Canadian Journal of
Forest Research

Perspective

Best practices for calibration of forest landscape models using fine-scaled reference information

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Abstract

Forest Landscape Models (FLMs) project responses to different climate, disturbance, and management scenarios and can inform decision-making that shapes ecosystems. However, use of FLM outputs by decision makers can be hampered by a lack of transparency and credibility in the calibration of modeled processes. Landscape modelers typically use fine-scaled (i.e., plot- or stand-level) information to calibrate the growth functions central to FLMs, but methods vary widely and are often poorly documented. We suggest best practices for calibration and assessment of tree growth in FLMs adapted from prior guidelines to increase rigor in ecological models and their application. Our proposed best practices include: (1) evaluating available information, (2) articulating assumptions, (3) accounting for scale, (4) formalizing model assessment stages, (5) grounding parameter ranges within empirical bounds, (6) considering parameter sensitivity, (7) verifying and corroborating output, (8) making iterative improvements, and (9) delivering sufficient documentation. We illustrate our approach across five case studies that involve a diversity of FLM designs centred on the tree-species, age-cohort structure available within the LANscape DIsturbance and Succession (LANDIS-II) modeling framework. We suggest that these best practices are applicable to many FLM platforms and provide the enhanced transparency essential for wider scientific acceptance of FLM projections.

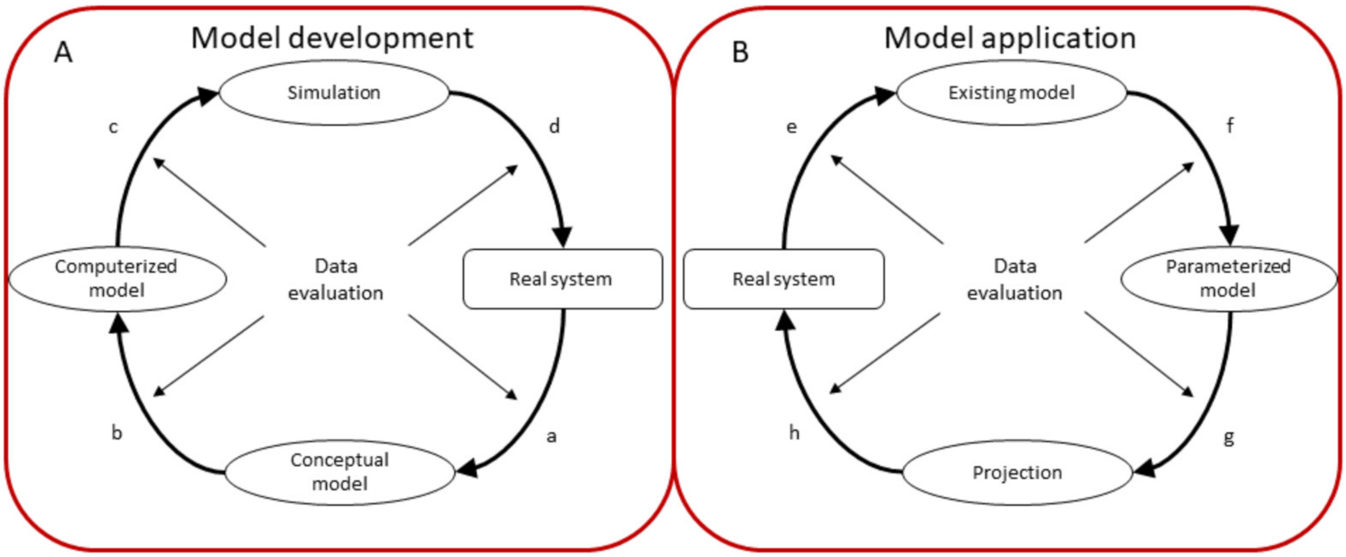
Key words: calibration, validation, modeling, growth and yield, evaludation

1. Introduction

Ecological models are fundamental to informed decision-making regarding forests in the context of global change, but such models and their applications must be trusted to be useful (Rastetter 1996). Transparency in terminology, methods, and evaluation are among the keys to establishing model credibility (Dietz et al. 2013; Yanai et al. 2021; McIntire et al. 2022). Still, recurring calls for comprehensive standards for model development, use, and documentation (Aber 1997; Grimm et al. 2014; Furniss et al. 2022) underscore a lack of coherency. For example, TRAnsparent and Comprehensive Ecological modeling documentation (TRACE) is a framework of best practices for documenting model design and model testing (Schmolke et al. 2010). Since its introduction, TRACE has been revised (Grimm et al. 2014) to include the six elements of "evaludation", a term combining evaluation and validation (Augusiak et al. 2014). TRACE, in turn, builds on a broader literature targeting the rigor of model development and testing (e.g., Sargent 1984; Oreskes et al. 1994; Rykiel 1996).

Models benefit from exposure to a diversity of applications (Huber et al. 2020). The TRACE framework was designed for model development, as Grimm et al. (2014) indicated, "Model application (i.e., the simulations carried out to answer specific environmental decision-making questions) will also need to be carefully documented. However, this is outside the scope of the TRACE documentation". Sargent (1984) split model validation into components including conceptual, i.e., the theories and assumptions upon which the model is based, and operational, i.e., the behavior of the model's output, providing useful categories for various steps in the modeling cycle. While not every TRACE element is implemented in every application, those overlapping with operational validity remain relevant, as described below. Additionally, when the application of an established model includes assessments of the model's operational behavior, the results can lead to refinement of the conceptualization and implementation stages of the modeling cycle, exemplifying the iterative nature of modeling (Fig. 1).

Fig. 1. Four main elements of: (A) the model development cycle (reprinted with permission) and (B) the model application cycle. Components include the steps: (*a*) conceptual model evaluation, (*b*) implementation and model output verification, (*c*) model analysis, (*d*) model output corroboration, (*e*) model selection, (*f*) calibration, (*g*) model output verification and corroboration, and (*h*) model summarization. Data evaluation is central to each step. This modified figure was originally published in Ecological Modelling, volume 280, Augusiak J., Van den Brink, P.J. and Grimm V., *Merging validation and evaluation of ecological models to "evaludation": a review of terminology and a practical approach*, pages 117–128, Copyright Elsevier.



We adapt past efforts to formalize rigor in the development, testing, and application of models via a set of best practices focused on the use of plot- and stand-level (fine-scaled) information to calibrate forest growth within Forest Landscape Models (FLMs). The goal is to increase confidence with transparent and consistent methods while remaining flexible to accommodate a diversity of model designs and available information. An FLM simulates landscape-scale responses to stochastic processes including seed dispersal, succession, natural disturbances, and management practices. These processes are typically simulated across multiple, interacting stands and large spatiotemporal extents, to assess long-term change in forest characteristics (e.g., Gustafson 2013; Dymond et al. 2016). Since their conception in the 1990s (Mladenoff and Baker 1999), FLMs have evolved to replace phenomenological patterns with underlying processes, including establishment, growth, mortality, and a diversity of disturbance agents (Sturtevant and Fortin 2021). FLMs have proven useful for developing solutions to critical landscape problems, for example, by projecting the consequences of forest management alternatives (Mairota et al. 2014; Gustafson et al. 2020; Hotta et al. 2021), shifts in land use (Thompson et al. 2016; Duveneck et al. 2017), climate change (Gustafson et al. 2010; Elkin et al. 2013; Liang et al. 2018), altered disturbance regimes (Sturtevant et al. 2009, 2012; De Jager et al. 2017), disturbance interactions (Lucash et al. 2018; Sturtevant and Fortin 2021), and combinations of these factors (Hof et al. 2017). We focus on FLMs that are based on a tree-species, age-cohort approach for scaling forest stand dynamics to broader landscapes (Lischke et al. 2006; Schumacher et al. 2006; Scheller et al. 2007; Wang et al. 2014*a*).

FLM processes, including growth, are dependent on site-specific conditions, requiring initialization and calibration for each new application (Fer et al. 2021). Successful calibration properly scales local tree species growth and emergent competition to landscape extents (e.g., Wang et al. 2014*b*; Boulanger et al. 2017). Ideally, required parameter values, such as life history parameters, are acquired directly from published empirical studies and silvics guides (e.g., Loehle 1988; Burns and Honkala 1990; Del Tredici 2001). Issues that prompt a model application and associated calibration are analogous to the problem formulation element in TRACE in that a given model is tuned to address specific questions and will not necessarily provide appropriate information outside of that context. Tree species growth calibration requires assessment by comparison with reference data, i.e., model output verification, and ideally also by comparison with independent or test data, termed model output corroboration (Augusiak et al. 2014; Grimm et al. 2014); separating these two steps allows assessment of the predictive power of a model (Pontius et al. 2004). Despite their critical role in model behavior and credibility, calibration procedures are often not documented with the detail needed for evaluation, replication, and emulation (Suárez-Muñoz et al. 2021). Such shortcomings can undermine model confidence (Scheller 2018) to the extent that results can be either discounted or misinterpreted when making important policy decisions (Shifley et al. 2017).

In this article, we describe procedures for defensibly and transparently calibrating FLMs in new environments. Local parameterization of any FLM application will share common stages and challenges specific to the selected FLM and its model configuration and the available fine-scaled informa-

Box 1. Best practice elements contributing to a rigorous and transparent calibration of forest growth in a forest landscape model. These elements fall within a broader framework (Fig. 2) that—consistent with the model evaludation guidelines of TRACE (Fig. 1)—is iterative in design. Iteration through the framework provides multiple opportunities to refine procedures according to new insights, additional information sources, and model improvements. The ability to meet specific best practices depends on resources and available information.

1. Synthesize and evaluate information sources available to define or guide forest growth
   - Document and understand quality, range, coverage, and scale
   - Systematically address the strengths and limitations of information sources
2. Articulate premises and assumptions underlying procedures
3. Account for scale in space and time, documenting decisions (e.g., grain, extent, aggregation versus stratification, etc.) affecting forest growth variability and evaludation
4. Designate independent datasets for model output verification and corroboration, or split the single dataset into training and test subsets
5. Select targets and set performance criteria, including stopping thresholds, based on purpose and context
   - Use quantitative methods where possible, and qualitative where necessary
6. Target the most influential parameters and remain within local empirical ranges
   - Use published parameter values directly where possible
7. Verify and corroborate calibration at different levels of organization
   - E.g., heterogeneity in drivers affecting growth, species competition, multiple state variables, and different scales in space and time
8. Allow for learning and model improvement via process iteration
9. Document and deliver
   - Premises, assumptions, and procedures
   - Results (parameter values, performance assessments)
   - Defendable justifications where performance criteria cannot be met
   - Strengths and limitations of the model application

tion. Our collective experience suggests a set of best practice (BP) elements (Box 1) general enough to adapt to the particulars of any given study while specific enough to provide concrete guidance. These elements can be crosswalked, though not always directly, to prior guidelines for increasing rigor in ecological models and their applications (Table 1; see also Fig. 2 in Grimm et al. (2014)). For example, we selected BPs to accommodate model applications, and they therefore correspond to elements on the (operational) top side of the model development cycle (Fig. 1), which we expanded into an iterative calibration, verification, and corroboration framework (Fig. 2). We organized this article around the sequence of BP elements within the proposed framework and present five case studies that illustrate applications of BPs across several variants of the LANdscape DIsturbance and Succession (LANDIS-II) FLM (see Supplementary materials A–E[1]), demonstrating commonalities and differences when calibrating forest growth across different model designs (Table 1).

2. Synthesis and evaluation of growth information (BP 1)

Data evaluation is central to all modeling components, and can ensure credible and reliable model development, analysis, and application (Fig. 1). Here, we describe some of the sources for fine-scaled growth (referred to hereafter simply as growth) information where each source presents unique opportunities and challenges when used to inform FLMs. Growth information provides important details about forest dynamics to forest managers. Not all sources will be available in every area; the goal is to acquire and synthesize the best available growth information and minimize limitations (i.e., Box 1, BP 1).

2.1. Forest growth data

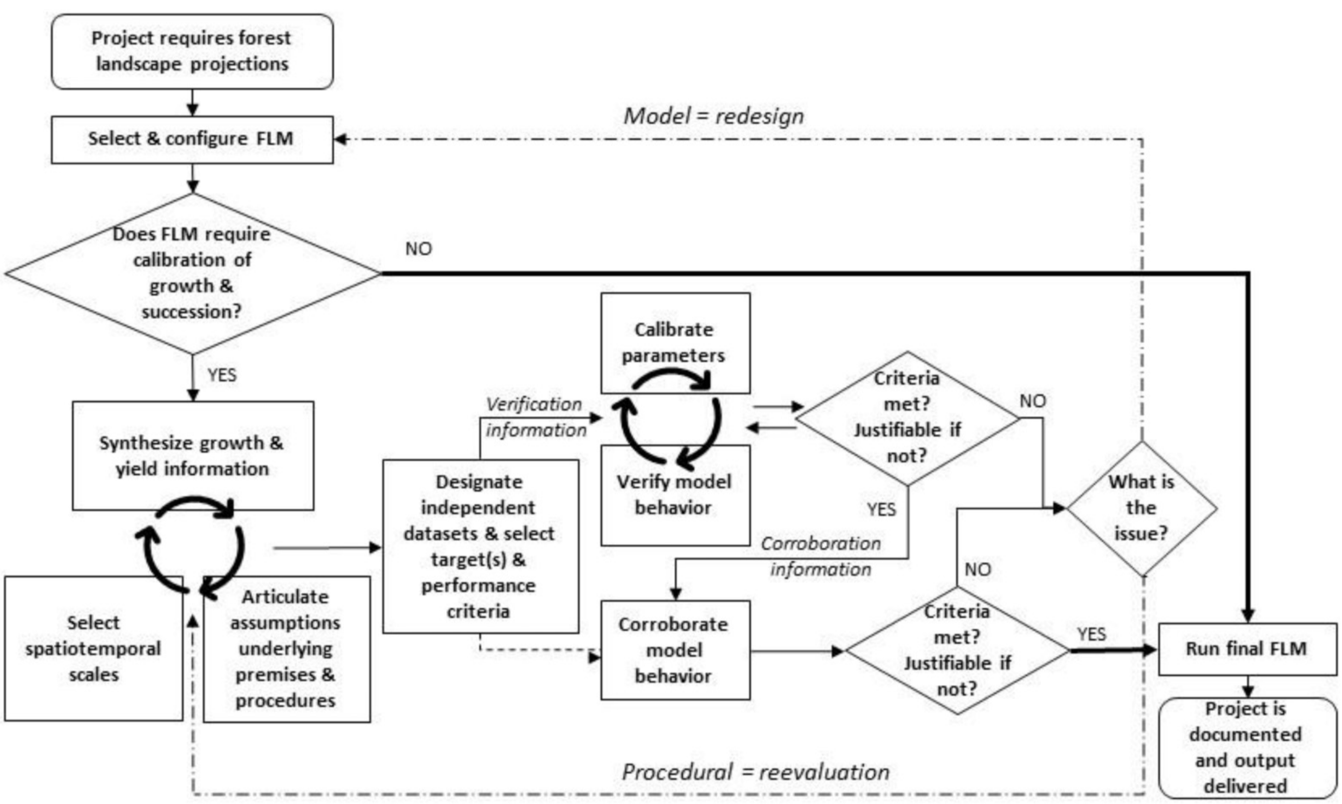
One important source of growth data comes from growth and yield studies that traditionally include wood volume by age and site quality within predominantly even-aged stands of a particular forest type or tree species (e.g., Sander 1977; Leary et al. 1993). Inventory plots are another common source of data that measure individual trees either once or periodically (aka, permanent plots) with plot sizes on the order of 0.04–0.07 ha. Permanent plots are typically resampled every 3–10 years, allowing estimates of individual tree growth, mortality, and variance (Dye et al. 2016). A broad inventory will capture variation in growth along natural gradients in climate, soils, elevation, and disturbance agents (Schmid et al. 2006) and can increase specificity (locational accuracy) when informing an FLM. Space-for-time substitutions can be used to estimate growth when plots provide diverse stand ages, assuming that soil, land-use, and other environmental conditions are similar (Pickett 1989; Rastetter 1996). Inventory data

Table 1. Crosswalk* of proposed best practices (Box 1) with evaluation and validation terms from existing, analogous reviews and frameworks.

Best calibration practice	Sargent (1984)	Rykiel (1996)	Schmolke et al. (2010)	Grimm et al. (2014)
1. Synthesize and evaluate information	Data validity	Data validation	Problem formulation and parameterization	Data evaluation
2. Articulate premises and assumptions	Multistage validation	Model context and multistage validation	Design and formulation	Conceptual model evaluation
3. Account for scale		Validation and scale		
4. Use independent datasets	Historical data and predictive validation	Historical data and predictive validation	Parameterization, calibration, verification, and validation	Data evaluation, model output verification, and model output corroboration
5. Choose targets and performance criteria	Operational validity	Performance criteria	Parameterization, calibration, verification, and validation	Model output verification, and model output corroboration
6. Modify influential parameters	Parameter variability—sensitivity analysis	Calibration and sensitivity analysis	Parameterization, calibration, verification, sensitivity analysis, results, and uncertainty analysis	Model output verification and model analysis
7. Verify and corroborate at different organization levels	*Validation techniques*			*Pattern-oriented modeling*
8. Allow for learning	*Testing during development*	*Iterative modeling cycle*	*Iterative modeling cycle*	*Iterative modeling cycle*
9. Document and deliver	Model documentation		TRACE documentation	TRACE documentation

*Links between terms are not always perfect; best practices can bridge multiple terms, each containing components of the best practice (see also fig. 2 in Grimm et al. 2014). Italicized terms indicate concepts more explicitly developed here, in the context of model application, than those from earlier reviews and frameworks.

Fig. 2. Best practice framework illustrated as an expansion of the model application cycle (Fig. 1B) and integrating best practices (Box 1) for evaludating the targeted growth within a forest landscape model (FLM). Solid lines represent the principal flow of procedures, the regular dashed line indicates a specific data flow, bold circular arrows represent tightly coupled iterations, and alternating dashed lines indicate higher level iterations (i.e., procedural feedbacks). Note that only a single positive response to the questions in the Criteria/Justifiable boxes is needed to proceed along the "yes" paths.



 Can. J. For. Res. 55: 1–19 (2025) | dx.doi.org/10.1139/cjfr-2024-0085

offer common and versatile targets for parameterizing FLMs, particularly where inventories are well established (Supplementary materials A–E[1]).

The growth data introduced above are not without limitations and trade-offs among data sources epitomize the complexity of the calibration problem. Growth and yield studies most directly related to the process of interest (i.e., tree species growth) are limited in scope (e.g., simplified species composition, unaffected by disturbance). Inventories are more representative of forest conditions, but individual tree species growth can be challenging to extract from such variability, and inventories often lack essential information such as tree age structure. Additionally, sampling density is often uneven across jurisdictions (Besnard et al. 2021), and repeated measurements can be expensive and therefore biased towards forest types that are common and/or of economic interest. Inventories often sample short durations, e.g., <20 years, and therefore provide limited information about long-term trends and rare events (see Rastetter 1996). Furthermore, few stands are older than about 100 years in much of the U.S. and Europe because of their land-use histories, limiting opportunities for chronosequences that capture the senescence of old trees. Consequently, we have substantially less data about growth within older forest stands (Gunn et al. 2014), despite the importance of individual tree mortality to stand biomass estimates (Dye et al. 2016) (Supplementary material C[1]). Although long-term experimental studies or intensively measured locations with infrastructure such as carbon flux towers can provide insight into processes underlying tree growth (e.g., Acker et al. 2002; Bormann and Likens 2012; Supplementary materials A and D[1]), they are limited in both number and scope.

Contrary to inventory data, tree-ring records can estimate annual growth retrospectively and, when available, add credibility to modeling results. They can complement plot data with information about productivity prior to, or between, monitoring years, be used for independent comparisons (Babst et al. 2014; DeRose et al. 2017), and be linked to climate patterns (Dye et al. 2016; Tei et al. 2017). Some tree-ring based studies capture mortality through dead and downed logs (Johnson et al. 1994). However, tree-ring studies are often limited to older trees and can thereby overlook important differences driven by microhabitats and competitive interactions among seedlings that influence patterns of forest growth (Babst et al. 2014; Nehrbass-Ahles et al. 2014; Foster et al. 2016).

Remote sensing represents another important information source (Coops 2015). Gross primary productivity (GPP) and net primary productivity (NPP) can each be estimated via the application of physiological principles to incoming and absorbed photosynthetically active radiation (Running et al. 2004), while foliar productivity can be related to leaf properties such as leaf area index (LAI) (e.g., Vose et al. 1994). GPP, NPP, and LAI are globally available from coarse-scale resolution (250–1000 m) platforms such as MODIS (Yu et al. 2018) and are becoming increasingly available over some regions via moderate-scale resolution (10–30 m) platforms such as Landsat and Sentinel (Robinson et al. 2018; Kang et al. 2021). Advantages of such forest productivity information include (1) continuous coverage across landscapes at resolutions consistent with that of most FLMs and (2) widespread availability for comparison with model output across the temporal extent of coverage. A disadvantage is the lack of context regarding the state of the system, i.e., tree ages, sizes, species composition, and disturbances underlying forest productivity at any given point in space or time. While other remote sensing products can provide such context (e.g., Wilson et al. 2012; Gao et al. 2020), the uncertainty involved when coupling separately produced remote sensing information is problematic. Consequently, the most accessible forest productivity information based on remote sensing has mostly been used for landscape model corroboration, rather than growth calibration per se (but see Maxwell et al. 2022).

Moderate or higher resolution remote sensing platforms that lack continuous coverage (or are not freely available) can estimate more detailed leaf characteristics with which to refine estimates of primary production (Ollinger and Smith 2005) and accurately map tree species composition (Likó et al. 2022). Dimensional analyses that estimate height, volume, biomass, and crown structure can be derived from moderate-to high-resolution platforms (Wolter et al. 2009; Rahimzadeh-Bajgiran et al. 2020), or high-resolution airborne laser scanners (Tompalski et al. 2016; Xu et al. 2020). Such structural data enable FLM calibration across key sources of environmental variability and across key internal determinants of observed forest growth patterns, but require considerable investment in time and resources and are therefore available across limited, although expanding, jurisdictions around the world (Fassnacht et al. 2024).

2.2. Forest growth models

Models of fine-scaled forest dynamics can serve as either alternatives or compliments to empirical growth data when evaludating local forest behavior in FLMs (Table 2). Pretzsch et al. (2015) categorized such models into three broad types: (1) empirical models (including charts and diagrams) based on statistical relationships derived from growth and yield studies and inventory data, (2) process-based models that simulate physiological processes affecting growth and how these are affected by the environment, and (3) hybrid models that couple empirical and process-based elements. Within this state space, as many as 10 modeling types can be defined according to fundamental concepts underlying their design, including stand structural relationships, horizontal and vertical positioning, tree physiology, ecosystem processes such as nutrient dynamics, and various combinations of these processes (Fabrika et al. 2018). Arguments for using process-based over empirical forest growth models are similar in kind to those applied to FLMs (Gustafson 2013). Empirical models, regardless of their level of sophistication, are limited by the range of conditions defined by their source data (Pretzsch et al. 2015). Nonetheless, there can be value in demonstrating consistency between the FLM outputs and empirical relationships documented for a given region (e.g., Supplementary materials A and C[1]). Process-based models can accommodate novel conditions such as changing climate, atmospheric CO_2, and community composition, but also require extensive parame-

Table 2. Overview of case studies as they relate to Best Practices (BP) of Box 1 and Fig. 2.

	Case study				
Best practice	A. Minnesota, USA	B. Minnesota, USA and Ontario, Canada	C. Fort Bragg, North Carolina, USA	D. New England, USA	E. North Carolina, USA
Forest landscape model selected and configured (Fig. 2)	LANDIS-II* PnET-Succession*	LANDIS-II Biomass Succession*	LANDIS-II NECN* and PnET-Succession	LANDIS-II PnET-Succession	LANDIS-II Forest Carbon Succession*
Synthesize and evaluate information for modeling forest growth (BP 1) and designate independent datasets (BP 4)	AmeriFlux tower† + FVS‡ (v§); FIA† (c§)	LINKAGES‡ and PnET-II‡ + published studies† (v); FIA (c)	FIA (v); published studies† (v)	FIA (v); published studies† (c)	FIA + FVS‡ + PnET-II (v); FIA (c)
Select appropriate biophysical stratification (s§) and scale (sc§) (BP 3)	climate, soil type (s); 0.81 ha cells, 120 years (sc)	climate, soil type, terrain (s); 1 ha cells, 100 years (sc)	climate, soil type (s); 1 ha cells, 100 years (sc)	climate, soil type (s); 6 ha cells, 100 years (sc)	ecological and geological zones (s); 2.25 ha cells, 26 years (sc)
Select targets (t§) and set performance and stopping thresholds (BP 5)	AET§ and C§ at flux site and biomass from FVS (t), qualitative based on premises (v); FIA (t), quantitative via reproducibility tests (c)	biomass (t), qualitative based on premises (v, c)	biomass (t), qualitative based on premises (v)	biomass (t), quantitative via variance tests (v); biomass (t), qualitative based on premises (c)	biomass (t), quantitative based on tests of means and variances (v, c)
Target influential parameters (p§), remaining within local empirical ranges (r§, BP 6)	shade and water tolerance, physiological (p); TRY plant trait database‖; FEIS‖ (r)	shade and water tolerance, physiological (p); silvics guide‖; published studies† (r)	physiological (p); silvics guide‖ (r)	Aber et al. (1995), Duveneck et al. (2017) (p); silvics guide‖ (r)	physiological (p) published studies†; gymnosperm database† (r)
Verify and corroborate calibration at different levels of organization (BP 7):	single sites (v, c)	single sites (v), landscape (c)	single sites (v)	landscape (v), single site (c)	single species and site (v), single site (c)
Biophysical	growth by soil type (v) and by drainage class (c)	growth by soil type, upland vs lowland (v)	growth within dominant soil type (v)	growth by site-specific soils (v)	growth by species and forest type (v, c)
Species competition; multiple state variables	two-species competitions; AET, C flux, biomass (v), biomass (c)	multiple species biomass dynamics (v); initial landscape species biomass (c)	biomass, decay rates of soil organic matter and wood, leaching (v)	biomass (v); multiple species competition (c)	biomass (v); biomass density distributions (c)
Different spatial and temporal scales	site-level (v, c); primary growth stages (v) and decadal (c)	site-level (v); landscape-scale (c)	site-level (v)	landscape (v), site-level (c), decadal	decadal (v)
Learn and improve models, where necessary (BP 8)	constrained growth (FVS); improved water balance (PnET-Succession)	not necessary	not necessary	not necessary	Added functionality on handling carbon pools by harvest prescriptions.
Document and deliver (BP 9)	in progress	in progress	Lucash et al. (2022)	Duveneck et al. (2017); MacLean et al. (2021)	Ling et al. (2020)

Note: The overarching BP is that the premises and assumptions underlying a study are explicit, i.e., BP 3 in Box 1. Further information is provided in each case study supplemental material (A–E[1]).

*Forest landscape models: Biomass Succession (Scheller and Mladenoff 2004); Forest Carbon Succession (Dymond et al. 2016); LANdscape DIsturbance and Succession (LANDIS-II; Scheller et al. 2007); Net Ecosystem Carbon and Nitrogen (NECN Succession; Scheller et al. 2011); Photosynthesis and EvapoTranspiration (PnET-Succession; de Bruijn et al. 2014; Gustafson et al. 2023*b*).

†Data and databases: AmeriFlux tower (Gough et al. 2023); Forest Inventory and Analysis (FIA; Gray et al. 2012); gymnosperm database (Earle 2016); published studies (Case study: [B.] Payandeh 1978; Schmidt and Carmean 1988; Pothier and Savard 1998; Carmean et al. 2001, 2006 [C.] Smith et al. 2006 [D.] Hollinger et al. 1999; Hadley and Schedlbauer 2002; Urbanski et al. 2007; Schuster et al. 2008; Battles et al. 2014; Eisen and Plotkin 2015 [E.] Carmean et al. 1989).

‡Forest growth models: Forest Vegetation Simulator (FVS; [A.] Crookston and Dixon 2005 [E.] FVS Staff 2008); LINKAGES (Post and Pastor 1996); Photosynthesis and EvapoTranspiration (PnET-II; Aber et al. 1992; Aber et al. 1995).

§Abbreviations: AET, Actual EvapoTranspiration; C, carbon; c, corroboration; p, parameters; r, empirical ranges; s, stratification; sc, scale; t, targets; v, verification.

‖Parameter databases: TRY plant trait database (Kattge et al. 2020); Fire Effects Information System (FEIS; Simmerman et al. 1998), silvics guides (Case study: [B–D.] Burns and Honkala 1990).

Can. J. For. Res. 55: 1–19 (2025) | dx.doi.org/10.1139/cjfr-2024-0085

terization, verification, and evaluation (Weiskittel et al. 2011; Pretzsch et al. 2015; Melo et al. 2019).

FLMs are designed to simulate competitive interactions among different tree species with different life history strategies, growth rates, sensitivity to environmental constraints, and climatic envelopes (Fig. 3). While many forest growth models have the capacity to simulate multiple species simultaneously, there are different levels of sophistication in the algorithms that simulate mixed species growth, ranging from simple weighted means of pure stand dynamics to spatially explicit competition among neighboring trees to behavior emerging from ecophysiological processes (Pretzsch et al. 2015). Our case studies focus on FLMs with a range of complexities within a common tree species cohort framework, placing them as intermediate in complexity within the Pretzsch et al. (2015) hierarchy, i.e., application of the mixing effects of multipliers with varying degrees of ecophysiology and/or ecosystem processes. This modeling domain provides important context for how growth models have traditionally been applied to parameterize or corroborate FLMs. For example, empirical growth and yield studies were often developed for even-aged monocultures or mixtures of species with similar physiology or life history strategies (Pretzsch et al. 2015; Shifley et al. 2017). While this would appear to be limiting, the simulation of monoculture stands, regardless of the degree of sophistication in the way a given model handles growth within mixed species stands, remains the most common application of forest growth models to parameterize FLMs (e.g., Boulanger et al. 2017). The underlying assumption when supporting models are applied in this way is that single-species growth will translate to realistic competition when simulating diverse, multi-aged, forested sites—requiring additional model verification, i.e., trust but verify (Supplemental materials A–E[1]). Projecting growth within mixed species stands and forests remains challenging and is an active area of model development (Pretzsch et al. 2015; Fabrika et al. 2018; Bravo et al. 2019). Nonetheless, opportunities remain to compare the growth dynamics of mixed species stands in FLMs to those simulated by sophisticated forest growth models more directly (Supplementary material D[1]).

Stand decline is another process that remains challenging for FLMs and forest growth models alike (Pretzsch et al. 2015). Stand decline has been modeled as a function of growth rate (Wyckoff and Clark 2002; Das and Stephenson 2015), resources and age (Franklin et al. 1987; Garman 2004), and stand density, increment thresholds, and relative size adjusted for shade-tolerant species (Dreyfus 2012). Modeling stand decline is often made difficult by limited knowledge about maximum longevity for many species, limited data about trees approaching their maximum possible age, and the difficulty of determining age in older trees. Differences in mortality algorithms can have larger effects than climate change (Irauschek et al. 2021) and can account for most of the variability in volume predictions (Stage and Renner 1988). Several of our case studies illustrate options for addressing uncertainty about tree species longevity (see Supplementary materials A–C[1]).

Disturbances and their interactions are often not explicitly accounted for in forest growth models, particularly empirical ones (Woods and Coates 2013; Glasby et al. 2019). For those growth models that represent disturbances (e.g., Vanclay 1991; Kangas 1999; Melo et al. 2019), the consequences, including effects from error propagation, are not fully understood. From the perspective of calibrating tree species growth for an FLM, it is important to understand the role of different disturbance agents as they affect empirical and modeled sources because some of those agents can be explicitly modeled within an FLM (e.g., Gustafson and Sturtevant 2013; Lucash et al. 2018), while others can be considered as background noise and are therefore an implicit constraint on observed or modeled growth.

Across our five case studies, we aim to help modelers increase model applicability and credibility by demonstrating a range of options for synthesizing growth information and allocating subsets to the assessment phases indicated in Fig. 2, via applications of procedural best practices summarized in the next section (Table 2, Supplementary materials A–E[1]). Each case study used inventory plot data in at least one assessment phase. We verified calibration of growth in FLMs against information from forest growth models in two of our case studies (see Supplementary materials A and C[1]), while in two others we applied meta-modeling techniques (Xu et al. 2012) to derive input parameters from a big-leaf model based on ecophysiology (see Supplementary materials B and E[1]).

3. Procedures

Following an evaluation of available fine-scaled information to support FLM parameterization, we recommend a set of interconnected assessment phases linked by feedback loops (Fig. 2) inherent to the iterative nature of model evaludation (Fig. 1). This workflow should increase efficiency, collaboration, and productivity. The following procedural phases represent most of the best practices (BPs) highlighted in Box 1: (1) articulation of assumptions and premises (BP 2), (2) accounting for spatiotemporal scales (BP 3), (3) designating datasets and setting performance criteria (BPs 4–5), (4) calibrating, verifying, and corroborating processes (BPs 6–7), (5) learning iteratively (BP 8), and (6) documenting procedures (BP 9).

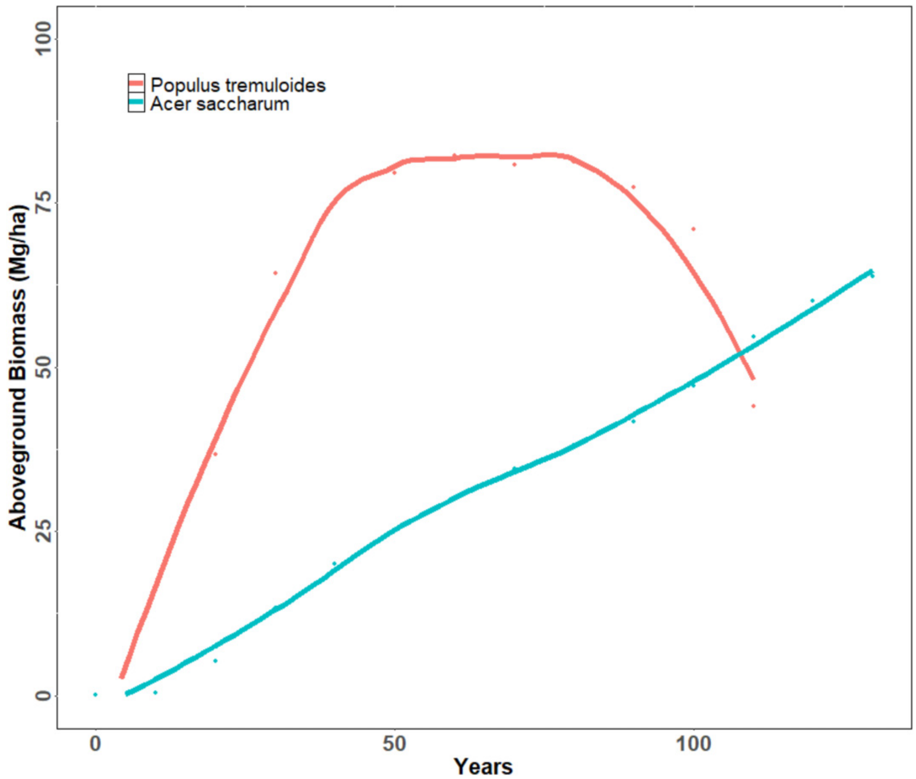
3.1. Articulate assumptions and premises (BP 2)

Models can be thought of as formal sets of assumptions and generalizations. Therefore, before using or calibrating a model, it is prudent to clearly articulate the assumptions and premises guiding the decisions for the applied procedures (Box 1; Fig. 2); doing so helps one to correctly calibrate an FLM and avoid inappropriate applications and interpretations (see Supplementary materials A–E[1]). Furthermore, explicit articulation of assumption and premises demonstrates deep understanding of the model and can be considered a component of the model analysis stage of evaludation (Fig. 1; Augusiak et al. 2014).

3.2. Account for spatiotemporal scales (BP 3)

Selection of spatiotemporal dimensions is fundamental to all phases of FLM development, parameterization, applica-

Fig. 3. Simulated growth of *Populus tremuloides* (quaking aspen), a fast-growing, shade-intolerant species, versus *Acer saccharum* (sugar maple), a slower growing, shade-tolerant species, by LANDIS-II PnET-Succession on a single site with a mesic soil type (very fine sandy loam) and constant climate, illustrating the verification of logical competitive interactions among tree species. Years (*x*-axis) is equivalent to cohort age. See Supplementary material A[1] for more information.



tion, and analysis (see Fritsch et al. 2020) because it is not possible to simultaneously optimize realism, precision, and generality in a tractable model, i.e., one dimension will always be compromised (Levins 1966). Hence, a recommended BP within the broader theme of data evaluation is to explicitly consider the scale of fine-scaled information and FLM application in the evaludation of growth patterns and processes (Box 1; Fig. 2). FLM simulation experiments have demonstrated that changing the spatiotemporal extents of analysis can impact the accuracy of response variables such as standing biomass and composition, with differences between coarse response variables often diminishing as spatial and temporal extents increase (Elkin et al. 2012; Temperli et al. 2013) (Supplementary material D[1]).

Like most ecological processes, forest growth is driven by processes that vary in both time and space—a phenomenon known as nonstationarity (Rollinson et al. 2021). Nonstationarity can emerge as a change in first order (mean) and/or second order (variance, covariance) statistical properties in the variable of interest (Rollinson et al. 2021), complicating the scaling of processes (e.g., Snell et al. 2014). The design of FLMs allows for nonstationarity in both space and time. Spatial factors such as soils, terrain, and climatic gradients provide physical templates underlying spatial variation in forest growth (Urban 2023). The sequence of vegetation initiation, growth, decline, and successional processes underlie temporal variation in forest growth. Disturbances interact with these processes in both space and time. Evaludation of spatiotemporal heterogeneity in growth can be challenging, and the process of reducing heterogeneity often necessitates simplifying assumptions within a given FLM. For example, many FLMs stratify the physical template as a compromise between approximation of the mean behavior for the landscape and the unique biophysical conditions present on individual cells (e.g., Scheller et al. 2007). Such stratification informs the aggregation of fine-scaled information used to parameterize these models.

Due to computational limitations, FLMs must optimize among spatial resolution (cell size), spatial extent (spatial coverage, number of cells), temporal resolution (time step), and temporal extent (duration). Under ideal circumstances, the fine-scaled information used for evaludation would align with the scale of application across these four dimensions. A more realistic goal is to match the scale of the fine-scaled information in as many dimensions as possible, to include scaling principles in the design of evaludation procedures, and to apply those principles to the interpretation of procedural results (see below).

Seeking parity in spatial scale between fine-scaled information and an FLM is a priority. Both the mean and the variance of growth must be considered. A common approach to growth calibration, for example, is to compare fine-scaled information to output from the simulation of a single FLM unit (typically a single cell or pixel) (De Bruijn et al. 2014; Suárez-

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Muñoz et al. 2021; see Section 3.4). In this case, if the inventory plots were measured at a finer spatial resolution than the FLM application, the variance in growth would not directly scale. Similarly, if there are relatively few plots, or if they sample a limited range of growing environments, or both, then the variance in growth from the reference data will not capture the full range of landscape variation. Thus, in addition to errors resulting from model uncertainty (Higgins et al. 2003), model output accuracy depends on scale discrepancies and sampling error (Melo et al. 2019). Examining the distribution of the mean and its variance, in both reference data and FLM output, can therefore be an informative verification step (Wang et al. 2014*b*; see Supplementary material C and E[1]), and interpretation can be required in instances where spatial scales differ substantively between the fine-scaled information and FLM application.

Temporal scaling considerations are similarly important. Several authors have emphasized the importance of evaluating changes across the full life cycle of trees (Song et al. 2013; Simons-Legaard et al. 2015; McKenzie et al. 2019). As noted in Section 2 (above), growth data are generally more restricted with respect to time, typically measuring growth across fully stocked conditions, but lacking information for stand initiation and senescence (Didion et al. 2009; Tinkham et al. 2018; Gray et al. 2023), processes that each affect species composition (Das and Stephenson 2015), yield (Franklin et al. 1987; Woods and Coates 2013), and long-term forest dynamics. Consequently, standing biomass within disturbed landscapes can be over- or underestimated if disturbance processes are not adequately captured (Simons-Legaard et al. 2015). Similarly, FLMs commonly simulate long durations (>30 years) to account for effects from ecological inertia when investigating the implications of alternative disturbance regimes or climate futures (Gustafson 2013; Serra-Diaz et al. 2018; MacLean et al. 2021). Long-term data are typically restricted in spatial extent (McKenzie and Perera 2015); consequently, FLMs are often evaluated at a single point in time (Petter et al. 2020) or over comparatively short time intervals (He et al. 2011). Given that any real landscape represents only one of many possible stochastic outcomes (He 2008), such evaluations can help establish plausibility, but cannot define the range of potential outcomes (Perera and Cui 2010; Petter et al. 2020). It is therefore ideal when existing information permits an assessment of how well the FLM tracks recent temporal trends. Additional challenges are presented when novel conditions are simulated. Climate change, for example, creates a moving target with large uncertainties (e.g., Maxwell et al. 2022), operating on time scales that have not been observed across the duration of available forest growth data.

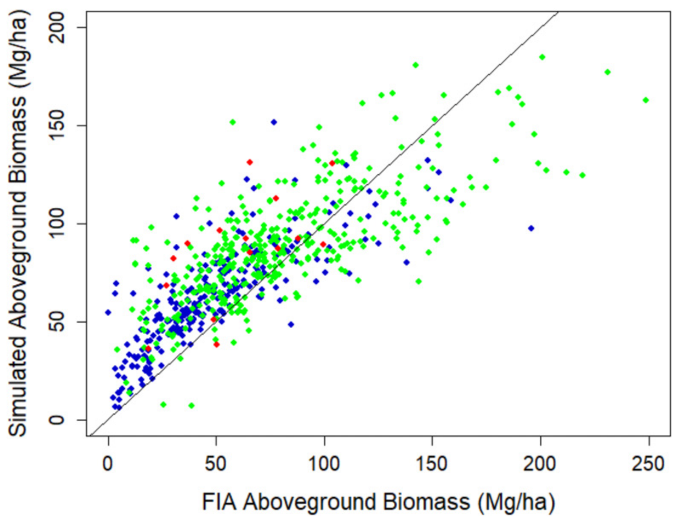
3.3. Designate datasets and set performance criteria (BPs 4, 5)

Selecting calibration targets and setting bounds of acceptable behavior (BP 5) are decisions that can benefit accountability and transparency. These decisions can be informed by calibrated forest growth models (Pokharel and Froese 2008; Petter et al. 2020; Bagdon et al. 2021), forest growth data, or some combination of the two. An alternative to plotting against time involves the assessment of stocks, e.g., the distribution of volume or biomass (see Thompson et al. 2011; Ling et al. 2020; Supplementary material E[1]). Derived calibration targets such as biomass, i.e., estimated from allometric equations, contain uncertainty that should be considered when evaluating fit (see Section 2). Whether one can allocate the fine-scaled information into independent datasets for model validation and corroboration (BP 4) will of course depend on information availability. Splitting a single dataset into training and test sets could be necessary.

Once calibration targets are selected, levels of congruence between FLM outputs and fine-scaled information can be assessed. Subjective, visual comparisons are common (see Boulanger et al. 2017; Seidel et al. 2018; Furniss et al. 2022; Supplementary materials A–C[1]), but statistical analyses can provide more objective criteria for determining calibration success (Mai 2023; Supplementary materials D–E[1]). Characteristics of the target information and simulation setup will largely determine which statistics are appropriate. Some are most useful when there are only single measurements at each point in time, i.e., without stochasticity or an error term. Summarizing at the landscape scale, where FLMs are most appropriate, can lead to such situations; working with a single site can present another (see Section 3.4 and Supplementary materials A and C[1]). Other methods can be useful when one has information about variance. Statistics that assess differences are most common, including goodness of fit (e.g., Garman 2004; De Bruijn et al. 2014; Wang et al. 2014*b*), root mean square error (RMSE), bias, Pearson's correlation coefficient (r), coefficient of determination (r^2), and the Nash–Sutcliffe modeling efficiency (Nash and Sutcliffe 1970). Reproducibility metrics that evaluate both the precision and accuracy of modeled versus reference data can also prove useful (Lin 1989; Fig. 4); standards from other fields (e.g., McBride 2005), however, could be too strict for comparably noisy ecological data (Sturtevant and Seagle 2004), a consideration for other metrics as well. Methods using variance information include equivalence testing (Robinson and Froese 2004; Blanco et al. 2007), regression (Fig. 5), and weighted least squares methods. Bayesian statistics are less common but increasingly used during model calibration (Smith et al. 2012; see Supplementary materials D and E[1]). Making the assumption that the reference target accurately represents truth will simplify assessments and allow for null hypothesis testing. Garman (2004), Ling et al. (2020), and Supplementary material E[1] each demonstrate such applications.

Care must be taken when applying and interpreting statistical metrics to evaluate model performance. It is important to consider that typical univariate statistics can indicate that a trivial difference is significant when there are thousands or millions of data points (Lin et al. 2013; Faber and Fonseca 2014)—a possibility with simulation projects. At large extents, spatial arrangements can also be evaluated. For example, the multiple-resolution method (Costanza 1989) can be used to compare FLM maps with remotely sensed data or predictive ecosystem maps (Garman 2004; Freitas et al. 2018). Stochasticity typically exists as a complicating factor for sta-

Fig. 4. Assessment of model output corroboration via reproducibility statistics (Lin 1989). Each circle represents a Forest Inventory and Analysis (FIA) plot, classified in 2006 as either hydric (blue), mesic (green), or xeric (red). Single cells were simulated for 10 years on very fine sandy loam that was the most common upland soil type in the study area and representative of mesic soil conditions. The concordance correlation coefficients (CCC) were larger when FIA plots were simulated on a suitable soil type, in this case mesic plots simulated on very fine sandy loam where the CCC = 0.90. Note that both hydric and xeric plots (CCC = 0.87 and 0.68, respectively) overestimated observed biomass when simulated on the mesic soil type. See Supplementary material A[1] for more information.



tistical comparisons (Shifley et al. 2008), however, applications of Monte Carlo simulations have been used to produce uncertainty intervals in individual tree modeling approaches that better reflect stochastic model components (Fortin et al. 2009).

The above metrics can also be used when assessing performance during model output corroboration which should use independent information to be most beneficial to credibility (BP 4; see Supplementary material D[1]). Splitting information for training and testing is a commonly applied approach when independent information is unavailable (see Supplementary material E[1]), but can lead to inflated performance estimates and autocorrelation issues. Because data are not available for assessing the performance of future projections, other approaches are needed. Wang et al. (2014*b*), for example, compared projections to stocking charts and stand density diagrams to corroborate the plausibility of outputs.

3.4. Calibrate, verify, and corroborate outputs (BPs 6, 7)

When the processes, rates, and patterns of a system are known, a model can be developed via a forward modeling approach in which parameters are developed based on the best available evidence, and mismatches with observed patterns can be used to learn about a system. However, fine-scaled information is generally too limited to parameterize forested landscapes with this forward modeling approach. The best available alternatives are either inverse modeling, where a model is developed (or in our case, calibrated; see Fig. 1) to match a known response pattern (effect), or pattern-oriented modeling, where a model is developed or calibrated to simultaneously match multiple characteristic system patterns (Kramer-Schadt et al. 2007). Different assessment phases for growth within an FLM (Fig. 2) typically include some form of inverse modeling, and ideally some form of pattern-oriented modeling (i.e., BP 7), as illustrated by our case studies (Table 2; Supplementary materials A–E[1]).

For parameters without a directly estimated value, calibration is often initiated with values estimated for another region or time, followed by iterative tuning of the most influential parameters (BP 6). Identification of the most influential parameters requires an understanding of model sensitivity, which is another aspect of the model analysis stage of evaludation (Fig. 1). Parameters without empirical bases and data limitations are two complicating factors (Simons-Legaard et al. 2015). FLMs are sometimes calibrated by simulating single-species growth on a typical site, with extreme events minimized by applying a recent, constant climate (see Supplementary materials A and B[1]). Young seedling biomass is seldom modeled, partly because calibration efforts tend to favor the growth of established trees. Targeting the optimal conditions estimated by a growth model (see Supplementary material A[1]) or curves derived from the literature (see Supplementary materials B and C[1]) are two examples of calibration based on model-to-model comparisons (Fig. 6; Rastetter 1996).

Adequate representation of heterogeneity is a factor when upscaling to increase accuracy and reduce uncertainty (Dye et al. 2016; see also Section 3.2). This is complicated by the fact that empirical data often have high variability that typically must be reduced to single values for model input. Finally, there is always a risk that different combinations of model parameter estimates can produce similar output, i.e., equifinality (Luo et al. 2009; Mai 2023). To further improve confidence, fine-scaled information can be cross-referenced and synthesized, expanding the temporal resolution of datasets (Fuchs et al. 2009), and thereby reducing instances of equifinality (Dietze et al. 2013).

A separate calibration to each environmental region is required by some FLMs (Fig. 7, panel A; Supplementary material B[1]) whereas others can be calibrated once, to optimal growing conditions, since internal processes will determine tree growth based on environmental conditions and stressors (Fig. 7, panel B; see Supplementary materials A, C, and D[1]). Determining whether relevant factors exhibit enough variation across the landscape to warrant stratification is part of balancing realism against complexity. A common approach to defining those parameters is to derive them from the outputs of more physiological growth models (e.g., Xu et al. 2012; Boulanger et al. 2017; Brecka et al. 2020; Supplementary materials B and E[1])—also known as meta-modeling (Urban et al. 1999) (e.g., Fig. 8).

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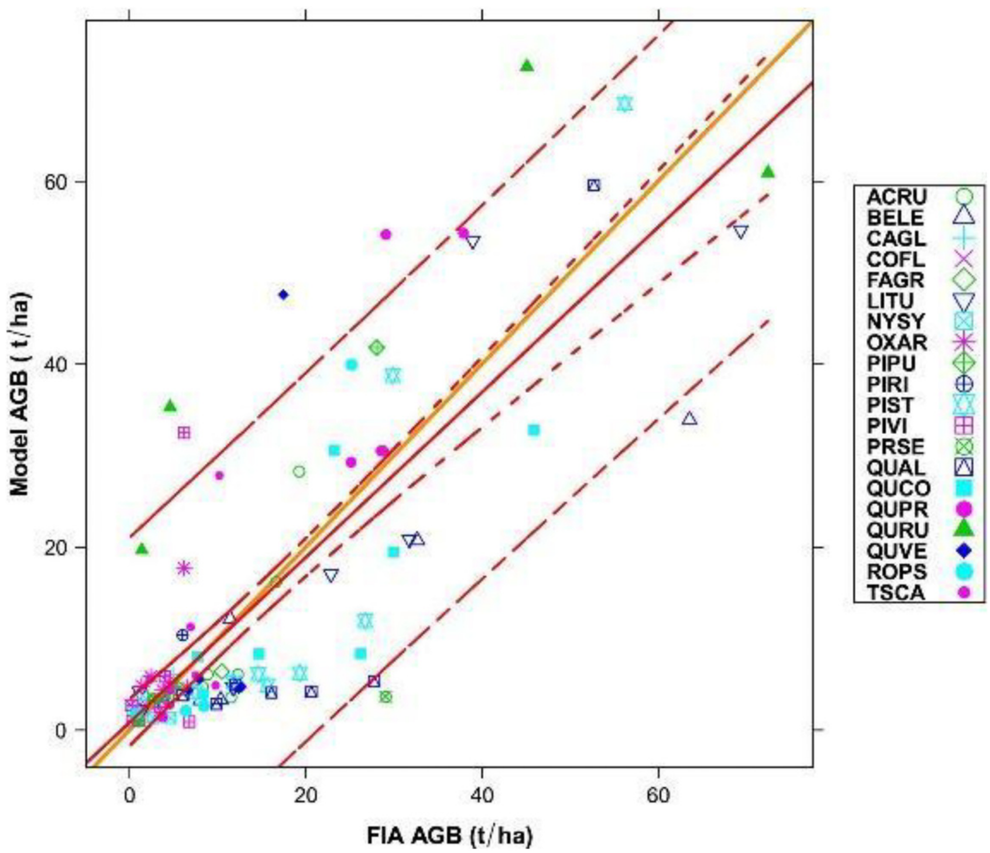
Fig. 5. Evaluation example from a study in North Carolina (Ling et al. 2020). The aboveground average biomass stocks for each dominant species are compared between the model output and Forest Inventory and Analysis (FIA) plot data. Compared are 109 FIA plots that were undisturbed between 2002 and 2010 and the output from the Forest Carbon Succession extension for LANDIS-II for the first 10 years of the simulation with no disturbances. Lines are the 1:1 relationship (orange), the linear regression of the model and the FIA data (solid red; slope = 0.90), 95% prediction interval (dashed red, outer pair), and the 95% confidence interval (dashed red, inner pair). The adjusted r-squared was 0.65, with a P-value < 0.01. For species abbreviations, see Ling et al. (2020). Figures used by permission, Wiley, USA. See Supplementary material E[1] for more information.

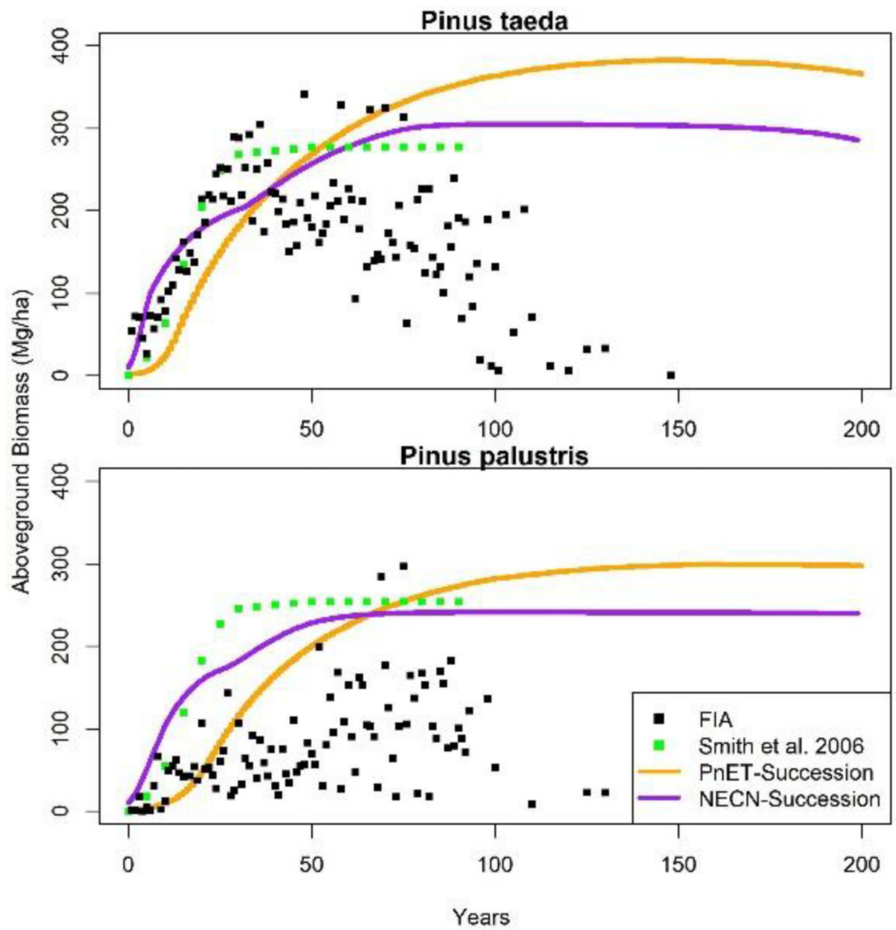


Including disturbances can result in more realistic simulations given that disturbances can have large, often species-specific, effects on successional trajectories and patterns (e.g., Hotta et al. 2021; Olson et al. 2021; Sturtevant and Fortin 2021). The disturbance processes that can be simulated vary among FLMs, but commonly include wildfire, timber harvesting, windthrow, and insect outbreaks. As highlighted in the previous section, a challenge in the use of plot data to inform FLMs is that such data often reflect poorly documented disturbance legacies (Glasby et al. 2019). The degree to which disturbance agents are problematic depends on the questions asked and degree to which such disturbance processes are explicitly simulated. For example, Supplementary material B[1] is focused on interactions between forest management and insect disturbance. If only plot data were used for calibration, then the legacies of past insect disturbances would affect the calibrated growth potential of insect host species and their competitive interactions. Applying a host-specific disturbance on top of those growth functions would effectively compound the impact of the insect artificially. It is therefore preferable in such cases to calibrate tree species according to their growth potential, and then use plot data for corroboration in a way that acknowledges or quantifies simulated disturbance processes (see Supplementary material B[1]).

4. Iterative learning (BP 8)

To better understand an FLM, i.e., model analysis, it is important to determine the reason for model output that fails to meet performance criteria. A discrepancy can be due to insufficient or incorrect model conceptualization and implementation, in which case the model's development should be revisited, and/or improper parameterization and operation, in which case the calibration procedures used for a model's application should be revisited (Figs. 1 and 2). Despite the best of intentions, not all issues in either model capabilities or supporting fine-scaled information can be foreseen. If the cumulative uncertainty exceeds the signal from the primary drivers of change under consideration, e.g., management or climate change, then the net result can be uninformative projections that cannot reliably distinguish among the drivers. However, if relative, e.g., rank order, outputs can be modeled with confidence and assumptions for relative changes across projected scenarios can be scientifically justified, one can

Fig. 6. Comparison of species biomass accumulation in Forest Inventory and Analysis (FIA) plot data, growth curves published in Smith et al. (2006), and as simulated by Net Ecosystem Carbon and Nitrogen (NECN Succession) and Photosynthesis and EvapoTranspiration (PnET) succession extensions for a study in Fort Bragg, North Carolina. The goal was to match the simulated maximum growth of the reference data. Note that the FIA data have many very young plots (<5 years old), especially for *Pinus taeda*. See Supplemental material C[1] for more information.



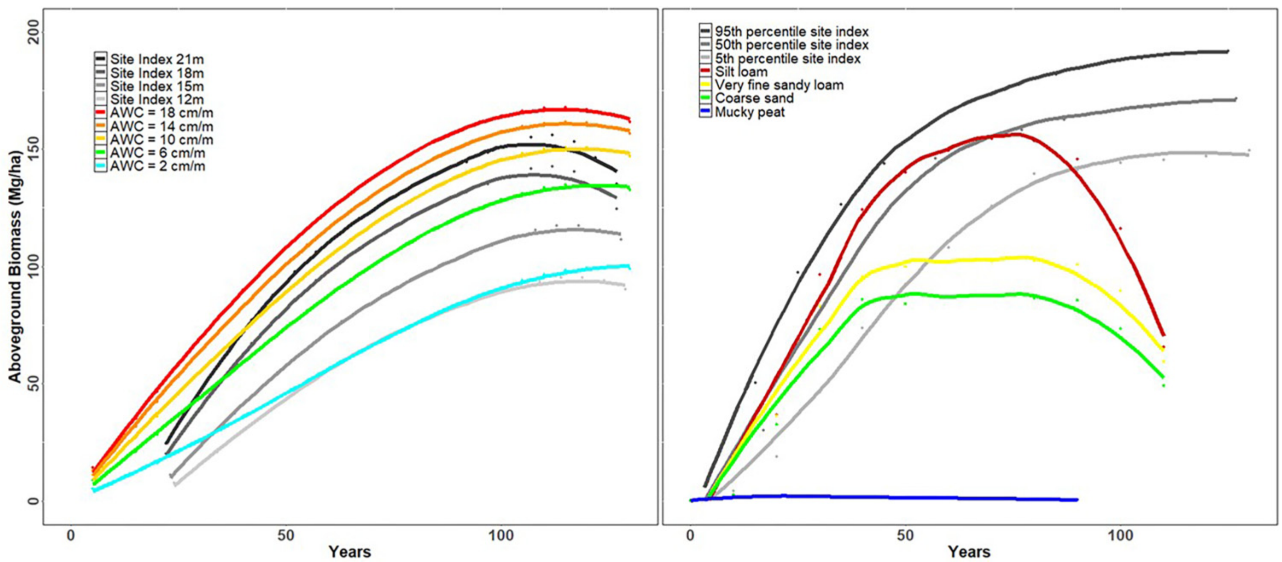
produce inference based on relative rankings despite the uncertainty (Gustafson et al. 2023*a*; Lucash et al. 2023). Furthermore, uncertainty itself is valuable information. Uncertainty can highlight which primary drivers limit our understanding of the future (e.g., Scheller et al. 2011; Maxwell et al. 2022). Uncertainty can also inform sensitivity analyses, highlighting important parameters for empirical studies or opportunities to improve model formulation (e.g., Petter et al. 2020).

Such realities partly underlie not only the iterative feedback loops in Fig. 2, but also situations in which performance criteria could not be met and were therefore justified by formal acknowledgement of limitations in either the model (e.g., Supplementary material B[1]), the supporting fine-scaled information (e.g., Supplementary material C[1]), or both (e.g., Supplementary material A[1]), and the degree to which such limitations affect interpretation of results. Appropriate documentation of analyses underlying model improvements: (1) demonstrates due diligence in model evaludation, (2) builds confidence in model results, and (3) informs and educates other modelers. During the calibration and evaludation of multiple studies, for example, several improvements to the PnET-Succession extension of the LANDIS-II model were identified, coded, and tested (e.g., Gustafson et al. 2023*a*), resulting in a new version that was documented as a formal publication (Gustafson et al. 2023*b*).

5. Procedural documentation (BP 9)

Research that relies on model application cannot be considered useful or complete until it is adequately documented, i.e., replication is feasible, and appropriate interpretation is conducted. Documentation of methods should include assumptions and premises as well as procedures for generating initial conditions, estimating parameters, and conducting accuracy assessments (e.g., Supplementary materials A–E[1]). The most obvious spot for such documentation is the methods section of peer-reviewed articles and technical reports; however, the detail required for full reproducibility generally exceeds journal length constraints. There is therefore an increasing trend of including more detail in the form of supplementary journal materials and as documentation embedded within code and model input files made available in public repositories (e.g., Lucash et al. 2023; Robbins et al. 2024). Articulating justifications and/or explanations for

Fig. 7. Site-level growth curves from Forest Landscape Models (FLM), following calibration to the targeted forest growth information (grayscale dots and lines). Panel A: The Biomass Succession extension of LANDIS-II was calibrated to each *Betula papyrifera* curve representing a range in tree species productivity that resulted from input parameters generated via meta-modeling with the PnET-II model (see Supplementary material B[1]). Species longevity and decline parameters were calibrated to match decline from empirical growth and yield curves from Quebec. Panel B: The PnET-Succession extension of LANDIS-II was calibrated to model output representing growth under the most favorable soil water availability and climate within the study area. In this case, the range in productivity for *Populus tremuloides* emerged from internal responses to varying water availability across different soil types (grayscale dots and lines). Species longevity and decline parameters were calibrated to be consistent with a literature review on stand break-up and longevity (J. Du Plissis, unpublished analyses). FLM models and growth information sources are defined and cited in Table 2. Years (*x*-axis) are equivalent to cohort age. See Supplementary materials A and B[1] for more information.

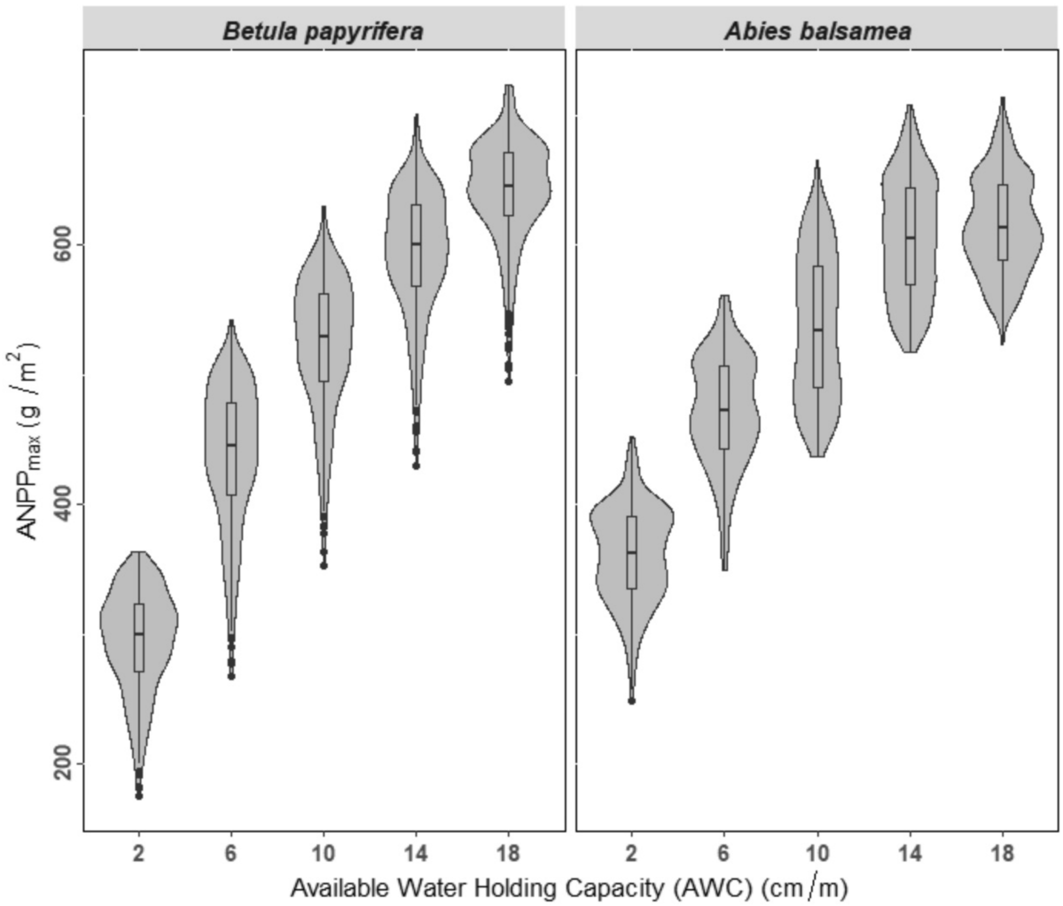


unfulfilled performance criteria could be useful for future applications of the model and suggest areas for additional data collection or model development. Clear articulation of the strengths and limitations of the model application is crucial for interpretation of the results.

6. Summary

A successfully completed calibration comprises many decisions that are, in part, project dependent. Our best practice guidelines are therefore broad and offer an array of options for many of the steps involved. Calibration issues are not unique to FLMs; however, due to factors such as succession, interdependent parameters, and stochasticity inherent to the many interacting external drivers, these steps can be difficult to complete for an FLM (Shifley et al. 2017). Many FLM applications use fine-scaled information, both empirical data and models, to calibrate the growth functions of FLMs. Here, we outlined important challenges for calibration, including issues of scale, trade-offs between empirical and process-based modeling, uncertainty regarding patterns of stand decline, undocumented disturbances, and extrapolation of processes across tree life stages. Our case study examples (Supplementary materials A–E[1]) include a diversity of FLM designs centered on the tree-species, age-cohort structure applied to landscapes across North America to illustrate how to apply our framework of best practices when using forest growth data and models to inform FLMs (see Box 1 and Fig. 2). Despite the importance of growth data, external reviews of many such government-supported systems have identified the need for additional and ongoing funding to support, maintain, and improve these systems (Society of American Foresters 2000; Bourgeois et al. 2018; Fassnacht et al. 2024). Also, in many parts of the world, data quantity and/or quality is poor (Matthews and Grainger 2002), causing the use of FLMs to be concentrated in the U.S., Canada, and Western Europe where inventory and species-parameter data exist. The accumulation of growth information can promote numerous opportunities and advancements such as increased automation (see Fer et al. 2021) and performance assessments that target successional processes (see Boulanger et al. 2017) and/or the most important environmental drivers (see Nadal-Sala et al. 2021). The topics we discussed and the details provided are not comprehensive, and thus our work is not designed to be a recipe book. In fact, each of the case studies differs in their strengths and weaknesses. Our goal was to overview many approaches that modelers use to parameterize and evaluate FLM behavior with respect to tree and forest growth, including competition, and place them within a generalized framework to encourage their adoption in future applications. Moving forward, we challenge others to utilize the best practices provided in Box 1 as well as the case studies summarized in Table 2 (see Supplementary materials A–E[1]) and further develop transparent methods

Fig. 8. Example meta-modeling approach using a more detailed model to derive tree species growth parameters for a forest landscape model. In this case, maximum annual net primary productivity ($ANPP_{max}$) was derived from the PnET-II model across a gradient in both soil available water-holding capacity (AWC) and climate (indicated by the distributions of $ANPP_{max}$ within AWC classes). Note the greater sensitivity of *Betula papyrifera* relative to *Abies balsamea* to variation in AWC. See Supplementary material B[1] for more information.



and reporting templates, thereby strengthening the validity and credibility of projections of forest change (Scheller 2018).

Acknowledgements

Dominic Cyr, Flora Krivak-Tetley, John Du Plissis, and four anonymous reviewers suggested edits and clarifications that greatly improved our manuscript. We further thank Jeffrey Suvada for his assistance with figure creation.

Article information

History dates

Received: 26 March 2024
Accepted: 13 August 2024
Accepted manuscript online: 23 August 2024
Version of record online: 25 November 2024

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

Funding information

This research was partly funded by the Great Lakes Restoration Initiative (GLRI, Focus Area 5; Project Template #936: Planning informed by alternative future watershed ecosystem services), NSF Grant No. DEB-LTER-18-32210, and the Bipartisan Infrastructure Law.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2024-0085.

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