Data-intensive modeling of forest dynamics

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Abstract

Forest dynamics are highly dimensional phenomena that are not fully understood theoretically. Forest inventory datasets offer unprecedented opportunities to model these dynamics, but they are analytically challenging due to high dimensionality and sampling irregularities across years. We develop a data-intensive methodology for predicting forest stand dynamics using such datasets. Our methodology involves the following steps: 1) computing stand level characteristics from individual tree measurements, 2) reducing the characteristic dimensionality through analyses of their correlations, 3) parameterizing transition matrices for each uncorrelated dimension using Gibbs sampling, and 4) deriving predictions of forest developments at different timescales. Applying our methodology to a forest inventory database from Quebec, Canada, we discovered that four uncorrelated dimensions were required to describe the stand structure: the biomass, biodiversity, shade tolerance index and stand age. We were able to successfully estimate transition matrices for each of these dimensions. The model predicted substantial short-term increases in biomass and longer-term increases in the average age of trees, biodiversity, and shade intolerant species. Using highly dimensional and irregularly sampled forest inventory data, our original data-intensive methodology provides both descriptions of the short-term dynamics as well as predictions of forest development on a longer timescale. This method can be applied in other contexts such as conservation and silviculture, and can be delivered as an efficient tool for sustainable forest management.

Keywords: data-intensive model, forest dynamics, Gibbs sampling, Markov chain model, Markov chain Monte Carlo, patch-mosaic concept, plant population and community dynamics

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1 Software and data availability

2   The software to estimate transition matrices based on forest inventory was implemented

3 by Jean Liénard in R version 2.15.1 (R Core Team, 2012) and is attached as a zip file to the

4 submission.

5   The database studied in this paper is available upon request to the Quebec provincial for-

6 est inventory database (`http://www.mffp.gouv.qc.ca/forets/inventaire/`). Straight-

7 forward modifications of the software allows to use with the USDA Forest Inventory and

8 Analysis program (`http://www.fia.fs.fed.us/`).

1. Introduction

Forest ecosystems are complex adaptive systems with hierarchical structures resulting from self-organization in multiple dimensions simultaneously (Levin, 1999). The patch-mosaic concept was actively developed in the second half of the twentieth century after Watt (1947) suggested that ecological systems can be considered a collection of patches at different successional stages. Dynamical equilibria arise at the level of the mosaic of patches rather than at the level of one patch. The classic patch-mosaic methodology assumes that patch dynamics can be represented by changes in macroscopic variables characterizing the state of the patch as a function of time (Levin and Paine, 1974). Forest disturbances are traditionally associated with a loss of biomass; however, Markov chain models based only on biomass do not capture forest succession comprehensively (Strigul et al., 2012). This limitation motivates the need for alternative formulations that are able to consider several forest dimensions instead of only one.

Here we develop a novel statistical methodology for estimating transition probability matrices from forest inventory data and generalize classic patch-mosaic framework to multiple uncorrelated dimensions. In particular, we develop a landscape-scale patch-mosaic model of forest stand dynamics using a Markov chain framework, and validate the model using the Quebec provincial forest inventory data. The novelty of our modeling framework lies in the consideration of forest transitions within multiple dimensional space of macroscopic stand-level characteristics (biomass, average age of trees, biodiversity and shade tolerance index) that constitutes a generalization of the one-dimensional model of forest biomass transitions developed earlier (Strigul et al., 2012). Our framework is also substantially distinct from previous models of forest dynamics, where successional stages are ordinated using empirical observations on successional pathways (Curtis and McIntosh, 1951; Kessell and Potter, 1980; Logofet and Lesnaya, 2000).

The Quebec forest inventory (Perron et al., 2011) is one of the extensive forest inventories that have been established in North America, among others led by the Canadian provincial governments and the USDA Forest Inventories and Analysis program in the USA. These

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37 inventories provide a representative sample of vegetation across the landscape through a

38 large number of permanent plots that are measured repeatedly. Although they were originally

39 developed for estimating growth and yield, they were rapidly found to be extremely useful

40 to studies in forest ecology, biogeography and landscape dynamics. Each permanent plot

41 consists of individually marked trees that are periodically surveyed and remeasured. Each

42 plot can be considered as a forest stand and then, theoretically, the forest inventories provide

43 empirical data sufficient for parametrization and validations of patch-mosaic models (Strigul

44 et al., 2012). However, practical development of the patch-mosaic forest models (i.e. their

45 parametrization, validation and prediction) is challenging due to the underlying structure of

46 the forest inventory datasets. These datasets are indeed collected at irregular time intervals

47 that are not synchronized across the focal area, and data collection procedures including

48 spatial plot design and tree measurement methods can be different at various survey times

49 and conducted by different surveyors (Strigul et al., 2012).

50 Our objective in this study is to develop a data-intensive method predicting the dynamics

51 of forest macroscopic characteristics. The idea of a data-intensive modeling approach is to

52 develop and explore a quantitative theory using statistical modeling, in contrast with the

53 hypothesis-driven theoretical approach in which selected mechanisms are used to design

54 and constrain models. We focus here on the development of the modeling framework and

55 illustrate the application of the framework to a large forest inventory dataset spanning 38

56 years of observations collected in Quebec. To overcome the issue of irregular samplings in

57 time specific to forest inventory data, we develop a Gibbs sampling procedure for augmenting

58 the data and infer the transition probabilities. Our particular use of Gibbs sampling

59 (Pasanisi et al., 2012) has a substantial scientific novelty, as this is the first application of

60 this statistical machinery to overcome the problems of irregularities in the forest inventory

61 sample design. In this paper, we demonstrate the power of this statistical methodology in

62 our application, and deliver it as ready-to-go tool for other applications by explaining every

63 step, providing pseudocode, and original R code. We anticipate that this novel statistical

64 methodology will be broadly used in forest inventory analysis as the issue of irregularities in

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65 inventories has previously been a substantial hindrance (e.g. Strigul et al., 2012).

66 We present in this paper the general methodology and demonstrate each of its steps on
67 the Quebec dataset. In particular, we consider the dimensionality of stand characteristics
68 in this dataset and present evidence that some characteristics are redundant. We apply
69 the method to predict long-term dynamics of Quebec forests, as represented by a subset of
70 macroscopic properties that best represent the variability in the data. We validate the model
71 utilizing two different cross-validation schemes to split the original data, based on survey
72 date (predicting later years using earlier years) and based on a random 2-folds partition of
73 plots (comparing long-term predictions inferred from two independent subsets). We finally
74 discuss the implications of this work, such as the effect of spatial and temporal variability,
75 the independence of most forest variables, the effect of changing external drivers and of
76 feedbacks.

2. Patch-mosaic modeling framework

78 The goal of this section is to introduce the modeling of patch-mosaic using Markov chains,
79 which is generalized and employed to predict forest dynamics in the main text. The patch-
80 mosaic concept assumes that the vegetation at the landscape level can be represented as
81 a collection of isolated spatial units - patches - where patch development follows a general
82 trajectory and is subject to disturbances (Watt, 1947; Levin and Paine, 1974). Patch-mosaic
83 models are derived using the conservation law, which takes into account patch aging and
84 other changes to macroscopic variables representing succession, growth of patches in space,
85 and disturbances (Levin and Paine, 1974). The same general idea as well as mathematical
86 derivations are broadly used in population dynamics to describe age- and size-structured
87 population dynamics. Patch-mosaic models can be partial differential equations or discrete
88 models depending on whether time and patch stages are assumed to be continuous or discrete.
89 Classic continuous patch-mosaic models are based on the application of the conservation
90 law to continuously evolving patches that can be destroyed with a certain probability, and
91 can be represented by the advection equation (model developed by Levin and Paine, 1974,

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92 for fixed-size patches) or equivalently by the Lotka-McKendick-von Foerster model (Strigul

93 et al., 2008). The continuous patch-mosaic models have been used in forest ecology to model

94 the dynamics of individual canopy trees within the stand or forest gap dynamics (Kohyama

95 et al., 2001; Kohyama, 2006).

96   In the case of patches changing in discrete time, the derivation of the conservation law

97 leads to discrete-type patch-mosaic models. In particular, the advection-equation model

98 (Levin and Paine, 1974) is essentially equivalent to several independently developed discrete

99 models (Leslie, 1945; Feller, 1971; Van Wagner, 1978; Caswell, 2001). These models consider

100 only large scale catastrophic disturbances (patch "death" process), destroying the patch,

101 which then develops along the selected physiological axis until the next catastrophic dis-

102 turbance Levin and Paine (1974). The stochastic model we are considering here employs a

103 Markov chain framework (Waggoner and Stephens, 1970; Usher, 1979a; Facelli and Pickett,

104 1990; Logofet and Lesnaya, 2000; Caswell, 2001) that is capable of taking into account all

105 possible disturbances.

106   In a Markov chains model, the next state of a forest stand depends only on the previous

107 state, and the probabilities of going from one state into another are summarized in what is

108 called a transition matrix, denoted T.

109   We summarize the distribution of states at time t as the row vector X_t, with length equal

110 to the number of discrete classes of patch state and with a sum equal to 1. We can predict

111 $X_{t+\Delta t}$ by multiplying the transition matrix:

$$X_{t+\Delta t} = X_t.T \tag{1}$$

112   To project an arbitrary number n time steps into the future, one simply multiplies by

113 T^n instead of T. The Perron-Frobenious Theorem guarantees the existence of the long-term

114 equilibrium, which can be practically found as the normalized eigenvector corresponding to

115 the first eigenvalue, or by iterative sequence of state vectors. In this paper we employ the

116 iterative method as it allows to derive forest states at different time steps in the future, for

117 example allowing to make predictions in 10, 20 or 30 years from now. To derive the long-term

118 equilibrium we simply choose an n large enough to satisfy the condition:

$$|X_{t+n\Delta t} - X_{t+(n-1)\Delta t}| < \epsilon \qquad (2)$$

119 Three illustrative examples of simplified Markov chains are available in Appendix 1.

120 3. Materials and Methods

121 We address here the issue of constructing transition matrices from forest inventory data

122 stemming from irregular sampling intervals and variable numbers of plots sampled in each

123 year. We outline in the following the general concepts of the methodology along with prac-

124 tical guidelines using the inventory led by the provincial Ministry of Natural Resources and

125 Wildlife in Quebec (Appendix 1). The key steps to use Gibbs sampling to estimate a tran-

126 sition matrix from irregular measurements are:

127 1. Compute stand level characteristics for each plot and for each survey year. Analyze

128 the dimensionality of these characteristics using correlation and principal component

129 analysis;

130 2. Construct temporal sequences of uncorrelated characteristics depending on forest sur-

131 vey dates. Use Gibbs sampling to infer the transition matrix. This algorithm consists

132 of random initialization of missing values followed by iteration of parameter estimation

133 and data augmentation:

134 • Parameter estimation: Compute the transition matrix using the (augmented)

135 sequences of plot transitions.

136 • Data augmentation: Draw new sequences conditional on the new transition ma-

137 trix.

138 The transition matrices for Quebec forests were obtained using this method with a three-

139 year time step. Future and equilibrium landscape characteristics were predicted according

140 to equations 1 and 2 (cf. Appendix 1).

¹⁴¹ *3.1. Step 1: stand characteristics and dimensional analysis*

¹⁴² This step consists of (a) the selection of a set of stand-level forest characteristics, (b) the

¹⁴³ dimensional analysis of these characteristics, (c) their decomposition into uncorrelated axes,

¹⁴⁴ and (d) the discretization of these uncorrelated axes.

¹⁴⁵ Our modeling method can be applied for the prediction of any forest stand characteristic

¹⁴⁶ under the condition that it is computable from every single plot survey. The particular choice

¹⁴⁷ of the characteristics depends on available data and research objectives. A general guideline

¹⁴⁸ is that these characteristics should summarize data from individual trees into macroscopic

¹⁴⁹ indicators of stand structure, which can then be used to compare forests across different

¹⁵⁰ ecosystems. We consider six characteristics of Quebec forests according to the rationale pre-

¹⁵¹ sented in Strigul et al. (2012) and Lienard et al. (2014). These characteristics are computed

¹⁵² based on trees with a diameter at breast height larger than 90mm (see Appendix 1.1 for

¹⁵³ more details about the Quebec forest inventory measuring protocol). We denote $\mathbb{S}$ the set of

¹⁵⁴ species inside each plot and $\mathbb{T}$ the set of trees inside each plot, and compute for each single

¹⁵⁵ plot survey the following characteristics:

¹⁵⁶ • dry weight biomass, estimated from Jenkins et al. (2003), using the formula: $\sum_{i \in \mathbb{T}} e^{\mathrm{B1}_i + \mathrm{B2}_i log(d_i)}$

¹⁵⁷ where B1 and B2 are species specific density constants , and d is the trunk diameter

¹⁵⁸ at breast height in cm. B1 and B2 have been derived from both US and Canadian

¹⁵⁹ studies, making it a suitable approximation for Quebec forests (Jenkins et al., 2003).

¹⁶⁰ The resulting aboveground biomass is expressed in 10^3 kg/ha.

¹⁶¹ • basal area, computed as the sums of trunk diameters at breast height d: $\sum_{i \in \mathbb{T}} \pi \left(\frac{d_i}{2}\right)^2$.

¹⁶² The basal area is expressed in m^2/ha.

¹⁶³ • intra-plot diversity (evenness), computed as the Gini-Simpson index (Hill, 2003), with

¹⁶⁴ $\Omega(s)$ referring to the number of trees with species s and $\Omega(\mathbb{T})$ referring to the total

¹⁶⁵ number of trees inside each plot: $1 - \sum_{s \in \mathbb{S}} \left(\frac{\Omega(s)}{\Omega(\mathbb{T})}\right)^2$. This provides an index in the

¹⁶⁶ 0-1 range describing the species heterogeneity at the stand level, with high values

¹⁶⁷ indicating a high heterogeneity.

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168 • extra-plot diversity (species richness), computed as the number of species present in a

169 plot: $\Omega(\$)$. In the Quebec dataset, this indicator ranges from 1 to 8 species, and is

170 interpreted as another measure of diversity.

171 • shade tolerance index, a new metric introduced by Strigul and Florescu (2012) and

172 Lienard et al. (2014) describing the shade tolerance rank of species r: $\sum_{i \in \mathbb{T}} \frac{\Omega(s) r_i}{\Omega(\mathbb{T})}$.

173 This index ranges from 0 to 1, with high values denoting forest stands composed of

174 typically late successional species and low values denoting forest stands composed of

175 typically early successional species in Quebec (Lienard et al., 2014).

176 • average age, computed as the average of tree ages a : $\sum_{i \in \mathbb{T}} \frac{a_i}{\Omega(\mathbb{T})}$. This commonly-used

177 indicator approximates the stand age in the forest inventory analysis (see Strigul et al.

178 2012 for a discussion of this characteristic).

179 Statistical relations of these stand-level characteristics were analyzed using standard mul-

180 tivariate methods. First, we computed the Pearson correlation coefficients both in the whole

181 dataset and in the dataset broken down in decades (to avoid biases due to their temporal

182 autocorrelation). We then performed a principal component analysis (PCA) to examine

183 (a) the number of components needed to explain most of the variance as well as (b) the

184 projection of characteristics in the space defined by these components.

185 In general, it is possible for a multidimensional model to operate on the space of principal

186 components. Such a model would (a) project the characteristics into the low-dimensional

187 space given by the principal components, then (b) predict their dynamics in this new space,

188 and finally (c) perform the inverse transformation to obtain predictions on the characteristics.

189 In our application to the Quebec dataset, we discovered that four uncorrelated characteristics

190 approximate well the principal component space (namely biomass, average age of trees, Gini-

191 Simpson and shade tolerance indexes, *cf.* Results). Our model employs this approximation

192 and is based on transition matrices of these forest characteristics. It substantially simplify

193 interpretation of modeling predictions.

194 Prior to the computation of transition matrices in the Markov chain framework, it is

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¹⁹⁵ necessary to discretize continuous variables into distinct states (Strigul et al., 2012). The
¹⁹⁶ general approach is to subdivide data into uniformly spaced states, with a precision that is
¹⁹⁷ small enough to capture the details of the distribution but large enough to be insensitive
¹⁹⁸ to statistical noise in the dataset. In addition, the computational effort needed to infer
¹⁹⁹ transition matrices is proportional to the square of the number of states, and available
²⁰⁰ computational power may constitute a practical limitation to the number of states. In the
²⁰¹ Quebec dataset, the stand-level characteristics span different ranges (see Figs. 2 and 3 in
²⁰² Appendix), with the biomass distribution in particular showing a long tail for the highest
²⁰³ values. In order to capture enough details of the distributions of the Quebec characteristics,
²⁰⁴ we opted to remove plots in the long tail of the biomass (those with a biomass higher
²⁰⁵ than 50,000 kg/ha, representing roughly 4% of the total dataset) and then subdivided the
²⁰⁶ remaining plots into 25 biomass states. An alternative approach would be to merge the rarely
²⁰⁷ occurring high-biomass states into the last state as was implemented in Strigul et al. (2012).
²⁰⁸ We conducted a comparison of these two approaches and found no significant differences.
²⁰⁹ For the other characteristics investigated (i.e. the internal diversity, shade tolerance index,
²¹⁰ and average age), we found that 10 states were enough to capture their distributions with
²¹¹ sufficient detail.

²¹² *3.2. Step 2: Gibbs sampling methodology*

²¹³ Inferring a Markov Chain model for characteristics computed with field data sampled at
²¹⁴ irregular intervals is a challenging problem. Indeed, the usual direct approach of establishing
²¹⁵ the n-year transition matrix by simply counting the number of times each state changes to
²¹⁶ another after n years can not be employed in most forest inventories, as successive mea-
²¹⁷ surements on the same plot are not made with constant time intervals. This irregularity
²¹⁸ in sampling results in states of the forest plots that are not observed, and can be modeled
²¹⁹ as missing data. Two classes of algorithms can be used to parameterize a transition matrix
²²⁰ describing the dynamics of both observed and missing data: expectation-maximization (EM)
²²¹ and Monte Carlo Markov Chain (MCMC), of which Gibbs sampling is a specific implemen-
²²² tation. Both classes of algorithms are iterative and can be used to find the transition matrix

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that best fits the observed data. EM algorithms consist of the iteration of two steps: in the expectation step the likelihood of transition matrices is explicitly computed given the distribution of the missing data inferred from the previous transition matrix estimate, and in the maximization step a new transition matrix maximizing this likelihood is chosen as the new estimate (Dempster et al., 1977). MCMC algorithms can be seen as the Bayesian counterpart of EM algorithms, as at each iteration a new transition matrix is stochastically drawn with the prior information of estimated missing data, and in turn new estimates for the missing data are stochastically drawn from the new transition matrix (Gelfand and Smith, 1990). EMs are deterministic algorithms, and as such they will always converge to the same transition matrix with the same starting conditions; conversely, MCMCs are stochastic and are not guaranteed to converge toward the same estimate with different random seeds. While both algorithms are arguably usable in our context, the ease of implementation and lower computational cost of MCMC algorithms led us to prefer them over EM (Deltour et al., 1999). We selected Gibbs sampling as a flexible MCMC implementation (Geman and Geman, 1984). We provide in the following a brief presentation of Gibbs sampling. Additional implementation details are in Appendix 1.2, and we refer to Robert and Casella (2004) for the general principles underlying MCMC algorithms and to Pasanisi et al. (2012) for an extended description of Gibbs sampling to infer transition probabilities in temporal sequences. In addition to the full explanation below, we also provide a pseudocode of the procedure (Box 1).

To apply Gibbs sampling for the estimation of the transition matrices, it is required to include plot characteristics in a set of temporal sequences. For each plot p, this is done by inserting each characteristic $s_{(p,i)}$ measured in the i-th year at position i of a row vector S_p representing the temporal sequence of this plot. For example, if a plot p was sampled only at years 1 and 3 during a 5-year inventory, allowing for the computation of characteristics $s_{(p,1)}$ and $s_{(p,3)}$, then its sequence would be the row vector $S_p = [s_{(p,1)}, \bullet, s_{(p,3)}, \bullet, \bullet]$, where $\bullet$ denotes a missing value. The sequences are mostly composed of unknown values as only a fraction of the forest plots were surveyed each year. In the application to the Quebec

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²⁵¹ dataset, a reduction of the size of these temporal sequences was performed (see Appendix

²⁵² 1.2 for a detailed description of this reduction and an illustrative example); however it is not

²⁵³ a pre-requisite for the general application of Gibbs sampling. Let further Y be the matrix

²⁵⁴ constructed using all the sequences S, with rows corresponding to successive measures of

²⁵⁵ different plots and columns corresponding to different years. The preliminary step of Gibbs

²⁵⁶ sampling consists of replacing the missing values $\bullet$ in Y at random, resulting in so-called

²⁵⁷ augmented data $Z^{[0]}$. Then, the two following steps are iterated a fixed number of times H,

²⁵⁸ with h the index of the current iteration:

²⁵⁹ 1. in the **parameter estimation** step, we draw a new transition matrix $\Phi^{[h]}$ conditional

²⁶⁰ on the augmented data Z^{h-1}, using for every row i:

$$\Phi_i^{[h]}|Z^{[h-1]} \sim Dir(\gamma_{i,1} + w_{i,1}^{[h-1]}, ..., \gamma_{i,r} + w_{i,n}^{[h-1]}) \tag{3}$$

²⁶¹ with Dir is the Dirichlet distribution, γ are biasing factors set here uniformly to 1 as

²⁶² we include no prior knowledge on the shape of the transition matrix (Pasanisi et al.,

²⁶³ 2012). $w_{i,j}$ are the sufficient statistics reflecting the transitions in the augmented data

²⁶⁴ $Z^{[h-1]}$, formally defined as

$$w_{i,j} = \sum_{t \,\in\, \text{years}} \sum_{k \,\in\, \text{plots}} \mathbb{1}_{\{Z_{k,t-1}^{[h-1]}=s_i \,\,\&\,\, Z_{k,t}^{[h-1]}=s_j\}} \tag{4}$$

²⁶⁵ with $\mathbb{1}_{\{Y_{k,t-1}=s_i \,\,\&\,\, Y_{k,t}=s_j\}}$ the count of sequences elements in the state s_i at time $t-1$

²⁶⁶ and in the state s_j at time t.

²⁶⁷ 2. in the **data augmentation** step, we draw new values the missing states, based to the

²⁶⁸ probabilities of the transition matrix $\Phi^{[h]}$. The probabilities $\mathbb{P}$ used to augment the

²⁶⁹ data $Z^{[h]}$ are derived from their values in the previous iteration ($Z^{[h-1]}$) as well as their

²⁷⁰ values in the current iteration but in an earlier year ($Z_{k,t-1}^{[h]}$ for $t \geq 2$):

$$\text{for the earliest data } t = 1, \quad \mathbb{P}(Z_{k,1}^{[h]} = s_j | Z_{k,2}^{[h-1]} = s_i, \Phi^{[h]}) \propto \Phi_{j,i}^{[h]} \tag{5}$$

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$$\text{for the latest data } t = T, \quad \mathbb{P}(Z_{k,T}^{[h]} = s_j | Z_{k,T-1}^{[h]} = s_i, \Phi^{[h]}) \propto \Phi_{i,j}^{[h]} \tag{6}$$

$$\text{otherwise,} \quad \mathbb{P}(Z_{k,t}^{[h]} = s_j | Z_{k,t-1}^{[h]} = s_{i_1}, Z_{k,t+1}^{[h-1]} = s_{i_2}, \Phi^{[h]}) \propto \Phi_{i_1,j}^{[h]} \times \Phi_{j,i_2}^{[h]} \tag{7}$$

Pseudocode 1: Estimate of the transition matrix of one stand characteristic

Data: Y, a matrix whose rows are sequences S of repeated measurements.

Result: M, the transition matrix

begin

  transitions list $\leftarrow \emptyset$;

  for $r \leftarrow 1$ **to** R **do**

    /* initialization   */

    Obtain $Z^{[0]}$ by filling missing states from Y at random;

    for $h \leftarrow 1$ **to** H **do**

      /* Parameter estimation   */

      Compute the sufficient statistics $w_{i,j}$, $\forall(i,j) \in [1,n]^2$ using Eq. 4;

      Initialize $\Phi^{[h]}$ as an empty $n \times n$ matrix;

      for $i \leftarrow 1$ **to** n **do**

        $\Phi^{[h]}_{i,1\ldots n} \leftarrow$ random values drawn from Eq. 3;

      end

      /* Data augmentation   */

      $Z^{[h]} \leftarrow Y$;

      for $k \leftarrow 1$ **to** K **do**

        if missing, $Z^{[h]}_{k,1} \leftarrow$ random value drawn from Eq. 5;

      end

      for $t \leftarrow 2$ **to** $T-1$ **do**

        for $k \leftarrow 1$ **to** K **do**

          if missing, $Z^{[h]}_{k,t} \leftarrow$ random value drawn from Eq. 6;

        end

      end

      for $k \leftarrow 1$ **to** K **do**

        if missing, $Z^{[h]}_{k,T} \leftarrow$ random value drawn from Eq. 7;

      end

    end

    if $h > B$ **then**

      transitions list $\leftarrow \{$transitions list, $\Phi^{[h]}\}$;

    end

  end

end

$M \leftarrow$ mean of all matrices in transitions list

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271 As Gibbs sampling is initialized by completing the missing values at random, the first

272 iterations will likely result in transition matrices far away from the optimal. The usual

273 workaround is to ignore the first B transition matrices corresponding to so-called "burn-in"

274 period, leaving only $H - B$ matrices. Furthermore, as Gibbs sampling relies on a stochastic

275 exploration of the search space, a good practice to ensure that Gibbs sampling converged

276 to the optimal transition matrix is to run the whole algorithm R times. There are no

277 general guidelines for setting the H, B and R parameters (Robert and Casella, 2004). We

278 empirically settled with $H = 1000$, $B = 100$ and $R = 50$ in order to ensure that the transition

279 matrices were reproducible for the Quebec dataset, leading to $R \times H = 50000$ iterations of

280 parameter estimation and data augmentation steps and resulting in $R \times (H - B) = 45000$

281 transition matrices. This process was repeated independently for each plot characteristic.

282 The algorithm was implemented in R version 2.15.1 (R Core Team, 2012) and took a total

283 runtime of 4 days on a 1.2 Ghz single-core CPU to compute the transition matrices for all 4

284 characteristics studied here.

285 **4. Results**

286 *4.1. Multivariate analysis of stand characteristics*

287 The correlation analysis performed on the Quebec forest inventory (Perron et al., 2011,

288 Appendix 1.1) revealed that biomass and basal area were highly correlated ($r = 0.96$), as

289 well as the external and internal diversity indices ($r = 0.90$, see Appendix 1.3 for the other

290 coefficients). These correlations are further preserved when the correlation analysis is done

291 separately on each decade, from the 1970s until the 2000s (*cf.* tables in Appendix 1.3),

292 confirming the presence of time-independent strong correlations between these two pairs of

293 characteristics.

294 A PCA applied to the dataset further confirmed that the biomass and basal area on one

295 hand, as well as the external and internal diversity on the other hand, have nearly identical

296 vectors in the principal components space (*cf.* Appendix 1.4). Furthermore, this analysis

297 showed that 4 principal components are required to adequately explain variance in the data;

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298 using 3 components accounts for only 87 % of the variance, while 4 components explain up
299 to 98 % of the variance. The PCA revealed that biomass, the internal diversity index, the
300 shade tolerance index, and the average age are close approximations of the different principal
301 components and explain most of the variance. Therefore, these variables have been employed
302 in the following analysis.

303 *4.2. Interpretation of the transition matrices*

304   We present here in detail the transition matrix for biomass with a 3-year time interval,
305 shown in Fig. 1 (the other characteristics are to be found in Appendices, in Figs. 7 and 8).
306 In this matrix, each value at row i and column j corresponds to the probability of transition
307 from state i into state j after 3 years. By definition, rows sum to 100%. This transition
308 matrix, as with the others in Appendix, is dominated by its diagonal elements, which is
309 expected because few plots show large changes in a given 3-year period. The values below
310 the diagonal correspond to transitions to a lower state (hence, they can be interpreted as
311 the probabilities of disturbance), while values above the diagonal correspond to transitions
312 to a higher state (i.e., growth). The transitions in the first column of the matrix correspond
313 to major disturbances, where the stand transitions to a very low biomass condition. As
314 the probabilities above the diagonal are larger than below the diagonal, the overall 3-year
315 prediction is of an increase in biomass. This matrix also shows that plots with a biomass
316 larger than 40,000 kg/ha have a roughly uniform 10% probability of ending with a biomass of
317 less than 20 000 kg/ha 3 years later, which is interpreted as the probability of high-biomass
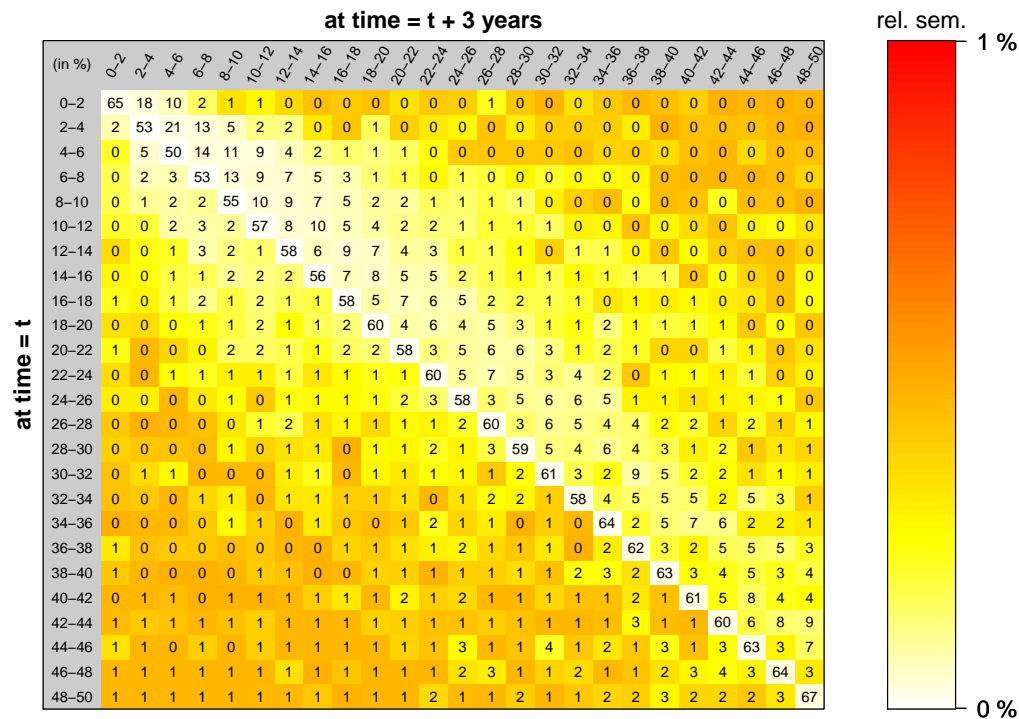318 stand to go through a moderate to high disturbance.

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at time = t + 3 years

(in %)	0–2	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–20	20–22	22–24	24–26	26–28	28–30	30–32	32–34	34–36	36–38	38–40	40–42	42–44	44–46	46–48	48–50
0–2	65	18	10	2	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
2–4	2	53	21	13	5	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4–6	0	5	50	14	11	9	4	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6–8	0	2	3	53	13	9	7	5	3	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
8–10	0	1	2	2	55	10	9	7	5	2	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0
10–12	0	0	2	3	2	57	8	10	5	4	2	2	1	1	1	1	0	0	0	0	0	0	0	0	0
12–14	0	0	1	3	2	1	58	6	9	7	4	3	1	1	1	0	1	1	0	0	0	0	0	0	0
14–16	0	0	1	1	2	2	2	56	7	8	5	5	2	1	1	1	1	1	1	1	0	0	0	0	0
16–18	1	0	1	2	1	2	1	1	58	5	7	6	5	2	2	1	1	0	1	0	1	0	0	0	0
18–20	0	0	0	1	1	2	1	1	2	60	4	6	4	5	3	1	1	2	1	1	1	1	0	0	0
20–22	1	0	0	0	2	2	1	1	2	2	58	3	5	6	3	1	2	1	0	0	1	1	0	0	0
22–24	0	0	1	1	1	1	1	1	1	1	1	60	5	7	5	3	4	2	0	1	1	1	1	0	0
24–26	0	0	0	0	1	0	1	1	1	1	2	3	58	3	5	6	6	5	1	1	1	1	1	1	0
26–28	0	0	0	0	0	1	2	1	1	1	1	1	2	60	3	6	5	4	4	2	2	1	2	1	1
28–30	0	0	0	0	1	0	1	1	0	1	1	2	1	3	59	5	4	6	4	3	1	2	1	1	1
30–32	0	1	1	0	0	0	1	1	0	1	1	1	1	1	2	61	3	2	9	5	2	2	1	1	1
32–34	0	0	0	1	1	0	1	1	1	1	1	0	1	2	2	1	58	4	5	5	5	2	5	3	1
34–36	0	0	0	0	1	1	0	1	0	0	1	2	1	1	0	1	0	64	2	5	7	6	2	2	1
36–38	1	0	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	2	62	3	2	5	5	5	3
38–40	1	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	2	3	2	63	3	4	5	3	4
40–42	0	1	1	0	1	1	1	1	1	1	2	1	2	1	1	1	1	1	2	1	61	5	8	4	4
42–44	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	60	6	8	9
44–46	1	1	0	1	0	1	1	1	1	1	1	1	3	1	1	4	1	2	1	3	1	3	63	3	7
46–48	1	1	1	1	1	1	1	1	1	1	1	1	2	3	1	1	2	1	1	2	3	4	3	64	3
48–50	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	2	2	3	2	2	2	3	67

at time = t (row label, left side)

rel. sem. — 1 % (top) to 0 % (bottom)

Fig. 1. 3-year transition matrix for the biomass. The states are the biomass ranges in 10^3 kg/ha, spanning from $0 - 2$ to $48 - 50$ 10^3 kg/ha, and represented here on the left and on top of the matrix. The values $M(i,j)$ inside the matrix correspond to the rounded probability of transition from state i to state j. The color represents the relative standard error of the mean and indicates the robustness of the stochastic search, as explained in Section 4.3. Lighter colors thus indicate a better confidence in the transition value; all relative standard errors of the mean (RSEM) are below 1%, corresponding to a very high confidence, and furthermore the smallest errors are found for the higher transition probabilities close to the diagonal.

4.3. Model validation

Two main types of error should be considered when designing a model with a parameter search based on real data. The first error relates to the robustness and efficiency of the estimation of the optimal transition matrix, which was performed with Gibbs sampling in our case. The second type of error encompasses more broadly the capacity of the chosen theoretical framework to predict the system beyond the range of the dataset. In our case, the theoretical framework we relied on is patch-mosaic concept, implemented with the Markov chain machinery, to describe the dynamics of our four characteristics.

17

327   To estimate the errors of the parameter search, we used the $R(H - B)$ transition matri-

328   ces to compute for each transition the standard error of the mean (SEM) and the relative

329   standard error of the mean (RSEM, defined as the ratio of the SEM over the transition prob-

330   ability, and expressed as a percentage). The SEM were below 1% throughout the matrices,

331   with the highest errors occurring for very low transition probabilities (i.e., far from the diag-

332   onals). Furthermore, the RSEM were very low, and particularly so for the transitions with

333   the highest probability (Fig. 1 in main text as well as Figs. 7 and 8 in Appendix). We finally

334   computed the SEM in the long-term predicted equilibriums and found values below 0.01%,

335   strengthening the conclusion that negligible errors are to be attributed to the stochastic fit

336   procedure.

337   An independent dataset would be most suited to estimate the more general errors in

338   the ability of a Markov-Chain model to predict future forest characteristics. As there is no

339   such dataset available, we performed two cross-validations of our methodology by splitting

340   this dataset in two different ways. In the first, we ran the Gibbs sampler with only the

341   first 18 years of records (from 1970 to 1988). We then used the model to predict forest

342   state for the period corresponding to the second half of the dataset (i.e., 1989 to 2007), and

343   we compared the predicted dynamics with the aggregated distribution of the second half

344   of the dataset (Fig. 2). Overall, the predictions were highly accurate, with R^2 between

345   observation and prediction ranging from 0.8 to 0.95, indicating that the second half of the

346   dataset is predictable with a Markov chain model based solely on the first half. In the

347   second validation, we randomly split the data into two sets, regardless of year. We then

348   computed the transition matrix and corresponding equilibrium conditions for each half (Fig.

349   9 in Appendix). Here again, the predictions match closely with values of R^2 higher than 0.98

350   for the internal diversity, shade tolerance index and average age. The R^2 was near 0.6 for

351   the biomass, indicating that this variable is more sensitive to small changes than the others;

352   however the difference in predictions were small, typically around 1% for each biomass state.

353   This second validation overall showed that the data contained in the inventory is redundant,

354   and that half of it is enough to provide highly accurate long-term estimates for the internal

18

355 diversity, shade tolerance index and average age. Considering only half of the data at random

356 would likely result in errors of around 1% in the long-term estimates of the biomass.
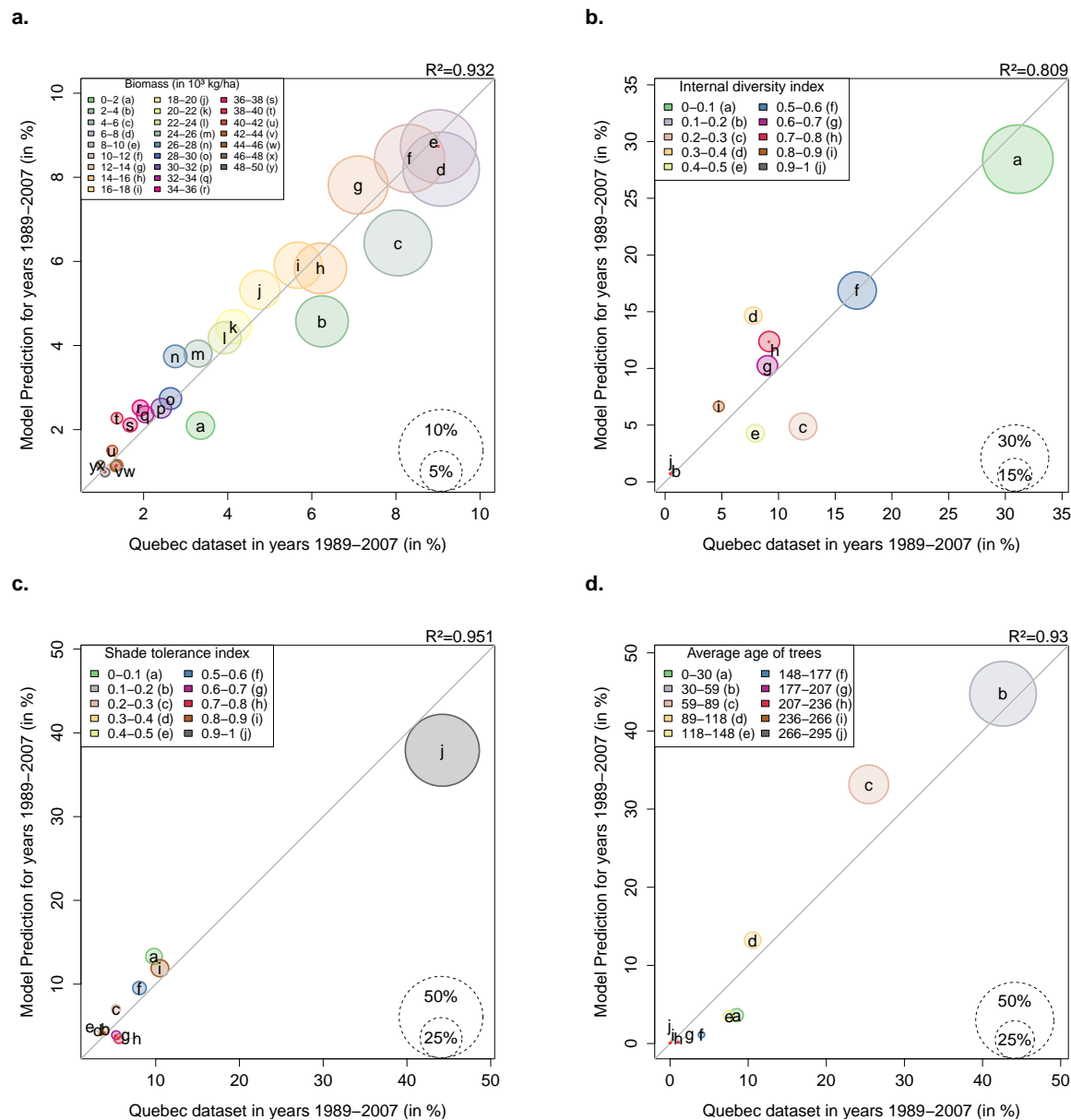

Fig. 2. Results of model validation, showing the second half of the dataset *vs* the model prediction for the classes of each characteristic (distribution in %). For each class, the circle size denotes the number of stands belonging to it in the real dataset. The R^2 measure is indicated on the top right of each plot. The model used to make the prediction was computed using only the first half of the dataset, corresponding to years 1970 to 1988 (see Materials & Methods for details).

19

357 *4.4. Predictions of temporal dynamics and long-term equilibrium*

358   We applied the inferred transition matrix to predict the state of forest in 2010s, 2020s

359 and 2030s based on their distribution in 2000s. We also predicted the long-term dynamics

360 of the forest stands, by computing the equilibrium states of the transition matrices. Overall,

361 the predictions showed an increase in biomass and stand age (Fig. 3 e and h), along with

362 a slight increase in biodiversity (Fig. 3 f) and a slight decrease of the prevalence of late

363 successional species accompanied by a slight increase of early successional species (Fig. 3 g).

364 These predictions are obvious for the biomass and average age of trees by looking at their

365 distributions in the existing dataset (Fig. 3 a and d), while they are less clearly seen when

366 looking at the average distributions of the biodiversity and shade tolerance index (Fig. 3 b

367 and c).

20
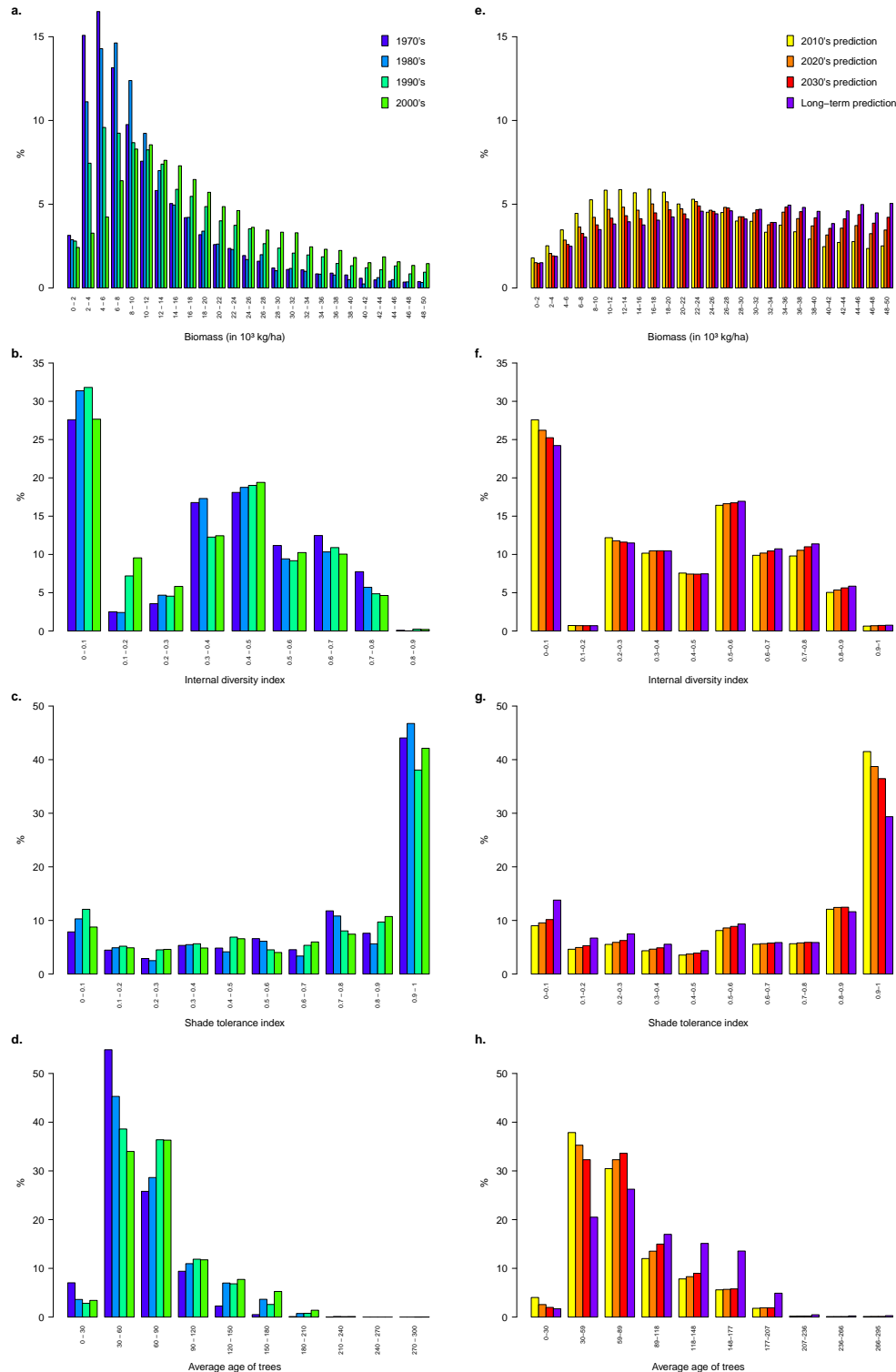
Fig. 3. Current distribution of relevant characteristics from the database, along with the long-term predictions of our models.

368   These long-term predictions were reached at different timescales depending on the char-

369 acteristics. For biomass, equilibrium was reached by approximately year 2030, but the other

370 characteristics, and in particular the average age of trees in plots, showed much slower dy-

371 namics to reach their equilibria (Fig. 3 e to h). The model predicted average relative changes

372 of +38.9% and +14.2% by the 2030s for biomass and stand age, and +44.0% and +37.9% by

373 the time they reach their long-term equilibrium state. Relative changes for the Gini-Simpson

374 diversity index were +5.2% by the 2030s and +7.1% in the long term, and early successional

375 species will become slightly more abundant with a change of -4.7% of the shade tolerance

376 index by the 2030s and -13.6% in the long term.

377 5. Discussion

378 We developed a data-intensive approach to multiple-dimensional modeling of forest dy-

379 namics. The modeling steps include 1) dimensional analysis of forest inventory data, 2)

380 extraction of non-correlated dimensions, and 3) the application of stochastic optimization to

381 compute probability transition matrices for each dimension. We applied this approach to the

382 Quebec forest inventory dataset and validated the model using two independent subsets of

383 data. Our study demonstrates that there exist at least four uncorrelated dimensions in Que-

384 bec forests: the biomass, biodiversity, shade tolerance index and averaged age of trees. The

385 most pronounced changes predicted for Quebec forests are increases in biomass and stand

386 age. Our model also predicted smaller increases in biodiversity in the prevalence of early

387 successional species. Our results demonstrate the utility of this methodology in predicting

388 long-term forest dynamics given highly dimensional, irregularly sampled data; the model was

389 computationally efficient and validation procedures demonstrated its ability to make short

390 and long-term predictions. Therefore, the framework will be useful both in applied contexts

391 (e.g., conservation, silviculture) as well as in developing our conceptual understanding of

392 how forested ecosystems are organized through dimensional analysis of forest characteristics

393 under the current disturbance regime.

22

5.1. Contribution to Markov chain forest modeling framework

Markov chain models have a rich history of application in ecology, and, in particular, in forest modeling (Facelli and Pickett, 1990; Caswell, 2001). This modeling framework has been employed to describe forest transitions at different scales with various focal variables, for example, succession models defined on the species and forest type level (Usher, 1969, 1981; Waggoner and Stephens, 1970; Horn, 1974; Logofet and Lesnaya, 2000; Korotkov et al., 2001), gap mosaic transition models (Acevedo et al., 1996, 2001) and biomass transition models (Strigul et al., 2012). Markov chain successional models (Usher, 1969, 1981, 1979b; Facelli and Pickett, 1990) are able to predict changes in species abundance, but require a comprehensive knowledge of successional sequence of species replacement and transition probabilities between different successional stages. The empirically-based Markov chain forest succession model, which operates at the species level and assumes that the underlying Markov chain is stationary, requires only substantially large observations to estimate transition probabilities (Waggoner and Stephens, 1970; Stephens and Waggoner, 1980). On the contrary, the mechanistic Markov chain modeling approach developed by Horn (1974, 1981) employs shade tolerance and gap dynamics to predict species replacement in the forest canopy given the species composition in the understory. However, this approach requires a detailed survey of the understory vegetation that is not commonly available in forest inventories. Also, gap dynamics individual-based models can be coupled with Markov chain models for scaling of gap dynamics to patch level (Acevedo et al., 1996, 2001). These transitional models have been demonstrated to be useful and relevant tools in forest prognosis, however their practical applications are often limited. The Bayesian methodology proposed in this study allows to extend the scope of transition matrices by allowing their computation directly from forest inventory data, with corresponding modifications of the R code provided as a supplementary material. The proposed methodology of matrix estimation could be employed to test the validity of the Markov chain homogeneity assumption.

23

⁴²⁰ *5.2. A data-intensive approach to understand forest dynamics*

⁴²¹   Modeling complex adaptive systems such as forest ecosystems requires capturing the

⁴²² dynamics of biological units at multiple scales and in multiple dimensions (Levin, 1998,

⁴²³ 2003). Ideally, a mechanistic model based on the physiological processes and interactions

⁴²⁴ of individual organisms should simulate the observed forest structure and predict forest

⁴²⁵ dynamics over different time horizons and environmental variables. However, such individual-

⁴²⁶ based modeling is very challenging as interactions between individual organisms within the

⁴²⁷ forest stand result in new properties at the stand level, where essential mechanisms, spatial

⁴²⁸ dimensions of variables, and functional relationships between variables are largely unknown.

⁴²⁹ Given these unknowns, a data-intensive approach can be useful for gaining insight into

⁴³⁰ ecosystem dynamics provided that sufficient amounts of relevant data are available (Kelling

⁴³¹ et al., 2009; Michener and Jones, 2012). In particular, the matrices we estimated (see Fig.

⁴³² 1 in main text and Figs. 7 and 8 in Appendices) incorporate all forest changes related to

⁴³³ different magnitude disturbances. This opens a possibility of the future investigation of how

⁴³⁴ particular disturbances are reflected in the forest macroscopic characteristics and can lead

⁴³⁵ to a logical extension of classic models that take into account only major disturbances, in

⁴³⁶ particular, birth-and-disaster Markov chains (Feller, 1971), forest fire models (Van Wagner,

⁴³⁷ 1978), and advection-reaction equations for patch dynamics (Levin and Paine, 1974) .

⁴³⁸   A potential limitation to a mechanistic interpretation of the transition matrices arises

⁴³⁹ from the Markovian assumption that the transition toward the next state depends solely

⁴⁴⁰ on the current state. If this assumption is not valid, it could bias these models. This

⁴⁴¹ assumption warrants further attention as it has not been yet comprehensively evaluated in

⁴⁴² forest modeling.

⁴⁴³   Integral Projection Model (IPM) is another modeling framework that could be used in

⁴⁴⁴ place of Markov chains (Easterling et al., 2000; Caswell, 2001). In IPM, continuous kernel

⁴⁴⁵ functions are used instead of discrete transition probabilities. While IPM are by design suited

⁴⁴⁶ to handle well data irregularly distributed across the states, they do not address explicitly

⁴⁴⁷ the issue of sampling irregularities in time. The data augmentation approach developed here

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448 can however be transposed to parameterizing IPM as well. Markov chains are preferable in

449 our application because they are not restricted by the choice of IPM kernels. Indeed, biomass

450 and stand age transitions can be decomposed into several kernels using commonly accepted

451 assumptions of growth and disturbances, however there is no obvious way to choose kernels

452 for biodiversity and shade tolerance index as their dynamics can not be understood in terms

453 of a monotonic progression toward high values (Lienard et al., 2014).

454 The application of MCMC procedures allows to compute transition matrices for datasets

455 with irregular sampling intervals and sample sizes. While Gibbs sampling has been intro-

456 duced 30 years ago (Geman and Geman, 1984), its application to handle missing data in

457 ecology has been mostly limited to stochastic patch occupancy models with a low number of

458 free parameters (5-6) and either artificially simulated data or relatively restricted datasets

459 (e.g. 72-228 resampled locations in ter Braak and Etienne, 2003; Harrison et al., 2011; Risk

460 et al., 2011). From the technical point of view, our application of MCMC differs by taking

461 advantage of the absolute time independence of Markov chains (allowing us to align sub-

462 sequences starting with a known observation, see Methods and Appendix 1.1). This makes

463 the use of MCMC possible in a data-intensive context, in which both the number of free

464 parameters (600 for the biomass matrix, 90 for each of the biodiversity, shade tolerance and

465 stand age matrices) and the number of samples (32,552) constitute increases of several or-

466 ders of magnitude. Similar irregularity problems are quite common in ecological datasets,

467 and the presented approach may have numerous applications beyond the statistical analysis

468 of forest inventories. This methodology can also be applied to other datasets, even with

469 regular samplings, and the same methodology can be applied to deduce transitions with a

470 finer temporal scale.

471 In this study we have analyzed the Quebec forest inventories without explicitly taking

472 into account the geographical location of plots, as well as the environmental and climatic

473 variables. We have obtained transition matrices covering temperate to boreal forests, with

474 a disturbance regime varying from canopy gaps to disastrous fires. We have repeated the

475 developed approach after subdividing the Quebec dataset into the major ecological domains

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476 and have not observed substantial differences between the resulting transition matrices and
477 the general matrices presented in this study (Liénard et al. unpublished data). In addition
478 to this, the biomass transition matrices computed for the Lake States in the US (see Strigul
479 et al. (2012) Tables 2 and 3) and the shade tolerance index transition matrices computed in
480 northeastern parts of the US (Lienard et al., 2014) are quite similar to the ones presented
481 in this study. It is quite amazing in fact that we could represent the dynamics of stand
482 level characteristics given the neglection of geography. We hypothesize that the forest stand
483 dynamics as well as disturbance regimes have substantial similarities across a large number
484 of boreal and temperate forest types, and this will be specifically addressed in our future
485 studies. We believe that the ability to make broad predictions on the forest stand dynamics
486 without going into the fine details of geography is one of the major strengths of our approach.

487 The patch-mosaic framework has been already extensively employed in forest model-
488 ing (Kohyama et al., 2001; Kohyama, 2006; Scherstjanoi et al., 2013). Our approach has
489 substantial similarities with the previous studies using the same scientific background (see
490 Appendix 1), however there are distinctions related to the definitions of the forest patch.
491 The forest stand or (forest patch) in this work represent a unit of forest which is large
492 enough to be a community of trees, where individual tree gap dynamics is averaged, but
493 at the same time small enough to be a subject to intermediate and large scale disturbances
494 (Strigul et al., 2012)[p.72]. This definition results in an estimate of about 0.5-1 ha, which
495 allows to use forest inventory permanent plots directly as an approximate forest stand rep-
496 resentations (the size of the standard Quebec forest inventory plot is about 625 m^2 and the
497 USDA FIA plot is 675 m^2). In other application of patch-mosaic concept to forest dynamics
498 the patches (stands) are often defined differently. The size of patches varies from the size
499 of large individual trees (in this case the patch dynamics is essentially equivalent to the gap
500 dynamics Kohyama et al., 2001; Kohyama, 2006; Moorcroft et al., 2001), through patches
501 similar to employed in our study (Acevedo et al., 2001) to the much large forest patches
502 representing many hectares of forest (Boychuk et al., 1997). The difference in definitions of
503 the patch essentially reflects the different applications and questions that can be addressed

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504 with particular models (see Strigul et al. (2012)[p.71] for an additional discussion).

505 5.3. Predictions for forest dynamics in Quebec

506 Our model made several notable predictions about future forest dynamics in Quebec.
507 The most pronounced predicted changes are substantial short-term increase in biomass and
508 a longer-term increase in average age of trees (Fig. 3). The increase in biomass is intuitively
509 consistent with the increase in stand age, and both demonstrate a progression toward more
510 mature stands. This progression is to be sustained throughout the next 20 years and beyond
511 (Fig. 3), thus meaning that the unmanaged forests sampled in the inventory are currently
512 far from their equilibrium state. The model also predicted smaller changes in biodiversity
513 and the shade tolerance index. To understand stand maturation occurring with the small
514 increase in the prevalence of early successional species, we must recall that neither biomass
515 nor stand age are significantly correlated with shade tolerance index in the dataset (e.g.,
516 $r = -0.02$ with 95% confidence interval [-0.03,-0.01] for biomass and shade tolerance, see
517 Fig. 5 in Appendix). Thus, it is unsurprising that the predictions are not correlated.
518 Further, the predicted changes happen with different temporal dynamics and have different
519 magnitudes, and have probably distinct mechanisms. In particular, while biomass and stand
520 age are affected by both individual tree growth (leading to an increase) and disturbances
521 (leading to a decrease), the shade tolerance index is affected only by disturbances. On
522 the one hand, small disturbances (e.g., individual tree mortality) will typically promote
523 the recruitment of late successional species into the canopy through gap dynamics. On
524 the other hand, intermediate and large-scale disturbances will facilitate early successional
525 species via the development of large canopy openings (e.g. Taylor and Chen, 2011). Thus,
526 increase of intermediate and large-scale disturbances may promote early successional species,
527 while the overall increase in biomass and stand age would result largely from individual tree
528 growth. Our work thus suggests that Quebec forests are not progressing toward higher shade
529 tolerance states despite their continuous biomass and stand age growth. This result echoes
530 recent studies which showed that shade tolerance is not the sole driver for forest succession
531 in Canadian central forests (Taylor and Chen, 2011; Chen and Taylor, 2012).

₅₃₂ The accurate prediction of the second half of the dataset obtained using only the first half

₅₃₃ of the dataset demonstrate that the natural disturbance regime in the forest plots sampled

₅₃₄ in the Quebec inventory did not change substantially over the last 30 years. In the context

₅₃₅ of global warming, this could mean either that (a) there is no substantial consequence yet

₅₃₆ on the macroscopic dynamics of Quebec forests or that (b) the climatic change consequences

₅₃₇ were already present in the first half of the dataset or that (c) our analysis is not fine enough

₅₃₈ to catch the signal of the recent climate change (in particular moving climatic boundaries,

₅₃₉ cf. McKenney et al., 2007, are not taken into account as the approach developed here is not

₅₄₀ spatially explicit). In all cases, the inclusion in the transition matrices of future disturbances

₅₄₁ induced by climatic change (e.g. the increase of forest fire reviewed in Flannigan et al.,

₅₄₂ 2009) could be a promising follow-up of our work by providing quantitative insights on the

₅₄₃ consequences of global warming on forests. The study of changes in disturbances was not

₅₄₄ the focus of the current study, and we have to be careful in generalizing conclusions about

₅₄₅ global warming as the gradual non-stationary disturbance regimes might take from 50 to

₅₄₆ 100 years to show significant departures (Loudermilk et al., 2013; Rhemtulla et al., 2009;

₅₄₇ Thompson et al., 2011).

₅₄₈ The multidimensional nature of forest stands creates substantial challenges for modeling.

₅₄₉ Our study demonstrates that at least four dimensions are uncorrelated in the Quebec dataset,

₅₅₀ and that stand characteristics cannot be collapsed around one variable. The data intensive

₅₅₁ model could be based on uncorrelated principal component axes. However, such a model

₅₅₂ would not lend itself to a simple mechanistic interpretations in terms of macroscopic forest

₅₅₃ characteristics. Therefore, we have developed the model using the mostly uncorrelated stand

₅₅₄ characteristics: biomass, biodiversity, shade tolerance index, and average age of trees. In

₅₅₅ this model, the small correlations between these characteristics (Figure 3 in Appendix) will

₅₅₆ propagate to the model predictions, potentially resulting in slightly correlated predictions,

₅₅₇ in contrast with a model developed on the principal components. However, this choice of

₅₅₈ dimensional variables has the decisive advantage of allowing for the meaningful interpretation

₅₅₉ of the transition matrices and predictions.

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560 The constructed transition matrices have predictive power, as demonstrated in Section

561 4.3. However, the universality of the predictions is intrinsically dependent on the repre-

562 sentativity of the dataset, and a bias in data collection will be reported in the predictions.

563 For this particular dataset for instance, we observed (and also predicted) increasing biomass,

564 diversity, age and slight decreasing shade tolerance over time. However we should not expect

565 forest stands affected by additional silvicultural operations, such as logging, to follow the

566 trajectory recorded in the Quebec dataset. Thus, predictions made with this dataset should

567 not be extended to them.

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