for potential integration into EnSym. University of Melbourne: Victoria, Australia.
- Bartels, S.F., H.Y.H. Chen, M.A. Wulder and J.C. White. 2016.** Trends in post-disturbance recovery rates of Canada's forests following wildfire and harvest. *Forest Ecol. Manag.* 361: 194-207. <https://doi.org/10.1016/j.foreco.2015.11.015>
- Basquill, S. and K. Baldwin. 2020.** Acadian Temperate Forest [online]. Sault Ste. Marie, Ontario, Canada: Canadian National Vegetation Classification. January 2020; generated January-31-2020; 14 p. Canadian National Vegetation Classification Macrogroup: CM744. Available from <http://cnvccnvc.ca>. ISSN 1916-3266. <https://doi.org/10.13140/RG.2.2.16859.52000>
- Battaglia, M. and P.J. Sands. 1998.** Process-based forest productivity models and their application in forest management. *Forest Ecol. Manag.* 102(1): 13-32. [https://doi.org/10.1016/S0378-1127\(97\)00112-6](https://doi.org/10.1016/S0378-1127(97)00112-6)
- Biggs, R., M., Schlüter, D. Biggs, E.L. Bohensky, S. BurnSilver, G. Cundill, V. Dakos, T.M. Daw, L.S. Evans, K. Kotschy, A.M. Leitch, C. Meek, A. Quinlan, C. Raudsepp-Hearne, M.D. Robards, M.L. Schoon, L. Schultz, and P.C. West. 2012.** Toward Principles for Enhancing the Resilience of Ecosystem Services. *Ann. Rev. Environ. Resour.* 37(1): 421-448. <https://doi.org/10.1146/annurev-environ-051211-123836>
- Botkin, D. B. 1993.** *Forest Dynamics: An Ecological Model.* Oxford University Press, Incorporated. <http://ebookcentral.proquest.com/lib/unb/detail.action?docID=3051918>
- Botkin, D. B., J.F. Janak, and J.R. Wallis. 1972.** Some Ecological Consequences of a Computer Model of Forest Growth. *Journal of Ecology* 60(3), 849-872. <https://doi.org/10.2307/2258570>
- Boucher, D., Y. Boulanger, I. Aubin, P.Y. Bernier, A. Beaudoin, L. Guindon, and S. Gauthier. 2018.** Current and projected cumulative impacts of fire, drought, and insects on timber volumes across Canada. *Ecological Applications* 28(5): 1245-1259. <https://doi.org/10.1002/eap.1724>
- Boulanger, Y., A. R. Taylor, D.T. Price, D. Cyr, and G. Sainte-Marie. 2018.** Stand-level drivers most important in determining boreal forest response to climate change. *Journal of Ecology* 106(3): 977-990. <https://doi.org/10.1111/1365-2745.12892>
- Bourque, C., Q. Hassan, and D. Swift. 2010.** Modelled Potential Species Distribution for Current and Projected Future Climates for the Acadian Forest Region of Nova Scotia, Canada.
- Braziunas, K. H., W.D. Hansen, R. Seidl, W. Rammer, and M.G. Turner. 2018.** Looking beyond the mean: Drivers of variability in postfire stand development of conifers in Greater Yellowstone. *Forest Ecol. Manag.* 430: 460-471. <https://doi.org/10.1016/j.foreco.2018.08.034>
- Brissette, J. C. 1996.** Effects of intensity and frequency of harvesting on abundance, stocking, and composition of natural regeneration in the Acadian Forest of eastern North America. <https://helda.helsinki.fi/handle/1975/9242>
- Bugmann, H. 2001.** A Review of Forest Gap Models. *Climate Change* 51: 259-305. <https://doi.org/10.1023/A:1012525626267>
- Burns, R.M. and B.H. Honkala. 1990.** *Silvics of North America: 1. Conifers; 2. Hardwoods.* Agriculture Handbook 654. U.S. Department of Agriculture Forest Service. Washington, DC. Vol 2: 877 pp.
- Cale, J. A., M.T. Garrison-Johnston, S.A. Teale, and J.D. Castello. 2017.** Beech bark disease in North America: Over a century of research revisited. *Forest Ecol. Manag.* 394: 86-103. <https://doi.org/10.1016/j.foreco.2017.03.031>
- Contosta, A. R., N.J. Casson, S. Garlick, S.J. Nelson, M.P. Ayres, E.A. Burakowski, J. Campbell, I. Creed, C. Eimers, C. Evans, I. Fernandez, C. Fuss, T. Huntington, K. Patel, R. Sanders-DeMott, K. Son, P. Templer, and C. Thornbrugh. 2019.** Northern forest winters have lost cold, snowy conditions that are important for ecosystems and human communities. *Ecological Applications* 29(7): e01974. <https://doi.org/10.1002/eap.1974>
- Cuddington, K., M. -J. Fortin, L. R. Gerber, A. Hastings, A. Liebhold, M. O'Connor, and C. Ray. 2013.** Process-based models are required to manage ecological systems in a changing world. *Ecosphere* 4(2). <https://doi.org/10.1890/ES12-00178.1>
- Dobor, L., T. Hlásny, W. Rammer, I. Barka, J. Trombik, P. Pavlenda, V. Šebeň, P. Štěpánek, and R. Seidl. 2018.** Post-disturbance recovery of forest carbon in a temperate forest landscape under climate change. *Agricultural and Forest Meteorology* 263: 308-322. <https://doi.org/10.1016/j.agrformet.2018.08.028>
- Dhar, A., L. Parrott, and C.D.B. Hawkins. 2016.** Aftermath of mountain pine beetle outbreak in British Columbia: Stand dynamics, management response and ecosystem resilience. *Forests* 7(8): 171. <https://doi.org/10.3390/f7080171>
- Drescher, M., A. H. Perera, L.J. Buse, K. Ride, and S. Vasiliauskas, S. 2008.** Uncertainty in expert knowledge of forest succession: A case study from boreal Ontario. *The Forestry Chronicle* 84(2): 194-209. <https://doi.org/10.5558/tfc84194-2>
- Ek, A.R. and R.A. Monserud. 1974.** FOREST: A computer model for simulating the growth and reproduction of mixed species forest stands. *Univ Wisconsin-Madison, Coil Agric and Life Sci Res Rep* R2635: 90 p.
- Environment Canada. 2021.** Canadian Climate Normals 1981-2010. [https://climate.weather.gc.ca/climate\\_normals/index\\_e.html](https://climate.weather.gc.ca/climate_normals/index_e.html) (Accessed Nov 14, 2021)
- ESRI. 2018.** ArcMap 10.6.1. <https://support.esri.com/en/products/desktop/arcgis-desktop/arcmap/10-6-1>
- Evans, P., and C.D. Brown. 2017.** The boreal-temperate forest ecotone response to climate change. *Environmental Reviews.* <https://doi.org/10.1139/er-2017-0009>
- Farrar, J.L. 1995.** *Trees in Canada.* Canadian Forest Service. Fitzhenry & Whiteside Limited. 502 pp.
- Forrester, D. I., M.L. Hobi, A.S. Mathys, G. Stadelmann, and V. Trotsiuk. 2021.** Calibration of the process-based model 3-PG for major central European tree species. *European Journal of Forest Research* 140(4): 847-868. <https://doi.org/10.1007/s10342-021-01370-3>
- Fraver, S., A. S. White, and R. S. Seymour. 2009.** Natural disturbance in an old-growth landscape of northern Maine, USA. *Journal of Ecology* 97: 289-298. <https://doi.org/10.1111/j.1365-2745.2008.01474.x>
- Frelich, L. E. and P.B. Reich. 1995.** Neighborhood effects, disturbance, and succession in forests of the western Great Lakes Region1. *Écoscience* 2(2) : 148-158. <https://doi.org/10.1080/11956860.1995.11682279>
- Gauthier, S., D. Boucher, J. Morissette, and L. De Grandpre. 2010.** Fifty-seven years of composition change in the eastern boreal forest of Canada. *Journal of Vegetation Science* 21: 772-785. <https://doi.org/10.1111/j.1654-1103.2010.01186.x>
- Gandhi, K. J. K., and D.A. Herms. 2010.** Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions*, 12(2): 389-405. <https://doi.org/10.1007/s10530-009-9627-9>
- Golladay, S. W., K.L. Martin, J.M. Vose, D.N. Wear, A.P. Covich, R.J. Hobbs, K.D. Klepzig, G.E. Likens, R.J. Naiman, and A.W. Shearer. 2016.** Achievable future conditions as a framework for guiding forest conservation and management. *Forest Ecology and Management* 360: 80-96. <https://doi.org/10.1016/j.foreco.2015.10.009>

- Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. Mooij, S. Railsback, H. -H. Thulke, J. Weiner, T. Wiegand, and D. Deangelis. 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. *Science* 310: 987–991. <https://doi.org/10.1126/science.1116681>
- Gustafson, E. J. 2013. When relationships estimated in the past cannot be used to predict the future: Using mechanistic models to predict landscape ecological dynamics in a changing world. *Landscape Ecology* 28(8): 1429–1437. <https://doi.org/10.1007/s10980-013-9927-4>
- Ho, D. 2023. Notepad++ (v 8.3.3). <https://notepad-plus-plus.org/> (accessed January 21, 2023)
- Honer, T.G., M.F. Ker, and I.S. Alemdag. 1983. Metric timber tables for the commercial tree species of central and eastern Canada. Information Report M-X-140. Maritime Forest Research Centre. Fredericton, NB.
- Honkaniemi, J., W. Rammer, and R. Seidl. 2021. From mycelia to mastodons – A general approach for simulating biotic disturbances in forest ecosystems. *Environmental Modelling & Software* 138: 104977. <https://doi.org/10.1016/j.envsoft.2021.104977>
- Johnsen, K., L. Samuelson, R. Teskey, S. McNulty, and T. Fox. 2001. Process Models as Tools in Forestry Research and Management. *Forest Science* 47: 2–8.
- Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I.C. Prentice, P. Leadley, S. Tautenhahn, G.D.A. Werner, T. Aakala, M. Abedi, A.T.R. Acosta, G.C. Adamidis, K. Adamson, M. Aiba, C.H. Albert, J.M. Alcántara, C. C. Alcázar, I. Aleixo, H. Ali, ... *et al.* 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* 26(1): 119–188. <https://doi.org/10.1111/gcb.14904>
- Keane, R. E., R. A. Loehman, and L.M. Holsinger. 2019. Selecting a Landscape Model for Natural Resource Management Applications. *Current Landscape Ecology Reports* 4(2): 31–40. <https://doi.org/10.1007/s40823-019-00036-6>
- Korzukhin, M. D., M.T. Ter-Mikaelian, and R.G. Wagner. 1996. Process versus empirical models: Which approach for forest ecosystem management? *Canadian Journal of Forest Research*. <https://doi.org/10.1139/x26-096>
- Landsberg, J. 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. *Can. J. Forest Res.* 33: 385–397. <https://doi.org/10.1139/X02-129>
- Leak, W. B. 2006. Sixty Years of Change in the Sapling Understories of Northern Hardwood Selection Stands in New Hampshire. *Northern Journal of Applied Forestry* 23(4): 301–303. <https://doi.org/10.1093/njaf/23.4.301>
- Le Guerrier, C., D.J. Marceau, A. Bouchard, and J. Brisson. 2003. A modelling approach to assess the long-term impact of beech bark disease in northern hardwood forest. *Canadian Journal of Forest Research* 33(12): 2416–2425. <https://doi.org/10.1139/X03-170>
- Lidestav, G., S. Bergstén, E.C.H. Keskitalo, and L. Linck. 2020. Forest social values: The case of Dalasjö, Sweden. *Scandinavian Journal of Forest Research* 35(3–4): 177–185. <https://doi.org/10.1080/02827581.2020.1754454>
- Long, J. N. 2009. Emulating natural disturbance regimes as a basis for forest management: A North American view. *Forest Ecology and Management* 257(9): 1868–1873. <https://doi.org/10.1016/j.foreco.2008.12.019>
- Loo, J. and N. Ives. 2003. The Acadian Forest: Historical condition and human impacts. *For. Chron.* 79(3): 462–474.
- MacLean, D.A., A.R. Taylor, P.D. Neily, J.W. Steenberg, S.P. Basquill, E. Quigley, C.K. Boone, M. Oikle, P. Bush, and B. Stewart. 2022. Natural disturbance regimes for implementation of ecological forestry: a review and case study from Nova Scotia, Canada. *Environmental Reviews* 30(1): pp.128–158. Marquet, P. A., A.P. Allen, J.H. Brown, J.A. Dunne, B.J. Enquist, J.F. Gillooly, P.A. Gowaty, J.L. Green, J. Harte, S.P. Hubbell, J. O’Dwyer, J.G. Okie, A. Ostling, M. Ritchie, D. Storch, and G.B. West. 2014. On Theory in Ecology. *BioScience* 64(8): 701–710. <https://doi.org/10.1093/biosci/biu098>
- Mayer, D.G. and D.G. Butler. 1993. Statistical validation. *Ecological Modelling* 68(1): 21–32. [https://doi.org/10.1016/0304-3800\(93\)90105-2](https://doi.org/10.1016/0304-3800(93)90105-2)
- McEwan, A., E. Marchi, R. Spinelli, and M. Brink. 2020. Past, present, and future of industrial plantation forestry and implication on future timber harvesting technology. *Journal of Forestry Research* 31(2): 339–351. <https://doi.org/10.1007/s11676-019-01019-3>
- McKenney, D. W., M.F. Hutchinson, P. Papadopol, K. Lawrence, J. Pedlar, K. Campbell, E. Milewska, R.F. Hopkinson, D. Price, and T. Owen. 2011. Customized Spatial Climate Models for North America. *Bulletin of the American Meteorological Society* 92(12): 1611–1622. <https://doi.org/10.1175/2011BAMS3132.1>
- McKenzie, P. F., M.J. Duveneck, L.L. Morreale, and J.R. Thompson. 2019. Local and global parameter sensitivity within an ecophysiological based forest landscape model. *Environmental Modelling and Software* 117: 1–13. <https://doi.org/10.1016/j.envsoft.2019.03.002>
- Miller, C. I., N.L. Stephens, and S.L. Stephens. 2007. Climate Change and Forests of the Future: Managing in the Face of Uncertainty. *Ecological Applications* 17(8): 2145–2151. <https://doi.org/10.1890/06-1715.1>
- Miller, K. M., B.J. McGill, A.S. Weed, C.E. Seirup, J.A. Comiskey, E.R. Matthews, S. Perles, and J. Paul Schmit. 2021. Long-term trends indicate that invasive plants are pervasive and increasing in eastern national parks. *Ecological Applications* 31(2): e02239. <https://doi.org/10.1002/eap.2239>
- Noseworthy, J. and T.M. Beckley. 2020. Borealization of the New England – Acadian Forest: A review of the evidence. *Environmental Reviews* 28(3): 284–293. <https://doi.org/10.1139/er-2019-0068>
- NSDNR. 2004. [Nova Scotia Department of Natural Resources]. Forest Inventory Permanent Sample Plot Field Measurement Methods and Specifications. Report FOR 2004-3. 31pp.
- Paluch, J.G. 2005. The influence of the spatial pattern of trees on forest floor vegetation and silver fir (*Abies alba* Mill.) regeneration in uneven-aged forests. *Forest Ecol. Manag.* 205(1): 283–298. <https://doi.org/10.1016/j.foreco.2004.10.010>
- Petter, G., P. Mairota, K. Albrich, P. Bebi, J. Brûna, H. Bugmann, A. Haffenden, R.M. Scheller, D.R. Schmatz, R. Seidl, M. Speich, G. Vacchiano and H. Lischke. 2020. How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. *Environ. Model. Software* 134: 104844. <https://doi.org/10.1016/j.envsoft.2020.104844>
- Pitt, D., and L. Lanteigne. 2008. Long-term outcome of precommercial thinning in northwestern New Brunswick: Growth and yield of balsam fir and red spruce. *Canadian Journal of Forest Research*, 38(3), 592–610. <https://doi.org/10.1139/X07-132>
- Plonski, W.L. 1974. Normal yield tables (metric) for major forest species of Ontario.
- Porter, K. B., D.A. Maclean, K.P. Beaton and J. Upshall. 2001. New Brunswick permanent sample plot database (PSPDB v1.0): User’s guide and analysis.
- Rammer, W., & R. Seidl. 2015. Coupling human and natural systems: Simulating adaptive management agents in dynamically changing forest landscapes. *Global Environmental Change* 35 :475–485. <https://doi.org/10.1016/j.gloenvcha.2015.10.003>
- Régnière, J., R. Saint-Amant, and A. Béchar. 2014. BioSIM 10 user’s manual. Information Report LAU-X-137E. Nat. Res. Can., Can. For. Serv., Laurentian Forestry Centre. 72 pp.
- Ricklefs, R. E. 2006. The unified neutral theory of biodiversity: do the numbers add up? *Ecology* 87(6): 1424–1431. [https://doi.org/10.1890/0012-9658\(2006\)87\[1424:TUNTOB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1424:TUNTOB]2.0.CO;2)
- Rowe, J.S. 1972. Forest regions of Canada. Nat. Res. Can., Can. For. Serv., Ottawa, Canada.
- Ruiz-Benito, P., G. Vacchiano, E.R. Lines, C.P.O. Reyer, S. Ratcliffe, X. Morin, F. Hartig, A. Mäkelä, R. Yousefpour, J.E. Chaves,

- A. Palacios-Orueta, M. Benito-Garzón, C. Morales-Molino, J.J. Camarero, A.S. Jump, J. Kattge, A. Lehtonen, A. Ibrom, H.J.F. Owen, H. J. F., and M.A. Zavala. 2020. Available and missing data to model impact of climate change on European forests. *Ecological Modelling* 416:108870. <https://doi.org/10.1016/j.ecolmodel.2019.108870>
- Rykiel, E. J. 1996. Testing ecological models: The meaning of validation. *Ecological Modelling* 90(3): 229–244. [https://doi.org/10.1016/0304-3800\(95\)00152-2](https://doi.org/10.1016/0304-3800(95)00152-2)
- Salawa, P. 2020. SQLiteStudio (v3.2.1). Salssoft. <https://sqlitestudio.pl>. (Last accessed January 21, 2023)
- Seidl, R., W. Rammer, R.M. Scheller, R. M., and T.A. Spies. 2012a. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecological Modelling* 231:87–100. <https://doi.org/10.1016/j.ecolmodel.2012.02.015>
- Seidl, R., T.A. Spies, W. Rammer, E.A. Steel, R.J. Pabst, and K. Olsen. 2012b. Multi-scale drivers of spatial variation in old-growth forest carbon density disentangled with Lidar and an individual-based landscape model. *Ecosystems* 15(8):1321–1335. <https://doi.org/10.1007/s10021-012-9587-2>
- Seidl, R., W. Rammer, and K. Blennow. 2014a. Simulating wind disturbance impacts on forest landscapes: Tree-level heterogeneity matters. *Environmental Modelling & Software* 51:1–11. <https://doi.org/10.1016/j.envsoft.2013.09.018>
- Seidl, R., W. Rammer and T.A. Spies. 2014b. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecological Applications* 24(8):2063–2077. <https://doi.org/10.1890/14-0255.1>
- Seidl, R. and W. Rammer. 2017. Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. *Landscape Ecology* 32(7):1485–1498. <https://doi.org/10.1007/s10980-016-0396-4>
- Seidl, R., F. Vigl, G. Rössler, M. Neumann, and W. Rammer. 2017. Assessing the resilience of Norway spruce forests through a model-based reanalysis of thinning trials. *Forest Ecology and Management* 388:3–12. <https://doi.org/10.1016/j.foreco.2016.11.030>
- Shifley, S. R., R. Frank, I.I.I. Thompson, D.R. Larsen, D.J. Mladenoff, and E.J. Gustafson. 2000. Utilizing inventory information to calibrate a landscape simulation model. In: Hansen, Mark; Burk, Tom, Eds. *Integrated Tools for Natural Resources Inventories in the 21<sup>st</sup> Century*. Gen. Tech. Rep. NC-212. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station: 549–561(212). <http://www.fs.usda.gov/treesearch/pubs/15905>
- Shifley, S., H. He, H. Lischke, W. Wang, W. Jin, E. Gustafson, J. Thompson, I.I.I. Thompson, W. Dijk, and J. Yang. 2017. The past and future of modeling forest dynamics: From growth and yield curves to forest landscape models. *Landscape Ecology* 32:1–19. <https://doi.org/10.1007/s10980-017-0540-9>
- Steenberg, J. W. N., P.N. Duinker, and P. G. Bush. 2013. Modelling the effects of climate change and timber harvest on the forests of central Nova Scotia, Canada. *Annals of Forest Science* 70(1):61–73. <https://doi.org/10.1007/s13595-012-0235-y>
- Soares, P., M. Tomé, J.P. Skovsgaard, and J.K. Vanclay. 1995. Evaluating a growth model for forest management using continuous forest inventory data. *Forest Ecology and Management* 71(3):251–265. [https://doi.org/10.1016/0378-1127\(94\)06105-R](https://doi.org/10.1016/0378-1127(94)06105-R)
- Suárez-Muñoz, M., M. Mina, P.C. Salazar, R.M. Navarro-Cerrillo, J.L. Quero, and F. Bonet-García. 2021. A step-by-step guide to initialize and calibrate landscape models: a case study in the Mediterranean Mountains. *Frontiers in Ecology and Evolution* (9). <https://doi.org/10.3389/fevo.2021.653393>
- Taylor, A. R., H.Y.H Chen, and L. VanDamme. 2009. A Review of Forest Succession Models and Their Suitability for Forest Management Planning. *Forest Science* 55(1): 23–36. <https://doi.org/10.1093/forestscience/55.1.23>
- Taylor, A. R., D. A. McPhee, and J.A. Loo. 2013. Incidence of beech bark disease resistance in the eastern Acadian forest of North America. *The Forestry Chronicle* 89(05):690–695. <https://doi.org/10.5558/tfc2013-122>
- Taylor, A.R., Y. Boulanger, D. Price, D. Cyr, E. McGarrigle, W. Rammer, and J. Kershaw. 2017. Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region. *Forest Ecology and Management* 405:284–294. <https://doi.org/10.1016/j.foreco.2017.07.033>
- Taylor, A. R., D.A. MacLean, P.D. Neily, B. Stewart, E. Quigley, S.P. Basquill, C.K. Boone, D. Gilby, and M. Pulsifer. 2020. A review of natural disturbances to inform implementation of ecological forestry in Nova Scotia, Canada. *Environmental Reviews*. <https://doi.org/10.1139/er-2020-0015>
- Temperli, C., J. Zell, H. Bugmann, and C. Elkin. 2013. Sensitivity of ecosystem goods and services projections of a forest landscape model to initialization data. *Landscape Ecology* 28(7):1337–1352. <https://doi.org/10.1007/s10980-013-9882-0>
- Thom, D., W. Rammer and R. Seidl. 2017a. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. *Global Change Biology*, 23(1), 269–282. <https://doi.org/10.1111/gcb.13506>
- Thom, D., W. Rammer and R. Seidl. 2017b. The impact of future forest dynamics on climate: Interactive effects of changing vegetation and disturbance regimes. *Ecological Monographs* 87(4), 665–684. <https://doi.org/10.1002/ecm.1272>
- Thom, D., W. Rammer, R. Garstenauer and R. Seidl. 2018. Legacies of past land use have a stronger effect on forest carbon exchange than future climate change in a temperate forest landscape. *Biogeosciences* 15(18):5699–5713. <https://doi.org/10.5194/bg-15-5699-2018>
- Valle, D., C.L. Staudhammer, W.P. Cropper Jr. and P.R. Garding. 2009. The importance of multimodel projections to assess uncertainty in projections from simulation models. *Ecological Applications* 19(7):1680–1692. <https://doi.org/10.1890/08-1579.1>
- Vanclay, J. and J.P. Skovsgaard. 1997. Evaluating forest growth models. *Ecological Modelling*. 98:1–12. [https://doi.org/10.1016/S0304-3800\(96\)01932-1](https://doi.org/10.1016/S0304-3800(96)01932-1)
- Van Oijen, M., J. Rougier and R. Smith. 2005. Bayesian calibration of process-based forest models: Bridging the gap between models and data. *Tree Physiol.* 25(7): 915–927. <https://doi.org/10.1093/treephys/25.7.915>
- Wang, X., M. -A. Parisien, S.W. Taylor, J.-N. Candau, D. Stralberg, G.A. Marshall, J.M. Little and M.D. Flannigan. 2017. Projected changes in daily fire spread across Canada over the next century. *Environmental Research Letters* 12(2):025005. <https://doi.org/10.1088/1748-9326/aa5835>
- Westoby, M. 1984. The Self-Thinning Rule. In: A. MacFadyen & E. D. Ford (Eds.), *Advances in Ecological Research* (Vol. 14, pp. 167–225). Academic Press. [https://doi.org/10.1016/S0065-2504\(08\)60171-3](https://doi.org/10.1016/S0065-2504(08)60171-3)
- Yang, Y., R.A. Monserud and S. Huang. 2004. An evaluation of diagnostic tests and their roles in validating forest biometric models. *Can. J. For. Res.* 34(3): 619–629. <https://doi.org/10.1139/X03-230>
- Zhao, J., A. Daigneault and A. Weiskittel. 2022. Estimating regional timber supply and forest carbon sequestration under shared socioeconomic pathways: A case study of Maine, USA. *PLOS Climate* 1(5): e0000018. <https://doi.org/10.1371/journal.pclm.0000018>