Toward improved uncertainty quantification in predictions of forest dynamics: A dynamical model of forest change

Malcolm Itter[1] and Andrew O. Finley[2,3]

[1]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA, USA
[2]Department of Forestry, Michigan State University, East Lansing, MI, USA
[3]Department of Statistics and Probability, Michigan State University, East Lansing, MI, USA

Abstract

Models of forest dynamics are an important tool to understand and predict forest responses to global change. Despite recent model development, predictions of forest dynamics under global change remain highly variable reflecting uncertainty in future conditions, forest demographic processes, and the data used to parameterize and validate models. Quantifying this uncertainty and accounting for it when making adaptive management decisions is critical to our ability to conserve forest ecosystems in the face of rapidly changing conditions. Dynamical spatio-temporal models (DSTMs) are a particularly powerful tool in this setting given they quantify and partition uncertainty in demographic models and noisy forest observations, propagate uncertainty to predictions of forest dynamics, and support refinement of predictions based on new data and improved ecological understanding. A major challenge to the application of DSTMs in applied forest ecology has been the lack of a scalable, theoretical model of forest dynamics that generates predictions at the stand level—the scale at which management decisions are made. We address this challenge by integrating a matrix projection model motivated by the well-known McKendrick-von Foerster partial differential equation for size-structured population dynamics within a Bayesian hierarchical DSTM informed by continuous forest inventory data. The model provides probabilistic predictions of species-specific demographic rates and changes in the size-species distribution over time. The model is applied to predict long-term dynamics (60+ years) within the Penobscot Experimental Forest in Maine, USA, quantifying and partitioning uncertainty in inventory observations, process-based predictions, and model parameters for nine Acadian Forest species. We find that uncertainty in inventory observations drives variability in predictions for most species and limits the inclusion of ecological detail within the DSTM. We conclude with a discussion of how DSTMs can be used to reduce uncertainty in predictions of forest dynamics under global change through informed model refinement and the assimilation of multiple forest data sources.

Introduction

Models of forest dynamics (FDMs) have a long history in applied forest ecology where they provide predictions of forest demography, composition, structure, and function over time and space (Bugmann, 2001). They are applied in a range of settings including to assess alternative management strategies (under the broad heading of growth and yield modeling; Pretzsch, 2009), to test mechanisms of species co-existence (Falster et al., 2017), and to predict complex biogeochemical processes at large spatial scales as part of dynamic global vegetation models (Fisher et al., 2018). Contemporary FDMs are also an important adaptive management tool informing actions to promote ecosystem resilience and maintain valuable ecosystem functions under rapidly changing conditions (McDowell et al., 2020).

Despite recent advances in FDMs, predictions of forest responses to global change remain uncertain (Maréchaux et al., 2021). While contemporary models are generally consistent in their approximation of historic forest patterns, predictions of forest responses to global change vary widely among models (Fisher et al., 2010; Bugmann et al., 2019). This variation is driven by uncertainty in future conditions including altered climate and disturbance regimes, imperfect and variable representation of the demographic processes underlying forest dynamics, and noisy observations of forests under novel conditions (Bugmann and Seidl, 2022).

Quantifying the uncertainty affecting predictions of forest dynamics and accounting for it when making adaptive management decisions is critical to our ability to conserve forest ecosystems and sustain the myriad services they provide (Messier et al., 2016). Yet, as we demonstrate here, current approaches to model forest dynamics make it challenging to quantify and partition different sources of uncertainty in FDMs and propagate them to predictions of future forest states. In particular, the size and complexity of FDMs makes them difficult to integrate within statistical frameworks that formally compare ecological models and data while quantifying the respective uncertainty in each (Dietze et al., 2018). Here we review sources of uncertainty affecting predictions of forest dynamics along with current approaches to quantify them. We then present a scalable, dynamical statistical model that allows for quantification, partitioning, and propagation of uncertainty in predictions of forest dynamics across space and time.

Uncertainty in predictions of forest dynamics

Uncertainty in predictions of forest dynamics stems from multiple sources including the data used to parameterize and drive FDMs (observation uncertainty), the functions used to approximate the ecological processes underlying forest dynamics within FDMs (process uncertainty), and unknown model parameters that must be estimated in order to generate predictions (parameter uncertainty; Van Oijen, 2017). Observation uncertainty reflects the fact that the state of forest ecosystems and the factors that drive forest dynamics (e.g., disturbance, climate) are never observed perfectly. Process uncertainty reflects incomplete understanding of the complex processes underlying forest dynamics and accounts for potential model misspecification. Lastly, uncertainty in model parameters reflects their imperfect estimation based on noisy data.

Ideally, FDMs would provide predictions of forest dynamics that reflect all of the uncertainty sources described above. In practice, however, the structure of FDMs including multiple non-linear demographic functions with potentially correlated parameters along with non-Gaussian observations make it challenging to quantify and propagate uncertainty to predictions of forest dynamics (Wilson et al., 2019). The demographic functions included in FDMs are often parameterized in-

dependently for each demographic process and species furthering the challenge of uncertainty quantification. Given these challenges, it is common to utilize point predictions when modeling forest dynamics, under which a single predicted value is generated representing the best guess of the future of a forest ecosystem. A simple example of point prediction is to fix FDM parameters at maximum likelihood estimates and generate a single prediction approximating the mean of the future state of the forest. Point predictions do not reflect uncertainty in the future state of forest ecosystems as there is no variability in predicted values (Gneiting, 2011).

The alternative to point prediction is probabilistic prediction, under which a probability distribution is generated for each predicted value reflecting uncertainty in future forest states (Gneiting and Katzfuss, 2014). The generated probability distribution provides a measure of variability in predicted values (Dietze, 2017). In general, it is not possible to solve for the variance in predictions of forest dynamics directly given the complex structure of FDMs. Instead, probabilistic predictions of forest dynamics are generated numerically through techniques such as bootstrapping and Monte Carlo simulation (Van Oijen, 2017). These techniques are computationally demanding and require estimates of uncertainty for one or more of the sources described above (observation, process, parameters) and as a result are less commonly applied.

When probabilistic prediction is applied, uncertainty quantification is often limited to parameter uncertainty perhaps because it is more straightforward to quantify than other types. To account for parameter uncertainty in predictions of forest dynamics, FDM parameters are sampled conditional on respective variance estimates and used to generate a distribution of predicted future states reflecting uncertainty in model parameters—an ensemble forecast (Fisher et al., 2010). Accounting for parameter uncertainty is more straightforward if forest dynamics are modeled using a Bayesian approach given that a posterior predictive distribution exists for predicted forest states that integrates over the uncertainty in model parameters propagating it to predictions (Hartig et al., 2012). There are few examples of Bayesian FDMs under which all model parameters are estimated jointly allowing for probabilistic prediction reflecting parameter uncertainty (Purves et al., 2008; Wilson et al., 2019). Instead, demographic sub-models are often fit independently under Bayesian approaches, again necessitating an ensemble forecast to account for uncertainty in model parameters (Myllymäki et al., 2024). In some cases, uncertainty in future drivers of forest dynamics (e.g., climate, disturbance) are incorporated into probabilistic predictions (Spadavecchia et al., 2011). This is particularly challenging as it requires a probabilistic model for future scenarios. In lieu of such a probabilistic model, forest dynamics are sometimes predicted under a set of scenarios reflecting a non-probabilistic range of future conditions (Thom et al., 2017).

Other approaches to quantify uncertainty in predictions of forest dynamics include model inter-comparisons under which a selection of FDMs are used to make predictions of forest ecosystem change given a shared initial condition (Bugmann et al., 2019; Díaz-Yáñez et al., 2024). These inter-comparisons provide a measure of process uncertainty in FDMs, specifically the variable representation of the processes underlying forest dynamics. However, without performing some form of model averaging, these approaches do not allow for the propagation of process uncertainty to predictions. Further, to the extent that inter-comparisons utilize point rather than probabilistic predictions to compare FDMs, they do not account for the varying levels of uncertainty among models.

Dynamical statistical models

An alternative approach to quantify and propagate uncertainty in predictions of forest dynamics is to apply a dynamical statistical model. These models pair a process model driving changes in a system over space and time with one or more data models that account for uncertainty in observations within a broader probabilistic framework. In the current context, an FDM represents the process model providing predictions of the state of forest ecosystems over space and time. These predictions are subject to an explicit process error term that reflects uncertainty in the mathematical representation of forest dynamics. Predictions are informed by observations of the state of forest ecosystems at select times and locations. These observations are imperfect and variable, and are subject to an explicit observation error term. Conceptually, forest observations are generated conditional on the latent (true, unobserved) state of the forest ecosystem (the data generating mechanism) plus some observation error. Hereafter, we refer to these models as dynamical spatio-temporal models (DSTMs) noting that in some contexts they are also referred to as state-space models, although the latter do not generally allow for error in the process (Wikle and Hooten, 2010). When implemented as part of a broader Bayesian hierarchical framework, DSTMs incorporate parameter models allowing for the quantification of parameter uncertainty in addition to the process and observation uncertainty already described. In the context of modeling forest dynamics, Bayesian DSTMs generate probabilistic predictions of future forest states that reflect and allow for partitioning of uncertainty in data, models, and parameters.

Despite the capacity of Bayesian DSTMs to quantify and reduce uncertainty in predictions of dynamic ecological processes (Laubmeier et al., 2020), there has been limited application of such models to predict forest dynamics over space and time. Relevant examples include models to predict individual tree demography (Clark et al., 2010, 2011), and to predict changes in the size distribution of forest populations over time using an integral projection process model (Ghosh et al., 2012). An important factor contributing to the limited application of Bayesian DSTMs to model forest dynamics is the scale and complexity of modern FDMs. As previously noted, these models are computationally demanding, utilizing a number of non-linear functions to approximate demographic processes often operating at the scale of individual trees. Integrating these complex models into Markov chain Monte Carlo (MCMC) routines commonly used to fit Bayesian DSTMs is generally intractable particularly over large spatio-temporal domains. Recent research has focused on the use of statistical emulators to reduce this computational challenge while still allowing for improved uncertainty quantification (Fer et al., 2018; Raiho et al., 2021).

An alternative approach to overcome the computational challenges of modeling complex spatio-temporal processes is to utilize low-dimensional model parameterizations motivated by process-based models within a broader Bayesian hierarchical framework (Wikle and Hooten, 2010). This approach relates to seminal applications of DSTMs in ecology (Wikle, 2003; Clark and Bjørnstad, 2004) and relies on conditioning facilitated by a hierarchical model structure to simplify complex ecological processes into component parts that are easier to model. The goal of the current study is to apply this approach to generate predictions of forest dynamics that reflect the different sources of uncertainty described above at a scale that allows such uncertainty to be accounted for in adaptive management decisions.

The importance of scale

The scale at which forest dynamics are modeled is a key consideration in developing a computationally efficient DSTM. While individual-based approaches are common in current FDMs (Shugart et al., 2018), they greatly increase model dimensionality and make it difficult to scale models across multiple locations. The alternative is to approximate forest dynamics using stand-scale models, which are more computationally feasible to integrate within DSTMs given they generate population-level predictions (e.g., trees per hectare, basal area per hectare).

There are a number of reasons to prefer stand-scale models if the goal is to use predictions of forest dynamics to inform adaptive management. The stand is the fundamental management unit and, despite its operational rather than ecological origins, remains the scale at which adaptive management decisions are made (O'Hara and Nagel, 2013). The stand is also the scale at which forest resilience and adaptability to global change are most often considered (Clark et al., 2016). Aligning model predictions with adaptive management outcomes is important both to inform management decisions (accounting for the uncertainty in predictions), but also to maximize the benefit of new information gained through adaptive management experiments consistent with an iterative, near-term forecasting approach (Dietze et al., 2018).

A key challenge under stand-scale models is approximating the ecological complexity found in individual-based models, in particular, the competitive growing environment affecting forest demographic rates (Pacala and Deutschman, 1995). One way to do this is through a cohort-based approach which groups individual trees by species, size, or physiological traits into cohorts within which individuals are assumed to have the same mean demographic rates (De Roos, 1997). Despite this strong assumption, cohort-based approaches have been shown to well approximate the predictions of complex, individual-based FDMs (Strigul et al., 2008), and are applied in a wide range of dynamic global vegetation models (Fisher et al., 2018). The simplifying assumption of cohort-based models further aligns with forest management where decisions are made at a population-level, accounting for the differences in demographic rates driven by species, size, and crown class (a measure of tree competitive status; Ashton and Kelty, 2018). Consideration of individual variability comes later during the implementation of management interventions (e.g., marking individuals for removal).

Cohort-based approaches to model forest dynamics connect to theoretical models of structured population dynamics (where structure may refer to species, size, and/or traits). Under qualifying assumptions, cohort-based models of forest dynamics can be expressed as the well-known McKendrick-von Foerster partial differential equation (hereafter, "MvF PDE"; De Roos, 1997). Models of forest dynamics based on the MvF PDE have been used in a range of studies exploring the successional niches of species and plant functional types (Kohyama, 1993; Hurtt et al., 1998; Moorcroft et al., 2001; Strigul et al., 2008; Falster et al., 2011, 2017). In the context of the current study, the MvF PDE provides a computationally efficient, theoretical model of forest dynamics that can be integrated within a Bayesian DSTM.

Materials and methods

Here we develop a Bayesian hierarchical DSTM for forest dynamics based on the MvF PDE informed by continuous forest inventory data. The goal of the model is to provide near-term predictions (years to decades) of the state of forest ecosystems driven by stand-scale forest dynamics that can be used to inform adaptive management. The model is defined to predict forest dynamics

within individual stands over time (i.e., it is a dynamical temporal model), providing a proof-of-concept of uncertainty quantification, data integration, and probabilistic prediction in models of forest dynamics. We demonstrate the capacity of the model to approximate complex forest dynamics while accounting for different sources of uncertainty in predictions through its application to long-term data from the Penobscot Experimental Forest.

Continuous forest inventory data

We construct our Bayesian DSTM using continuous forest inventory (CFI) data because of its broad spatio-temporal availability, its role as a foundational data type in forestry, and its history as a primary data source in FDMs. CFI refers to the periodic re-measurement of a network of permanent sample plots providing observations of forest composition, size, and structure over time and space that can be used to inform FDMs. Permanent sample plots share a common structure with fixed or variable radius plots used to measure overstory trees and, sometimes, small fixed area subplots to observe seedlings and saplings. Large-scale CFI networks such as the USDA Forest Service Forest Inventory and Analysis (FIA) program are well-known examples, but regional- and state-level networks and long-term observations from historic experimental forests provide additional CFI data often with greater spatio-temporal resolution.

Under current approaches to modeling forest dynamics, CFI data are used to construct estimates of forest demographic rates over fixed time intervals corresponding to the number of years between remeasurements. Estimates of demographic rates are then pooled for a regional selection of plots and used to parameterize FDMs (Purves et al., 2008). Time- and location-specific information such as the current state of the forest ecosystem and local drivers including physiography, weather, and disturbance are used as further inputs to the model, but otherwise data are pooled across time and space (but see Liang and Zhou, 2010, for a counter example). CFI data may also be used to define initial conditions for predictions of future forest states applying previously parameterized FDMs (Didion et al., 2009).

Under the Bayesian dynamical model defined here, CFI data are treated as repeat observations of forest ecosystem states over time and space. Within a given location, forest dynamics are modeled as a formal time series using a process-based FDM to predict the temporal evolution of the forest ecosystem (Fig. 1). CFI data are observed conditional on the modeled state of the system at different time points. The dynamical model generates predictions of the forest ecosystem state regardless of whether inventory observations are available to inform it. An immediate benefit of this approach is its ability to accommodate missing data (i.e., non-inventory years) and irregular inventory intervals without having to assume equal demographic rates between remeasurements. There is no temporal differencing applied to estimate demographic rates in order to parameterize models. Instead, demographic parameters are estimated directly based on CFI observations over time and space (sometimes referred to as inverse or Bayesian calibration; Van Oijen et al., 2005).

Dynamical model of forest change

The MvF PDE provides the theoretical basis for the process of forest dynamics within our dynamical model. The MvF PDE describes changes in the density of individuals of a given species and size (and/or trait value) over time. Directly applying the MvF PDE as the process model within a Bayesian DSTM requires numerically solving the PDE as part of a broader MCMC routine used to sample from the joint posterior distribution. While numerical approximations to PDEs are often used as process models within Bayesian DSTMs (Wikle and Hooten, 2010), we prefer to utilize

a matrix projection model to predict forest dynamics motivated by the discretization of the MvF PDE in size and time. Specifically, we model changes in the species-specific density of trees in specified size classes over time (i.e., the size-species distribution).

Matrix projection models refer to a diverse class of population models in which discrete age, size, physiological trait, or life history stage define cohorts used to predict population dynamics in discrete time (Caswell, 2001). When applied in the context of forest dynamics with discrete size classes defined by diameter at breast height (DBH), these models represent a natural extension and formalization of size-class models that have been used for over a century to predict stand-level growth and yield under alternative management scenarios (Weiskittel et al., 2011). Our use of a matrix projection model relates to maximizing the dynamical model's applicability to CFI data. While most contemporary CFI data include continuous observations of tree diameter as the primary measure of size, tally data that record the number of trees within specified diameter classes remain common, particularly in historic inventories. A matrix projection model allows us to make use of all forest inventory observations regardless of whether size-class or continuous size observations are available. Further, as we detail in the Discussion, we expect the matrix projection model to yield similar predictions to alternative approaches that model size continuously (e.g., integral projection models or direct application of the MvF PDE).

We utilize a Bayesian hierarchical approach (Fig. 1) to construct our dynamical model defined by separate data, process, and parameter models (Berliner, 1996).

Data model

We define our data model to work with counts of individual trees by species and DBH class within fixed radius CFI plots. Throughout, we utilize i to denote DBH classes ($i = 1, \ldots, k$), j to denote species ($j = 1, \ldots, m$), and t to denote time defined in years ($t = 1, \ldots, T$). The outcome variable $y_{ij}(t)$ denotes tree counts in DBH class i from species j in year t. DBH class counts are modeled using a Poisson distribution,

$$y_{ij}(t)|\lambda_{ij}(t) \sim \text{Poisson}(|A|\lambda_{ij}(t)) \tag{1}$$

where $|A|$ is the size of the plot expressed in hectares and $\lambda_{ij}(t)$ is a rate parameter defining the latent (unobserved) density of trees per hectare in DBH class i from species j in year t. Here $|A|$ is defined for a fixed radius plot in which all trees have the same inclusion probability regardless of size. In the case of variable radius plot data wherein the inclusion probability is proportional to DBH, each DBH class would have its own unique plot area ($|A| \rightarrow |A|_i$).

Variability in plot-level counts around the latent stem density is captured through the Poisson variance equal to its mean ($|A|\lambda_{ij}(t)$). When replicate plot data are available from the same stand, as is often the case with CFI data, the Poisson counts may be overdispersed. In the case of overdispersion, we incorporate a multiplicative observation error term, $\epsilon_{ij}(t)$, such that the conditional distribution for diameter class counts is given by,

$$y_{ij}(t)|\lambda_{ij}(t), \epsilon_{ij}(t) \sim \text{Poisson}(|A|\lambda_{ij}(t)\epsilon_{ij}(t)) \tag{2}$$

where $\epsilon_{ij}(t)$ is constrained to be positive. Common choices to model the error term include log normal or Gamma distributions (Kéry and Royle, 2015). Here we model the error term using a Gamma distribution,

$$\epsilon_{ij}(t) \sim \text{Gamma}\left(\frac{1}{\phi_j^2}, \frac{1}{\phi_j^2}\right) \tag{3}$$

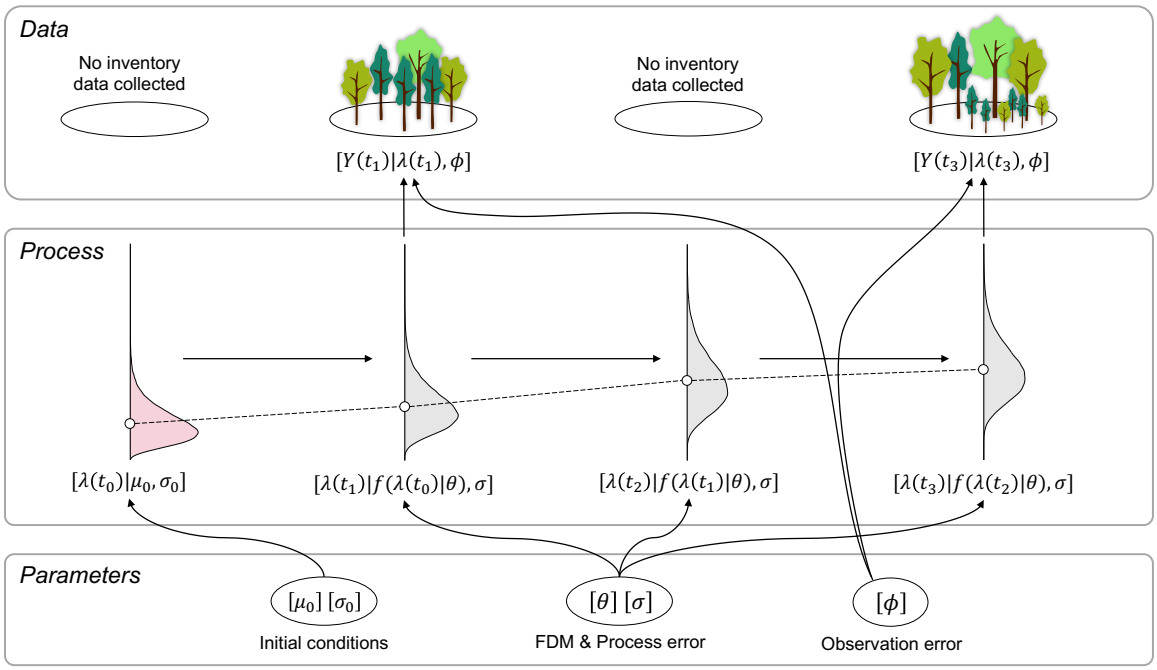

Figure 1: Structure of hierarchical Bayesian dynamical temporal model. Data ($Y(t)$) include periodic inventory observations observed within fixed area plots. The process ($\lambda(t)$) represents the latent (unobserved) state of the forest ecosystem driven over time by a model of forest dynamics ($f()$). Density plots are used to illustrate the fact that a probability distribution exists for each state with points indicating the mean. Parameters include those describing the initial condition of the forest (μ_0, σ_0), model of forest dynamics parameters (θ), as well as process (σ) and observation (ϕ) standard deviations. Square brackets, [], are used to denote probability distribution functions. Arrows indicate dependence among model components.

such that $\epsilon_{ij}(t)$ has a mean of 1.0 and variance equal to a species-specific overdispersion parameter ϕ_j^2. Under the Gamma error model, the marginal distribution for DBH class counts ($y_{ij}(t)$) integrating out the error term, is negative binomial with mean equal to $|A|\lambda_{ij}(t)$ and variance equal to $|A|\lambda_{ij}(t)(1+\phi_j^2|A|\lambda_{ij}(t))$ (Lawless, 1987). Hence, the Gamma error model has the computational benefit that we are able to model DBH class counts conditionally on $\lambda_{ij}(t)$ and ϕ_j^2 without having to sample the random error term $\epsilon_{ij}(t)$.

Process model

We apply a matrix projection model motivated by the MvF PDE discretized in size and time to predict the temporal evolution of the rate parameter ($\lambda_{ij}(t)$) equal to the underlying species- and size-specific stem density. Consistent with common matrix applications to model forest dynamics (Liang and Picard, 2013), we assume the size-species distribution in year t depends only on the distribution in the previous year $t-1$ (i.e., the temporal evolution of the size-species distribution is a first-order Markov process). The temporal evolution of the rate parameter is then modeled as,

$$\lambda_{ij}(t+1) = \mathbf{h}_{ij}(t;\boldsymbol{\theta}_j)\boldsymbol{\lambda}_j(t)\eta_{ij}(t+1) \tag{4}$$

where $\mathbf{h}_{ij}(t;\boldsymbol{\theta}_j)$ is the ith row of a $(k \times k)$ species-specific propagator matrix $\mathbf{H}_j(t;\boldsymbol{\theta}_j)$ that depends on time and a set of species-specific demographic parameters $\boldsymbol{\theta}_j$. The $\boldsymbol{\lambda}_j(t)$ term denotes a k-dimensional vector of latent DBH class densities for the jth species: $\boldsymbol{\lambda}_j(t) = (\lambda_{1j}(t), \lambda_{2j}(t), \ldots, \lambda_{kj}(t))^\intercal$ (where $^\intercal$ indicates the transpose). Lastly, $\eta_{ij}(t+1)$ is a multiplicative process error term reflecting unexplained variation in the temporal evolution of the latent process.

We apply a common parameterization for the propagator matrix ($\mathbf{H}_j$) that can be decomposed into separate matrices representing growth, mortality, and fecundity (Liang and Picard, 2013). Specifically, the propagator matrix is given by,

$$\mathbf{H}_j(t;\boldsymbol{\theta}_j) = \mathbf{G}_j(t;\boldsymbol{\theta}_j^{\text{gr}})\mathbf{M}_j(t;\boldsymbol{\theta}_j^{\text{mr}}) + \mathbf{F}_j(t;\boldsymbol{\theta}_j^{\text{fr}}) \tag{5}$$

where $\mathbf{G}_j$, $\mathbf{M}_j$, and $\mathbf{F}_j$ are $(k \times k)$ matrices describing growth, mortality, and fecundity across modeled DBH classes for species j conditional on demographic rate parameters (growth = $\boldsymbol{\theta}_j^{\text{gr}}$, mortality = $\boldsymbol{\theta}_j^{\text{mr}}$, fecundity = $\boldsymbol{\theta}_j^{\text{fr}}$, with $\boldsymbol{\theta}_j = (\boldsymbol{\theta}_j^{\text{gr}}, \boldsymbol{\theta}_j^{\text{mr}}, \boldsymbol{\theta}_j^{\text{fr}})$). The values of these matrices are estimated using species-specific demographic functions dependent on the defined demographic rate parameters. Here, $\mathbf{G}_j$ defines the proportion of individuals in a given DBH class growing into larger DBH classes, $\mathbf{M}_j$ defines the proportion of individuals that survive in a given DBH class, and $\mathbf{F}_j$ defines the number of individuals that recruit into the smallest DBH class. Consistent with common matrix models for forest dynamics (Liang and Picard, 2013), we assume the Usher property applies such that growth is limited to the next larger size class in a given time step: $i \to i+1$ for $t \to t+1$. This assumption combined with the above matrix decomposition leads to a sparse propagator matrix consisting of only $(3 \times k) - 1$ demographic rate terms for each species (see Section S3 in the Supporting information).

In the definition of the propagator matrix, we use t as a general representation of time-varying conditions that may affect forest demography including exogenous factors such as weather or disturbance and endogenous factors such as density-dependent competition for light, growing space, and other resources within a stand. In the latter case, the propagator matrix depends on the modeled size-species density, $\boldsymbol{\lambda}(t)$, across all species in a stand: $\boldsymbol{\lambda}(t) = (\boldsymbol{\lambda}_1(t)^\intercal, \ldots, \boldsymbol{\lambda}_m(t)^\intercal)^\intercal$. That is, the propagator matrix accounts for heterogeneous environments affecting demography to the extent that variables describing these environments are included in the applied demographic functions used to define the matrix (see Section S.4 in the Supporting information). Thus, the matrix model motivated by the MvF PDE results in a sparse, ecologically-meaningful representation of the complex dynamics of the size-species distribution over time, which closely follows a similar application of a matrix projection model within a Bayesian DSTM to predict the spatio-temporal dynamics of an ecological population (Hooten et al., 2007).

A wide range of demographic functions may be applied to populate the propagator matrix ($\mathbf{H}_j$). To the extent that demographic functions are taken from previously parameterized FDMs, existing estimates can be used to define prior distributions that help to constrain demographic parameters, while allowing for their refinement based on new data. We explored a number of demographic functions to describe growth, mortality, and fecundity in the propagator matrix including alternative representations of density-dependent competition as well as growth- and size-dependent demographic rates. Detailed definitions of the demographic functions tested and applied are provided in the Supporting information (Section S4). The general form of these functions is defined below.

Growth is modeled using an inverse probit function,

$$g_{ij}(t) = \Phi(\mathbf{x}_i^{\text{gr}}(t)^\intercal \boldsymbol{\theta}_j^{\text{gr}}) \tag{6}$$

where $g_{ij}(t)$ is the size- and species-specific growth rate (the proportion of individuals that grow into the next larger DBH class), Φ is the standard normal cumulative density function, and $\mathbf{x}_i^{\text{gr}}(t)$ is a vector of variables affecting growth at time t including functions of the size-species distribution ($\boldsymbol{\lambda}(t)$) in the case of density dependence. Survivorship is modeled in a similar fashion using an inverse logit function,

$$m_{ij}(t) = \frac{1}{1 + \exp(-(\mathbf{x}_i^{\text{mr}}(t)^\intercal \boldsymbol{\theta}_j^{\text{mr}}))} \tag{7}$$

where $m_{ij}(t)$ is the size- and species-specific survivorship rate and $\mathbf{x}_i^{\text{mr}}(t)$ is a vector of variables affecting survivorship at time t. Lastly, fecundity is modeled using an exponential function,

$$f_{ij}(t) = \exp(\mathbf{x}_i^{\text{fr}}(t)^\intercal \boldsymbol{\theta}_j^{\text{fr}}) \tag{8}$$

where $f_{ij}(t)$ is the size- and species-specific fecundity rate (the per capita number of individuals recruiting into the smallest DBH class) and $\mathbf{x}_i^{\text{fr}}(t)$ is a vector of variables affecting fecundity at time t.

Finally, we model the process error term (Eqtn. 4) using a log normal distribution,

$$\eta_{ij}(t) \sim \text{LogNorm}(0, \sigma_j^2) \tag{9}$$

where σ_j^2 is a species-specific, multiplicative process variance. The process error terms are modeled independently because the complex dependence in the density of trees across size classes, species, and time is captured by the time-varying (often density-dependent) propagator matrix. This highlights an important property of Bayesian hierarchical DSTMs under which complex spatio-temporal dependence in the process of interest is quantified through the dynamical model, rather than through modeled error terms where it is more difficulty to estimate (Wikle and Hooten, 2010).

Parameter models

The dynamical framework is completed by defining models for demographic rate parameters, initial size-species density values, and observation and process variance parameters. We apply a hierarchical prior to model demographic rate parameters,

$$\theta_{j\ell} \sim \text{Normal}(\mu_\ell, \tau_\ell^2) \tag{10}$$

where μ_ℓ is the mean rate across all m species and τ_ℓ^2 is the among-species variance for the ℓth demographic parameter ($\ell = 1, \ldots, p$, where p is the total number of demographic parameters). We assign semi-informative normal priors to the mean demographic rates with mean values set to match expected demographic rates and variance values set to the expected order of magnitude. Among species standard deviation parameters (τ_ℓ) are assigned half-Cauchy prior distributions (Gelman, 2006). The hierarchical prior allows for partial pooling of demographic data among species reflecting similarities in the demographic responses of species while allowing for inter-specific variability where it is supported by data. Hierarchical priors can also be helpful when estimating demographic rates of rare or underrepresented species (Dietze et al., 2008). Note that

demographic parameters are estimated based only on plot-level counts defined under the Data model (Eqtns. 1 and 2). This is because our inferential interest lies in population-level demographic rates and stand-level predictions (Ghosh et al., 2012). This is different from existing matrix projection approaches to model forest dynamics under which individual-level demographic parameters are estimated from pooled inventory data (similar to the approach to calibrating FDMs described earlier), and used to define the propagator matrix (Liang and Picard, 2013).

Initial size-species density values correspond to the latent Poisson rate at the initial time point ($\boldsymbol{\lambda}(0)$). Modeling initial density values is challenging given the model must balance sufficient flexibility to represent complex size-species distributions, while constraining variability in initial values to reasonable bounds (to prevent numerical instability in the dynamical model). We model initial values using a standardized normal density to represent the size distribution of each species scaled by an estimate of the overall density of the species at the initial time point. Specifically,

$$\lambda_{ij}(0) = n_j f(z_{ij}) \tag{11}$$

where n_j is the initial overall density of species j in terms of trees per hectare and $f(z_{ij})$ is the standardized size density. We apply a standard normal distribution to model the initial size density,

$$f(z_{ij}) = \frac{\phi(z_{ij})}{\sum_{i=1}^{k} \phi(z_{ij})} \tag{12}$$

where $\phi(z_{ij})$ is the standard normal density of z_{ij}, which is defined as $z_{ij} = v_j^{-1}(d_i - q_j)$ where d_i is the midpoint of the ith size class, q_j is the mean of the initial size distribution, and v_j is its standard deviation. Note that the standardized distribution sums to one across the modeled size classes: $\sum_{i=1}^{k} f(z_{ij}) = 1.0$ for $j = 1, \ldots, m$. Semi-informative log normal and normal priors are applied for the initial density (n_j) and mean of the initial size distribution (q_j) respectively, with mean values defined based on plot-level means of initial inventory observations and variances set to be consistent with the expected order of magnitude of each parameter. The initial size distribution standard deviation (v_j) is assigned a half-Cauchy distribution. We found the normal distribution to be sufficiently flexible to model a range of initial size class distributions, while being relatively easy to control. Note we use an empirical Bayes approach for the initial density and mean size distribution parameters. We found that using initial inventory observations was necessary to help constrain these parameters to reasonable neighborhoods for each species. Additional information on prior distributions are provided in the Supporting information.

Case studies

We develop our initial dynamical model using both simulated CFI data that approximates theoretical successional dynamics of an eastern temperate forest and long-term CFI data from the Penobscot Experimental Forest. We focus on the Penobscot case study here and provide details on the simulated analysis including long-term predictions of forest dynamics and the ability of the model to recover underlying demographic and uncertainty parameters in the Supporting information.

The Penobscot Experimental Forest (PEF) is a 1600 ha experimental forest north of Bangor, Maine (44°52'N, 68°38' W) jointly managed by the USDA Forest Service and the University of Maine to support long-term applied forest ecology research (Brissette and Kenefic, 2014). The forest is located within the Acadian Forest, a transition zone between the eastern temperate forest to the south and the boreal forest to the north. The PEF is characterized by a cold, humid climate

with a mean annual temperature of 6.8°C and mean annual precipitation of greater than 1000 mm with much falling as snow.

A long-term silviculture experiment was established in the PEF between 1952-1957 with replicated treatments initiated across 20 management units (Brissette and Kenefic, 2014). Permanent sample plots were installed prior to silvicultural treatments in the 1950s with plots remeasured every 5-10 years through present. Species identity and DBH are recorded for all trees within sample plots using a nested, fixed area design with 0.08 ha plots used to measure large diameter trees (> 11.4 cm) and either 0.02 ha or 0.008 ha nested subplots used to measure small diameter trees ($1.3 - 11.4$ cm). DBH values are measured to the nearest 0.25 cm except in historic inventories (prior to 1974) in which tree diameter was classified into 2.54 cm DBH classes.

We apply the dynamical model to predict long-term forest dynamics (1953-2012) using inventory data collected within a 2.4 ha control unit in the PEF long-term silviculture experiment: MU32B (Fig. S1). No silvicultural treatments were applied within this unit nor were there any major disturbance events during the model period. The forest within the unit is even-aged and characterized as being within the late stem exclusion to understory re-initiation phases of development within the model period (Brissette and Kenefic, 2014). The unit comprises a mixture of nine Acadian forest species including balsam fir (*Abies balsamea* (L.) Mill.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), eastern white pine (*Pinus strobus* L.), northern white-cedar (*Thuja occidentalis* L.), paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), and red (*Picea rubens* Sarg.), black (*P. mariana* Mill.), and white spruce (*P. glauca* (Mo.) A.V.). The management unit was inventoried 11 times between 1954-2009 (roughly every five years) across three (1954-1989) or ten (1993-2009) CFI plots (see Table S1 for inventory years and plot details).

Implementation

We sampled from the joint posterior distribution of the dynamical model parameters using MCMC simulation. Specifically, we applied a Hamiltonian Monte Carlo sampler written in STAN (Stan Development Team, 2024) and implemented using the RStan package (Stan Development Team, 2023) for the R statistical computing environment (R Core Team, 2023). For each version of the model, three MCMC chains were run for a total of 2,000 iterations with a burn-in of 1,000 iterations. Model convergence was assessed based on R-hat values (< 1.05), bulk effective sample size (minimum of 100 per chain), and visual inspection of chains for all parameters (Vehtari et al., 2021). Additional information on model implementation including generation of starting values is provided in the Supporting information.

Results

The Bayesian dynamical model approximates complex forest dynamics while accounting for different sources of uncertainty in predictions. The modeled PEF stand is even-aged and moves from the late stem exclusion to the understory re-initiation phase during the 60-year model period (Brissette and Kenefic, 2014). Predictions of overall changes in stand density reflect these stages of development exhibiting characteristic reduction in stem density coincident with increases in basal area density (Fig. 2). Fast growing, early successional white pine, which dominates the initial canopy of the stand and slow growing, shade tolerant eastern hemlock, which dominates the understory and midstory are responsible for most of the increases in basal area over the model period (Fig. 3). Changes in the size-species distribution over time reflect a similar pattern, with the largest size classes composed almost exclusively of white pine, the intermediate size classes

composed largely of eastern hemlock and mid-tolerant red maple, and the smallest size classes dominated by shade tolerant balsam fir (Fig. 4). Predictions at the end of the model period (e.g., 2005 and 2009 in Fig. 4) indicate the initial loss of large, overstory white pine and its replacement with with slow growing eastern hemlock consistent with expected successional patterns in eastern temperate forests. These patterns are further represented in modeled demographic rates with shade tolerant eastern hemlock having a low growth rate and high survivorship rate, and mid-tolerant white pine have a high growth rate and moderate survivorship rate (Fig. S3).

Uncertainty in predictions of forest dynamics within the modeled PEF stand is reflected in estimates of species-specific observation and process error standard deviations (Fig. 5). These standard deviations indicate the size-specific density of balsam fir has the highest observational uncertainty, while white pine has the lowest. In contrast, the size-specific density of white spruce has the highest process uncertainty, while eastern hemlock has the lowest. Uncertainty is further reflected in 95 percent credible intervals for overall stand density (Fig 2), species-specific density (Fig. 3), and changes in the size-species distribution over time (Fig. 4). These intervals combined with posterior mean of predictions (illustrated in the same figures) are used to summarize the posterior predictive distribution of the latent state of the forest at each time point. The posterior predictive distribution reflects the uncertainty in modeled demographic rates (Fig. S3), as well as the process uncertainty under the matrix projection model (Fig. 5). Our interest is in changes to the latent size-species distribution over time rather than noisy observations of it. Thus, we do not include observation uncertainty in predictions of the temporal evolution of the latent size-species density. Observation uncertainty is instead accounted for in the posterior predictive density of inventory plot observations, which have larger uncertainty bounds than the latent process on its own (Fig. 3) reflecting the fact that observations are generated conditionally on the latent state subject to their own error term.

Discussion

The goal of the Bayesian dynamical model introduced here is to generate probabilistic predictions of forest dynamics that account for and partition the different sources of uncertainty in the processes shaping forest change over time and space. The model is specifically aimed at generating near-term (years to decades), stand-level predictions to help inform adaptive management decisions in the face of future uncertainty. Here we detail the different sources of uncertainty affecting predictions in the PEF before describing approaches to reduce uncertainty in predictions.

Uncertainty in predictions of forest dynamics

Much can be learned by assessing changes in the uncertainty of predictions of the latent size-species distribution over the model period as reflected in the width of the modeled 95 percent credible intervals for the overall stand density (Fig. 2). There are relatively large levels of uncertainty in predictions of stem density early in the model period due to uncertainty in the initial condition of the forest (modeled as part of the broader Bayesian hierarchical model, Fig. 1), which slowly decline after the first ten years. Uncertainty levels decline (in the case of stem density) or remain relatively constant (in the case of basal area density) during the middle of the model period before increasing in the mid-1990s when additional forest plots are included in periodic inventories of the forest. While we expect uncertainty in predictions to be reduced with additional inventory plots (ten instead of three), the large variability among the ten plots (Fig. 2) contributes

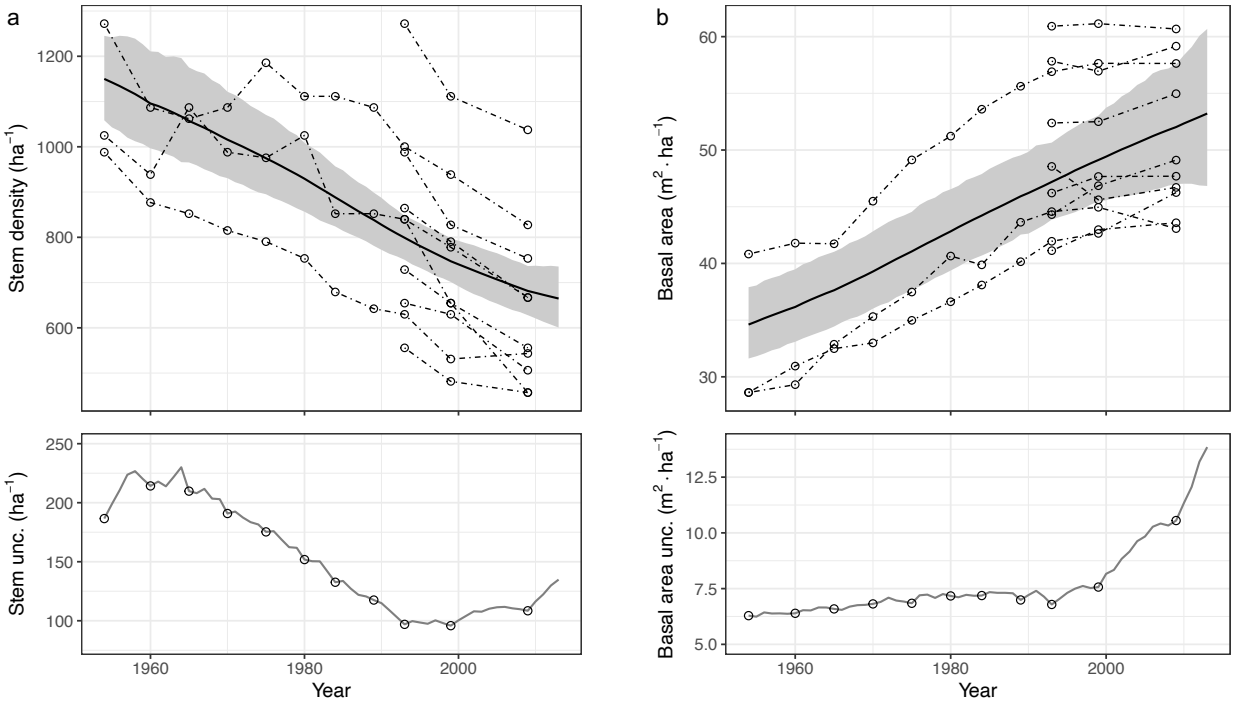

Figure 2: Changes in stand density over the model period (1954-2013) in terms of stems (a), and basal area (b) per hectare. Upper panel represents the posterior mean predicted density values (solid line) and 95 percent credible intervals (grey shading). Points represent plot-level observations of stand density during inventory years connected by dashed lines for reference. Lower panel represents the 95 percent credible interval width with points indicating inventory years.

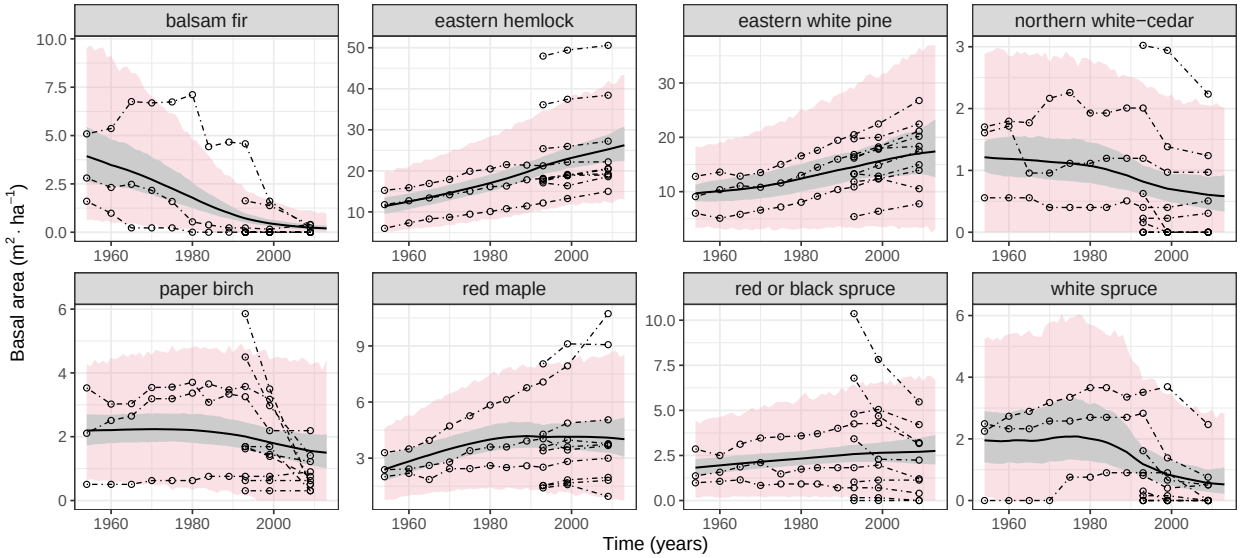

Figure 3: Changes in species-specific basal area per hectare over the model period (1954-2013). Solid lines represent the posterior mean predicted basal area along with 95 percent credible intervals (grey shading). Pink shading indicates the 95 percent credible interval of observed basal area per hectare values incorporating species-specific observation error.

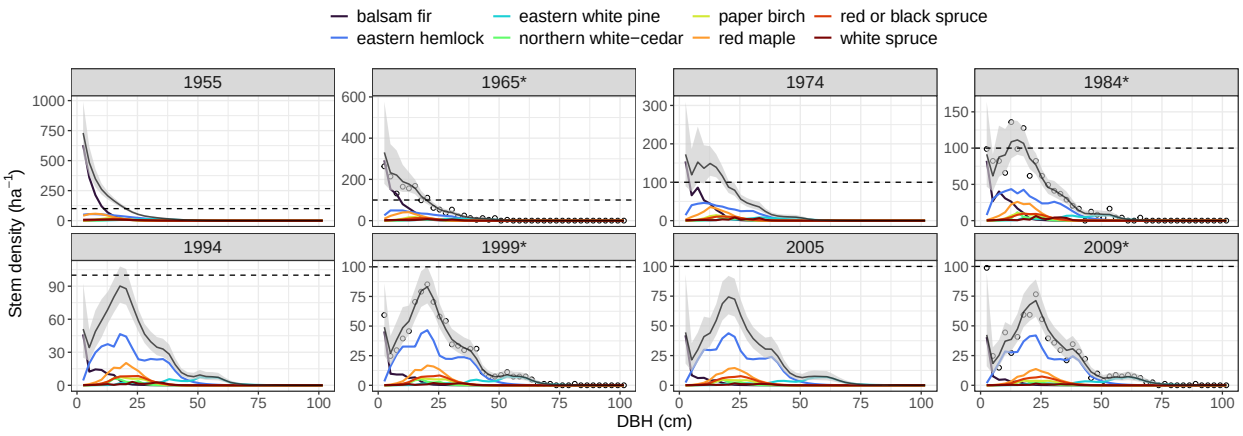

Figure 4: Predictions of the size-species distribution in eight years during the model period (inventory years are starred). Grey line is the posterior mean predicted overall size density (pooled across species) with 95 percent credible intervals shaded. Points in inventory years are the mean observed overall size density across plots. Colored lines are the posterior mean predicted size density by species. A dashed reference line is provided at 100 $m^2 \cdot ha^{-1}$ of basal area.

to an increase in uncertainty despite explicitly modeling observation error.

Throughout the model period, there is reduced uncertainty in predictions of the latent size-species distribution during inventory years for which observations of stand density exist relative to the surrounding years (those immediately preceding and following the inventory year). This is an expected outcome under a Bayesian dynamical model that pairs process and data models each with their own error terms (Clark and Bjørnstad, 2004), and relates to the fact that the latent state of the forest in an inventory year is informed by both the surrounding state values (the previous and subsequent states under the 1st order Markov process applied here) and the observed state of the forest. The importance of observations in constraining predictions of forest dynamics is further demonstrated by the rapid increase in uncertainty at the end of the model period (last three years) when predictions are no longer informed by inventory observations (Figs. 2, 3).

Additional insight on the sources of uncertainty impacting predictions of forest dynamics can be gained by comparing modeled process versus observation error. In general, species-specific process error has lower standard deviation than species-specific observation error within the modeled PEF stand (Fig. 5). This is likely due to the large variability among plots in a given inventory year (Figs. 2, 3). There is large observation error standard deviation for understory species with high stem density and small diameter individuals such as balsam fir and eastern hemlock relative to overstory species such as white pine characterized by low stem density and large diameter individuals (Fig. 5). In contrast to observation error, we find that eastern hemlock has one of the lowest process error standard deviations among modeled species (Fig. 5) perhaps due to a low understory mortality rate and a consistent growth rate across size classes (Fig. S3).

Reducing uncertainty in predictions of forest dynamics

Ecological forecasting approaches aimed at reducing uncertainty in predictions of ecological processes call for iterative refinement of models based on data (Dietze et al., 2018). These approaches are contingent upon quantification and separation of process versus observation error that allow

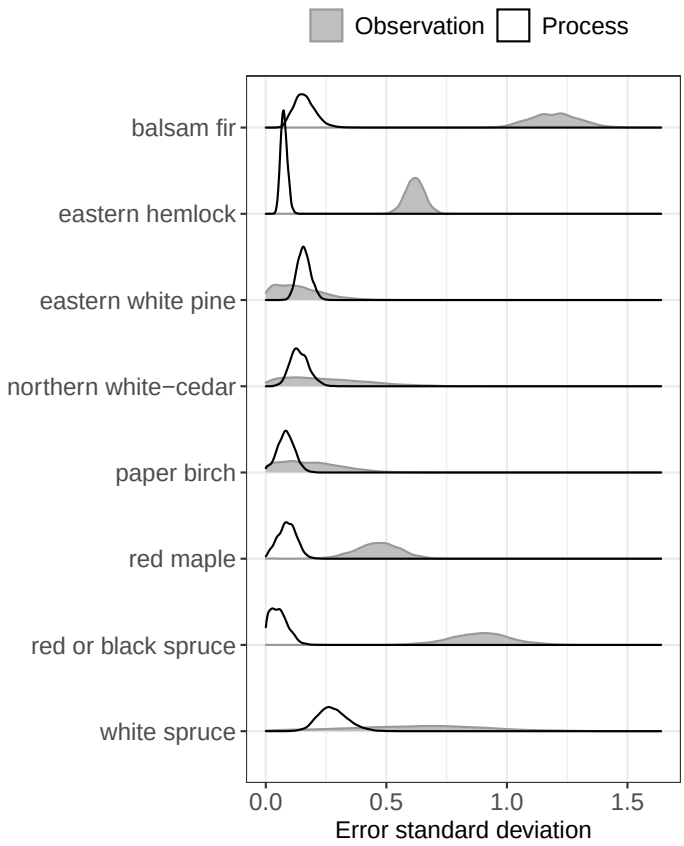

Figure 5: Posterior distributions of the species-specific process (σ_j) and observational error standard deviations (ϕ_j).

ecologists to determine primary sources of uncertainty in models and data and objectively measure reductions in uncertainty attributable to new data and/or model refinement (Dietze, 2017). The identification and separation of process and observation error is generally challenging even when both error types are explicitly defined in models (Hooten et al., 2007). In the current study, estimates of process and observation error are facilitated by the temporal structure of the dynamical model and replicate observations of the state of the forest ecosystem for select time points in the form of multiple inventory plots. Such error partitioning is not generally possible under alternative approaches that pool inventory observations over time and space to parameterize FDMs.

In addition to the targeted data collection and model refinement discussed above, uncertainty in predictions of forest dynamics may be further reduced by using multiple datasets to inform predictions. Additional data sources that might help to inform FDMs include remote sensing data products, paleo-ecological records, and functional trait data. Further, the inclusion of multiple forest inventory networks that intersect the spatio-temporal area of interest (e.g., national, regional, and ecosystem level networks) has the potential to further refine predictions of forest dynamics. The Bayesian dynamical model defined here supports synthesis of these diverse datasets within a single model framework that accounts for unique observational error structure in each and accommodates both missingness and differing spatio-temporal resolutions in observations. Synthesis of multiple datasets to reduce uncertainty in predictions is broadly connected to data assimilation

approaches under which new or future data are used to update the predicted states of a system (Dietze et al., 2018). Data assimilation is particularly important in the context of modeling forest dynamics under global change because future observations of forest responses to novel conditions may be more valuable than the historic observations used to parameterize the model. While data assimilation is not the focus of the current study, we note the Bayesian dynamical model developed here aligns with and facilitates the application of well-known approaches for Bayesian data assimilation (Wikle and Berliner, 2007).

Incorporating density-dependence in population-level models

Our initial Bayesian dynamical model applies a cohort-based approach to model forest dynamics approximating the ecological detail included in more complex individual-based FDMs within a size-structured population model. The challenge in these models is sufficiently capturing fine scale spatial variability in growing conditions (e.g., at the scale of individual trees or small patches approximating a canopy gap) to accurately predict forest dynamics while maintaining computational tractability (Pacala and Deutschman, 1995). The matter of computational tractability is particularly important in the context of dynamical models commonly fit using MCMC simulation (Wikle and Hooten, 2010). While simple approximations of the mean growing environment such as overall density or the basal area of trees larger in size than the target cohort are straightforward to implement within a dynamical model, they tend to oversimplify within stand spatial variability with potentially biased divergence from spatially explicit models (Pacala and Deutschman, 1995). On the other hand, more complex approximations that account for within stand spatial variability in the growing environment (Moorcroft et al., 2001) are computationally demanding and difficult to integrate within a broader dynamical model.

We initially constructed our dynamical model using the perfect plasticity approximation of the mean growing environment (Strigul et al., 2008). The perfect plasticity approximation (PPA) estimates access to light based on cohort height and crown size relative to a (theoretical) spatially homogeneous canopy base height under the assumption of extreme crown plasticity. Under the Bayesian hierarchical model applied here, the theoretical canopy base height is a derived parameter (i.e., it is a function of modeled parameters and as such has its own probability distribution). We found that using the PPA as a measure of density dependent competition led to identifiability issues in demographic parameters when applied to both the PEF and simulated datasets, the latter of which applied the PPA as the true data generating mechanism. We thus replaced the PPA with basal area larger as a measure of density-dependent competition within simulated datasets (similar to Kohyama, 1993), which did not present identifiability issues.

Several factors may have contributed to the observed identifiability issues. First, there was limited variability in the canopy position of modeled species with the most common species present in either the overstory (white pine) or the understory (balsam fir, eastern hemlock) during the model period. There was also a lack of size variability among species such that we were only able to estimate the effect of DBH on white pine growth given that all other species had low size variation within the PEF stand (Fig. S2). The lack of variability in the growing conditions within the PEF stand points to the need to integrate information from a network of plots providing observations of forest ecosystems in a diversity of states. This is one reason why regional plot data is pooled under common approaches to calibrate FDMs. Integrating information from of network of plots requires the current dynamical model be extended across space linking plots within a broader forested landscape.

Alternative model parameterizations

We constructed our Bayesian dynamical model using a matrix projection process model because it is straightforward to implement and scalable (Hooten et al., 2007). Alternatives to the matrix projection model include integral projection models under which size is continuous and time is discrete (Ghosh et al., 2012) or the direct application of the MvF PDE under which both size and time are continuous (Kohyama, 1993; Falster et al., 2011, 2017). Forest dynamics are commonly modeled on an annual (or multiyear) time step matching the temporal resolution of inventory data (Bugmann, 2001). Note that when applied on an annual time step, the MvF PDE is functionally continuous in size and discrete in time consistent with an integral projection model, although the form of the two models is different. When size is continuous rather than discrete, the Poisson data model applied to predefined size class counts in the current model (Eqtns. 1 and 2), is replaced with a heterogeneous Poisson point process data model under which observed tree sizes are proportional to the integral of a continuous size intensity function over a bounded size range (Ghosh et al., 2012). Under standard numerical approaches to approximate this integral, the continuous size space is discretized using a fine size grid (much finer than common forest inventory size classes). A similar discretization procedure is applied under common approaches to numerically approximate the MvF PDE (Zhang et al., 2017).

Without a large sample of individuals to fully represent the size intensity, a fine size grid may lead to irregular counts with a large number of zeros (many size ranges will have no observed values within them), which can lead to numerical stability issues. The solution is to coarsen the size grid resulting in size classes more closely approximating those used in a matrix projection model. Further, previous studies have shown that the observation error associated with diameter tape measurements of tree DBH (such as those collected within CFI plots) has a standard deviation of 1.0 cm (Clark et al., 2007), such that small predefined size classes (e.g., 2.54 cm classes as applied here) are close to the precision of DBH measurements. As such, the main benefit of an integral projection process model within a dynamical model of forest change is not that it treats size continuously, but rather that it is highly scalable. Specifically, there are well developed approaches to express the redistribution kernel of a spatio-temporal integral projection model as a low-dimensional, basis function expansion that when integrated within a broader Bayesian hierarchical model provides a computationally feasible approach to model complex dynamical processes at large spatial scales (Wikle and Hooten, 2010).

Conclusions

Here we have developed a Bayesian dynamical model to predict changes in forest ecosystems over time informed by long-term CFI data. The ultimate goal of the dynamical modeling approach is to connect a large regional network of plots across time and space. While previous studies have modeled spatio-temporal forest dynamics using similar structured population models (Kohyama, 1993; Falster et al., 2017), none have directly linked process models to data within a Bayesian DSTM that supports uncertainty quantification. The Bayesian DSTM developed here provides a sparse, process-based representation of the demographic processes underlying forest dynamics with high potential for scaling across space. Further it connects the challenge of modeling forest dynamics under global change to well developed statistical methods for predicting complex spatio-temporal processes (Wikle and Hooten, 2010) and to modern approaches to ecological forecasting aimed at reducing uncertainty in predictions (Dietze et al., 2018). As such, it provides an initial

step toward improved connection between FDMs and data, informed model refinement and future data collection, and ultimately reduced uncertainty in predictions of forest dynamics under global change.

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