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Modeling Population Dynamics and Woody Biomass in Alaska Coastal Forest

Randy L. Peterson, Jingjing Liang, and Tara M. Barrett

Alaska coastal forest, 6.2 million ha in size, has been managed in the past mainly through clearcutting. Declining harvest and dwindling commercial forest resources over the past 2 decades have led to increased interest in management of young-growth stands and utilization of woody biomass for bioenergy. However, existing models to support these new management systems are very limited in number and value. This study presents a density-dependent, size-specific, and species-specific matrix growth model for forest in coastal Alaska. This model enables short- and long-term predictions of stand basal area, volume, and biomass in a simple and accurate way and facilitates understanding of the ecological and economic effects of forest management alternatives. Components of forest growth were estimated from tree- and stand-level attributes from repeated measurements of 544 Forest Inventory and Analysis permanent sample plots located throughout coastal Alaska with a wide range of stand conditions. The model was tested on 293 postsample validation plots and found to have significantly higher accuracy than the Forest Vegetation Simulator, the only growth model available for the region. Analysis of residuals revealed no spatial autocorrelation, which indicates that this model is able to adequately account for the effects of physiographic factors and other differences between southeast and southcentral Alaska.

Keywords: matrix model, forest management, population structure, spatial autocorrelation

Alaska coastal forest is 6.2 million ha in size with 2.6 million ha of timberland (Barrett and Christensen 2011). Geographically, the region spans roughly 25° longitude and 8° latitude across seven ecoregions and numerous forest types (Nowacki et al. 2001). The region is composed of two distinct parts, southeast and southcentral Alaska (Viereck and Little 1975). Shade-tolerant conifers dominate the maritime southeast Alaska landscape that is often characterized by steep slopes and temperate weather. Coastal and boreal tree species occupy different niches across the transitional ecoregion zone in southcentral Alaska, where climatic conditions are a mixture of maritime and continental and vary by location (Nowacki et al. 2001).

Alaska's coastal forest is dominated by seven conifers of moderate to high shade tolerance—*Tsuga heterophylla* (Raf.) Sarg. (western hemlock), *Picea sitchensis* (Bong.) Carr. (Sitka spruce), *Tsuga mertensiana* (Bong.) Carr. (mountain hemlock), *Chamaecyparis nootkatensis* (D. Don) Spach (Alaska yellow-cedar), *Thuja plicata* Donn ex D. Don (western redcedar), *Picea glauca* (Moench) Voss (white spruce), *Picea mariana* (Mill.) B.S.P. (black spruce)—that comprise more than 90% of total basal area (Table 1). Deciduous *Betula papyrifera* Marsh. (paper birch), *Populus trichocarpa* Torr. & Gray (black cottonwood), *Populus tremuloides* Michx. (quaking aspen), *Alnus rubra* Bong. (red alder), and shade-intolerant *Pinus contorta* Dougl. ex. Loud. (lodgepole pine) account for less than 10% of the total basal area.

Forest management in the region has been dominated by harvesting old-growth forests using clearcutting (Deal 2007, Halbrook et al. 2009). Declining harvest and dwindling commercial forest resources over the past 2 decades (Brackley et al. 2009) have led to a new era of forest management that is characteristic of various efforts to stimulate the industry through strategies such as the alternatives to the clearcutting (ATC) program (McClellan et al. 2000), managing young-growth stands (Barbour et al. 2005, USDA Forest Service 2008), and utilizing woody biomass for bioenergy (Alexander et al. 2010). At present, there is little information available regarding the effects of uneven-aged forest management on coastal Alaska forest, despite its wide prescription in the region (USDA Forest Service 2008), and experimental results are not available yet (Deal 2007).

The existing growth-and-yield models are of limited value for these new management systems for several reasons. The Forest Vegetation Simulator (FVS) Southeast Alaska variant (FVS-

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Affiliations: *Randy L. Peterson, University of Alaska Fairbanks. Jingjing Liang (alpenbering@gmail.com), University of Alaska Fairbanks, Forest Sciences, Fairbanks, AK. Tara M. Barrett, USDA Forest Service, Pacific Northwest Research Station.*

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; square meters (m^2) = 10.8 ft^2; cubic meters (m^3): 1 m^3 = 35.3 ft^3; hectares (ha): 1 ha = 2.47 ac; millimeters (mm): 1 mm = 0.039 in.; kilometers (km): 1 km = 0.6 mi; kilograms (kg): 1 kg = 2.2 lb.

Table 1. Percent basal area and frequency of live trees in all sample plots.

Common name	Scientific name	Basal area	No. of trees
		.....(%).....	
Western hemlock	*Tsuga heterophylla*	35.11	32.77
Sitka spruce	*Picea sitchensis*	21.29	14.79
Mountain hemlock	*Tsuga mertensiana*	15.36	18.53
Alaska cedars		19.47	17.61
Alaska yellow cedar	*Chamaecyparis nootkatensis*	11.22	12.01
Western redcedar	*Thuja plicata*	8.25	5.59
Boreal spruce		2.21	6.22
White spruce	*Picea glauca*	1.72	4.20
Black spruce	*Picea mariana*	0.49	2.01
Other species		6.56	10.08
Lodgepole pine	*Pinus contorta*	2.67	4.13
Paper birch	*Betula papyrifera*	1.97	2.99
Black cottonwood	*Populus trichocarpa*	1.15	1.72
Quaking aspen	*Populus tremuloides*	0.54	0.74
Red alder	*Alnus rubra*	0.22	0.47
Subalpine fir	*Abies lasiocarpa*	0.02	0.03
All species		100.00	100.00

SEAPROG) lacks sufficient observations in model calibration for *Picea* species (Ritchie 1999, Keyser 2008) and has been found to be problematic when it is used to predict outcomes of silviculture treatments other than clearcutting (McClellan and Biles 2003, McClellan 2005). The three growth-and-yield tables (Taylor 1934, Meyer 1937, Barnes 1962) for the region are designed for even-aged stands and do not provide the details demanded by current resource managers (Ritchie 1999).

To better understand the ecological and economic effects of various ATC systems on Alaska coastal forest, in this study we developed a matrix model of forest dynamics and linear models of stem volume and biomass based on permanent sample plot data collected throughout the region. The prediction accuracy of the present model in comparison with that of existing growth-and-yield models for the region was evaluated with an independent validation data set. Spatial autocorrelation was investigated to determine whether the present model could be reliable in large-scale applications.

Data and Methods

Data

Data used to calibrate the matrix model of forest dynamics came from the Alaska Forest Inventory and Analysis (FIA) database (Grimm and Railsback 2005). FIA field data are from a systematic sample of forested areas across all private and public lands (excluding wilderness) in the coastal Alaska region and consist of four circular 0.017-ha (0.042-acre) subplots. Permanent sample plots (PSPs) selected for model calibration in this study met the following three criteria: a selected PSP must be classified as forested land (O'Connell et al. 2013) and remeasured at least once, at least one live tree must exist at the time of both measurements, and no evidence of silvicultural treatments or any other forms of vegetation manipulation is seen in a selected PSP. A total of 788 PSPs across the Alaska coastal region were selected with these criteria. To test model accuracy and spatial autocorrelation, we took a simple random sample of the modeling data and held 244 FIA PSPs for validation. This was combined with an independent sample data set of 49 Cooperative Alaska Forest Inventory (CAFI) (Malone et al. 2009) PSPs located in the boreal-coastal transition zone of southcentral Alaska, which made a total of 293 validation plots (Figure 1). CAFI plots were established and measured similarly to FIA plots, with the exception that each CAFI plot consisted of three 0.04-ha (0.1-acre) subplots.

The 13 tree species in Alaska coastal forest were integrated into six species categories (Table 1). Western hemlock, mountain hemlock, and Sitka spruce, each constituted an independent species category because of their abundance and commercial importance in the region. Western redcedar and Alaska yellow-cedar were grouped as Alaska cedars because they had similar growth characteristics and geographic distributions (Viereck and Little 1975). Similarly, black spruce and white spruce were combined into boreal spruce because of their similar growth patterns and natural range (see Liang 2010). All the remaining species account for less than 7% of the total stocking and were combined into one category labeled as other species.

All variables and their units are defined in Table 2. Stand diversity measures (H_d, H_s) were calculated by Shannon's formula

$$H_d = -\sum_{j=1}^{n}\frac{B_j}{B}\ln\left(\frac{B_j}{B}\right),\ H_s = -\sum_{i=1}^{k}\frac{B_i}{B}\ln\left(\frac{B_i}{B}\right) \quad (1)$$

where B_j, B_i, and B are, respectively, the basal area of size class $j = 1, \ldots, n$, species group $i = 1, \ldots, k$, and total basal area. According to the summary statistics of plot-level variables (Table 3), the average and maximum stand basal areas of Alaska coastal forest were higher than those of the productive Douglas-fir/western hemlock forests in the US Pacific Northwest (Liang et al. 2005), which together with the domination of climax species in terms of stem density (Table 3) are indicative of the large amount of Alaska coastal forest that maintains old-growth characteristics. Western hemlock has the highest recruitment (R) and total stem density (N), whereas Alaska cedars have the lowest recruitment but are medium in total stem density. Average stand basal area is 32.05 $m^2 \cdot ha^{-1}$ and gross aboveground timber volume is 271.29 $m^3 \cdot ha^{-1}$ (Table 3). High correlations between some plot-level variables, the highest being 71.2% between basal area (B) and tree size diversity (H_d), suggest that multicollinearity needs to be addressed in model development.

At the individual tree level (Table 4), Sitka spruce had the largest dbh (D) and highest average annual diameter growth (g). Boreal spruce had the highest mortality rate (m) and the second highest g, which was nearly twice the growth rate of the same species in interior Alaska (Liang 2010). The lowest diameter growth was seen for western hemlock, mountain hemlock, and Alaska cedars. The high SDs observed in all plot-level (Table 3) and tree-level (Table 4) variables reflect the wide variety of site and structural conditions represented by this data set.

Matrix Model Structure

A matrix model of forest dynamics (hereafter, matrix model) was developed to study the ecological and economic effects of various ATC systems. With use of transition or probability matrices to predict future plant and animal population structures, matrix models have been employed to study the dynamics of forests all over the world (for a review, see Liang and Picard 2013). We chose to develop a matrix model in this study for three major reasons. First, matrix models primarily deal with temporal changes of structured forest populations and can be directly coupled with a diameter-biomass model to predict the dynamics of woody biomass and aboveground carbon (e.g., Picard et al. 2009); matrix models, because of their demographic nature, have been used extensively to study the

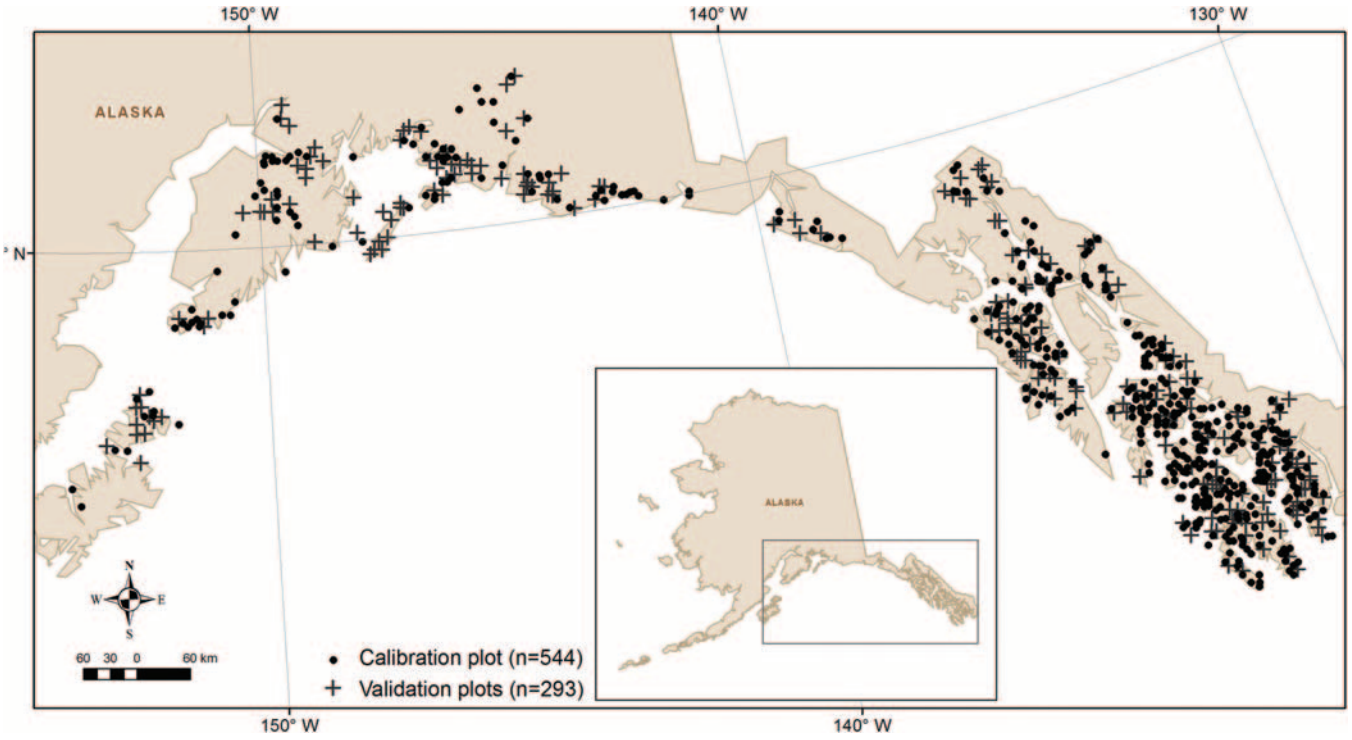

Figure 1. Location of the study area within the State of Alaska (inset) and geographic distribution of the sample plots used to calibrate and validate the matrix growth model. Alaska Albers Equal Area Conic projection.

Table 2. Definition and units for variables used in this study.

Variable	Units	Definition/explanation
$a°$		Plot aspect
B	$m^2 \cdot ha^{-1}$	Total stand basal area
C	$m^2 \cdot ha^{-1} \cdot yr^{-1}$	Site productivity
D	cm	Dbh
E	km	Plot elevation
g	$mm \cdot yr^{-1}$	Annual diameter growth
H_d		Tree size diversity
H_s		Tree species diversity
m	yr^{-1}	Average annual mortality rate
Q	$kg \cdot ha^{-1}$	Total stand gross biomass (oven-dry weight including top, stem, and limbs, except foliage)
N	$trees \cdot ha^{-1}$	No. of trees per ha
R	$trees \cdot ha^{-1} \cdot yr^{-1}$	Total stand recruitment, no. of trees per ha that grew into the smallest diameter class (12.70–18 cm) in a year
$S°$		Average slope of each subplot
T	yr	elapsed time between inventories
V	$m^2 \cdot ha^{-1}$	Total stand gross aboveground timber volume

Table 3. Summary statistics for plot-level variables.

Variables	Mean	SD	Maximum	Minimum
B ($m^2 \cdot ha^{-1}$)	32.05	23.08	138.09	0.19
C ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	2.89	2.45	17.02	0.66
H_d	1.66	0.57	2.50	0.00
H_s	0.59	0.40	1.45	0.00
Q ($kg \cdot ha^{-1}$)	182,597	184,749	1,545,519	357
T (yr)	8.03	2.64	13.10	1.00
V ($m^2 \cdot ha^{-1}$)	271.29	277.06	2,338.49	0.39
N ($trees \cdot ha^{-1}$)				
Western hemlock	134.03	168.65	1,323.51	0.00
Mountain hemlock	75.80	161.50	1,397.87	0.00
Sitka spruce	60.50	143.64	1,457.35	0.00
Alaska cedars	72.00	131.60	951.74	0.00
Boreal spruce	25.42	83.21	654.32	0.00
Other species	41.22	80.99	490.74	0.00
R ($trees \cdot ha^{-1} \cdot yr^{-1}$)				
Western hemlock	1.30	2.96	28.09	0.00
Mountain hemlock	0.59	1.96	24.78	0.00
Sitka spruce	0.93	3.74	40.78	0.00
Alaska cedars	0.48	1.41	13.64	0.00
Boreal spruce	0.93	3.23	26.77	0.00
Other species	0.59	3.62	69.98	0.00

T and R are between the two inventories, and all the remaining variables are at the time of the first inventory.

outcomes of a broad range of forest management regimes and silvicultural treatments (e.g., Buongiorno et al. 1995), and, last, but not least, matrix models can be easily incorporated into user-friendly computer simulation programs to facilitate forest management planning and education (e.g., Schulte et al. 1998, Liang et al. 2006).

Similar to the matrix models developed for Douglas-fir/western hemlock forest in the Pacific Northwest (Liang et al. 2005) and for Alaska boreal forest (Liang 2010), the matrix model presented here is stand-specific, i.e., the transition matrices and projections are derived not only from the structure and composition of forest populations but also from the site productivity and/or physiographic conditions at specific locations. A stem volume and a stem biomass model were also developed and incorporated into the matrix model to enable an analysis of the volume and biomass output of ATC systems.

A forest matrix model predicts the structured population dynamics of forest stands from time t to $t + 1$

$$\mathbf{y}_{t+1} = \mathbf{G} \cdot \mathbf{y}_t + \mathbf{R} + \boldsymbol{\varepsilon} \quad (2)$$

where $\mathbf{y}_t = [y_{ijt}]$ is a vector of live trees at time t of size class $j = 1, \ldots, n$ and species group $i = 1, \ldots, k$. $\boldsymbol{\varepsilon}$ is the error term. $\mathbf{G}$ and $\mathbf{R}$

Table 4. Summary statistics for tree-level variables.

	Species					
	Western hemlock	Mountain hemlock	Sitka spruce	Alaska cedars	Boreal spruce	Other species
D (cm)						
Mean	28.03	25.74	31.28	28.56	17.74	23.66
SD	16.38	12.99	19.48	16.46	5.28	9.32
Maximum	116.33	107.69	147.32	141.47	47.49	67.31
Minimum	12.70	12.70	12.70	12.70	12.70	12.70
n	4,521	2,573	2,066	2,483	826	1,366
g (cm · yr^{-1})						
Mean	0.12	0.09	0.22	0.09	0.21	0.17
SD	0.11	0.10	0.22	0.11	0.16	0.19
Maximum	0.64	0.51	1.21	0.58	0.74	0.95
Minimum	−0.18	−0.24	−0.16	−0.35	−0.24	−0.27
n	4,521	2,573	2,066	2,483	826	1,366
m (yr^{-1})						
Mean	0.005	0.005	0.006	0.003	0.018	0.009
SD	0.024	0.025	0.027	0.017	0.060	0.034
Maximum	0.476	1.000	1.000	0.169	0.476	0.476
Minimum	0.000	0.000	0.000	0.000	0.000	0.000
n	4,858	2,727	2,197	2,596	922	1,483

D is calculated at the first inventory; g and m are between the two inventories. n, number of observations.

are, respectively, the growth and recruitment matrices which are defined as

$$\mathbf{G} = \begin{bmatrix} \mathbf{G}_1 & & & \\ & \mathbf{G}_2 & & \\ & & \ddots & \\ & & & \mathbf{G}_k \end{bmatrix}, \mathbf{G}_i = \begin{bmatrix} s_{i,1} & & & & \\ g_{i,1} & s_{i,2} & \ddots & & \\ & \ddots & \ddots & & \\ & & g_{i,n-2} & s_{i,n-1} & \\ & & & g_{i,n-1} & s_{i,n} \end{bmatrix},$$

$$\mathbf{R} = \begin{bmatrix} \mathbf{R}_1 \\ \mathbf{R}_2 \\ \vdots \\ \mathbf{R}_k \end{bmatrix}, \mathbf{R}_i = \begin{bmatrix} R_i \\ 0 \\ \vdots \\ 0 \end{bmatrix} \quad (3)$$

where $\mathbf{G}$ is the transition matrix of live trees of size j and species group i that stay alive ($s_{i,j}$ denotes the annual stasis rate) or grow into the next size class ($g_{i,j}$ denotes the annual upgrowth rate), and $\mathbf{R}$ is the recruitment of trees for species group $i = 1, \ldots, k$ that enter the smallest size class. $s_{i,j}$ is calculated using the following relationship

$$s_{i,j} = 1 - g_{i,j} - m_{i,j} \quad (4)$$

where $m_{i,j}$ is the annual mortality rate. Trees in this study were sorted into 19 5.08-cm (2-in.) dbh classes. The smallest size class consisted of trees 12.7–17.8 cm (5–7 in.) in dbh, and the largest consisted of trees 104.1 cm (41 in.) and above.

The components of forest dynamics, diameter growth, mortality, and recruitment were modeled with the tree- and plot-level variables listed in Table 2 and so were volume and biomass models. More specifically, diameter and its square (D, D^2) were used in individual tree models (diameter growth, mortality, volume, and biomass) to capture the nonlinear effect of diameter on growth (e.g., Liang et al. 2005). To estimate stand-level recruitment of a species, R_i, we used the number of trees of that species and its square (N_i, N_2^i) to represent the size of the seed bank. Basal area (B) and site productivity (C) are considered key predictors in many existing matrix models, because of their prominent effect on forest dynamics (e.g., Namaalwa et al. 2005). Physiographic variables—elevation (E), slope (S), and aspect [cos(a), sin(a)]—were also included in the present matrix model, because it was hypothesized that each variable could individually affect forest dynamics. In addition, stand diversity measures (H_d, H_s), metrics of size and species diversity, were also used in the model to explicitly account for the effects of diversity on forest dynamics (Liang et al. 2007).

Upgrowth rate ($g_{i,j}$), the probability that a live tree in size class $j = 1, \ldots, n$ at time t would move into size class $j + 1$ at time $t + 1$, was calculated as the annual diameter increment ($d_{i,j}$), divided by 5.08 cm, the width of each size class, assuming that $g_{i,j}$ stays constant within each diameter class. $d_{i,j}$ was estimated with ordinary least squares, and the residuals (ψ_{ij}) were assumed to be independent $N(0, \sigma^2)$. The following equation represents the full model of diameter growth

$$d_{ij} = \alpha_{i1} + \alpha_{i2}D_j + \alpha_{i3}D_j^2 + \alpha_{i4}B + \alpha_{i5}C + \alpha_{i6}E + \alpha_{i7}S + \alpha_{i8}\cos(a) + \alpha_{i9}\sin(a) + \alpha_{i10}H_d + \alpha_{i11}H_s + \psi_{ij} \quad (5)$$

The average annual mortality, m_{ij}, was estimated from M_{ij}, a binary variable representing whether a tree of species i and diameter class j died ($M_{ij} = 1$) or not ($M_{ij} = 0$) between the two inventories over an elapsed time of T years

$$m_{ij} = \frac{P(M_{ij} = 1|\mathbf{x})}{\mathrm{T}} \quad (6)$$

where $P(M_{ij} = 1|\mathbf{x})$ was estimated with a probit model, and its full model is represented by the following equation

$$P(M_{ij} = 1|\mathbf{x}) = \Phi(\delta_{i1} + \delta_{i2}\mathrm{D_j} + \delta_{i3}\mathrm{D_j^2} + \delta_{i4}\mathrm{B} + \delta_{i5}\mathrm{C} + \delta_{i6}\mathrm{E} + \delta_{i7}\mathrm{S} + \delta_{i8}\cos(a) + \delta_{i9}\sin(a) + \delta_{i10}H_d + \delta_{i11}H_s + \xi_{ij}) \quad (7)$$

Recruitment of species i, R_i, was estimated with a Tobit model to explicitly account for total stand recruitment that is left truncated at 0

$$E(R_i|x_i) = \Phi(x_i\beta_i\sigma_i^{-1})x_i\beta_i + \sigma_i\varphi(x_i\beta_i\sigma_i^{-1}) \quad (8)$$

with the full model

Table 5. Estimated parameters of the diameter growth model.

	Model	BIC
Western hemlock		
Full	$1.7546^{***} + 2.2310D^{***} - 2.2513D^{2***} - 0.0064B^{***} + 0.1354C^{***} - 0.5952H_d^{***} - 0.2741H_s^{***} + 0.6753E^{***} + 0.0033S^{***} + 0.0054\cos(a) - 0.1050\sin(a)^{***}$	−7,534.8
Reduced	$1.7585^{***} + 2.2342D^{***} - 2.2541D^{2***} - 0.0065B^{***} + 0.1353C^{***} - 0.5949H_d^{***} - 0.2738H_s^{***} + 0.6747E^{***} + 0.0032S^{***} - 0.1044\sin(a)^{***}$	−7,543.2
Mountain hemlock		
Full	$1.8709^{***} - 0.0827D - 0.4595D^2 - 0.0003B + 0.0828C^{***} - 0.4512H_d^{***} - 0.5680H_s^{***} - 0.2919E^{**} + 0.0054S^{***} - 0.0550\cos(a)^{*} - 0.0082\sin(a)$	−4,574.3
Reduced	$1.8490^{***} + 0.0753D^{***} - 0.4672D^{2***} + 0.0798C^{**} - 0.4483H_d^{***} - 0.5674H_s^{***} - 0.2739E^{***} + 0.0053S^{***}$	−4,593.6
Sitka spruce		
Full	$3.1770^{***} + 4.8461D^{***} - 3.2500D^{2***} - 0.0327B^{***} + 0.2370C^{***} - 1.1379H_d^{***} + 0.1720H_s + 1.0926E^{**} + 0.0029S - 0.1886\cos(a)^{**} - 0.0411\sin(a)$	−1,030.6
Reduced	$3.1779^{***} + 4.8652D^{***} - 3.2700D^{2***} - 0.0328B^{***} + 0.2375C^{***} - 1.1374H_d^{***} + 0.1674H_s^{*} + 1.0497E^{***} + 0.0031S^{***} - 0.1895\cos(a)^{***}$	−1,037.9
Alaska cedars		
Full	$0.6783^{**} - 0.1229D + 0.3669D^2 - 0.0035B + 0.1385C^{***} + 0.3485H_d^{*} - 0.5262H_s^{***} - 1.1643E^{***} + 0.0049S^{***} + 0.1209\cos(a)^{***} + 0.0706\sin(a)^{*}$	−3,889.2
Reduced	$0.7351^{**} - 0.1248D^{***} + 0.3698D^{2***} - 0.0025B^{***} + 0.1342C^{***} + 0.2986H_d^{***} - 0.5168H_s^{***} - 1.1017E^{***} + 0.0048S^{***} + 0.1234\cos(a)^{***}$	−3,892.5
Boreal spruce		
Full	$1.6224^{**} - 9.5702D + 28.6283D^{***} - 0.0448B^{***} + 0.2841C^{***} + 0.8035H_d^{***} + 0.1309H_s + 1.4934E^{***} + 0.0003S - 0.2967\cos(a)^{**} + 0.3583\sin(a)^{***}$	−740.7
Reduced	$1.6312^{**} - 9.4605D^{***} + 28.442D^{2***} - 0.0451B^{***} + 0.2825C^{***} + 0.8411H_d^{***} + 1.4047E^{***} + 0.0006S^{**} - 0.2866\cos(a)^{***} + 0.3647\sin(a)^{***}$	−747.1
Other species		
Full	$3.4441^{***} - 1.7078D + 4.5096D^2 - 0.0042B + 0.2272C^{***} - 1.3176H_d^{***} - 0.6592H_s^{***} - 0.7719E + 0.0143S^{***} - 0.0096\cos(a) + 0.0508\sin(a)$	−977.7
Reduced	$3.0086^{***} + 0.9709D^2 - 0.0024B^{***} + 0.2309C^{***} - 1.3518H_d^{***} - 0.6210H_s^{***} + 0.0129S^{***}$	−1,001.7

Significance levels: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table 6. Estimated parameters of the mortality models.

	Model	BIC
Western hemlock		
Full	$-1.255^{***} - 0.972D + 0.815D^2 + 0.002B - 0.025C - 0.068H_d - 0.100H_s - 0.534E^{*} + 0.001S - 0.009\cos(a) + 0.036\sin(a)$	2,022.3
Reduced	-1.641^{***}	1,949.6
Mountain hemlock		
Full	$-1.705^{***} + 0.269D - 0.425D^2 - 0.013B^{***} + 0.027C - 0.082H_d + 0.457H_s^{**} + 4.686E + 0.003S - 0.034\cos(a) + 0.004\sin(a)$	918.2
Reduced	$-1.564^{***} - 0.013B^{***} - 0.029H_d^{*} + 0.409H_s^{*}$	865.1
Sitka spruce		
Full	$-1.984^{***} - 1.397D^{**} + 0.702D^{**} + 0.004B + 0.008C + 0.167H_d + 0.074H_s - 1.355E^{*} + 0.005S^{*} - 0.005\cos(a) + 0.018\sin(a)$	806.5
Reduced	$-1.840^{***} - 0.454D^2 + 0.007B^{**} - 0.640E^{**}$	764.4
Alaska cedars		
Full	$-1.467^{**} - 1.167D + 0.926D^2 + 0.004B + 0.048C - 0.308H_d + 0.268H_s + 0.329E - 0.006S^{*} - 0.021\cos(a) + 0.008\sin(a)$	668.4
Reduced	$-1.756^{***} - 0.005S^{**}$	603.7
Boreal spruce		
Full	$-2.466^{***} + 13.847D^2 - 22.459D^2 + 0.022B^{*} - 0.054C - 0.475H_d^{*} + 0.181H_s + 0.350E - 0.021S^{***} - 0.162\cos(a) - 0.059\sin(a)$	577.4
Reduced	$-2.718^{***} + 13.021D^{***} - 21.211D^{2***} - 0.016S^{***} - 0.038\cos(a)^{**}$	545.4
Other species		
Full	$-2.407^{***} + 2.201D - 5.087D^2 + 0.011B^{*} - 0.014C + 0.399H_d - 0.162H_s - 0.082E - 0.003S + 0.031\cos(a) + 0.119\sin(a)$	724.7
Reduced	$-2.207^{***} + 0.012B^{***} + 0.246H_d^{***}$	673.8

Probit mortality equations were estimated by maximum likelihood.
Significance levels: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

$$x_i\beta_i = \beta_{i1} + \beta_{i2}N + \beta_{i3}N^2 + \beta_{i4}B + \beta_{i5}C + \beta_{i6}E + \beta_{i7}S + \beta_{i8}\cos(a) + \beta_{i9}\sin(a) + \beta_{i10}H_d + \beta_{i11}H_s + \mu_{ij} \quad (9)$$

where Φ is the standard normal cumulative distribution function and φ is the standard normal probability density function.

Total stand volume and biomass were calculated with the following equation

$$\mathbf{v}_i = \mathbf{v}'\mathbf{y}_t \quad (10)$$

where $\mathbf{v}$ is a vector of single-stem volume and biomass by size and species (v_{ij}), which are represented by the following full model

$$\nu_{ij} = \theta_{i1} + \theta_{i2}D_j + \theta_{i3}D_j^2 + \theta_{i4}B + \theta_{i5}C + \theta_{i6}E + \theta_{i7}S + \theta_{i8}\cos(a) + \theta_{i9}\sin(a) + \theta_{i10}H_d + \theta_{i11}H_s + \omega_{ij} \quad (11)$$

Model Estimation and Quality Control

We aimed to develop a matrix model that is parsimonious and accurate. Parsimony of the present model was achieved by keeping

Table 7. Estimated parameters of the recruitment model.

	Model	Scale	BIC
Western hemlock			
Full	$-6.066^{***} + 0.039N^{***} - 0.027N^{****} - 0.044B^{*} + 0.342C^{**} - 1.222H_d + 2.597H_s^{**} - 0.134E + 0.003S - 0.661\cos(a) - 0.215\sin(a)$	5.238***	1,443.6
Reduced	$-6.109^{***} + 0.040N^{***} - 0.028N^{****} - 0.056B^{***} + 0.271C^{***} - 0.002S^{*} - 0.659\cos(a)^{**}$	5.308***	1,427.9
Mountain hemlock			
Full	$-9.863^{***} + 0.018N^{***} - 0.006N^{*} - 0.026B - 0.731C^{**} + 1.364H_d + 2.118H_s^{*} + 0.586E^{**} + 0.026S + 0.468\cos(a) + 0.383\sin(a)$	4.422***	846.1
Reduced	$-6.227^{***} + 0.021N^{***} - 0.010N^{****} - 0.892C^{**} + 0.395E^{***} + 0.030S^{**}$	4.462***	826.0
Sitka spruce			
Full	$-8.145^{**} + 0.050N^{***} - 0.021N^{**} - 0.124B^{*} + 0.565C^{*} - 3.718H_d^{*} + 1.383H_s - 0.500E + 0.081S^{*} - 0.773\cos(a) + 1.930\sin(a)$	9.780***	951.6
Reduced	$-7.408^{**} + 0.048N^{***} - 0.021N^{****} - 0.094B^{***} + 0.532C^{***} - 2.919H_d^{***}$	9.981***	932.2
Alaska cedars			
Full	$-7.843^{***} + 0.036N^{***} - 0.034N^{****} - 0.041B - 0.001C - 0.465H_d + 3.392H_s^{**} - 0.219E + 0.022S + 0.179\cos(a) + 0.207\sin(a)$	3.756***	695.3
Reduced	$-9.100^{***} + 0.035N^{***} - 0.036N^{****} - 0.129C^{**} + 3.310Hs^{***}$	3.878***	665.3
Boreal spruce			
Full	$-5.834^{*} + 0.138N^{***} - 0.183N^{****} - 0.341B^{***} + 0.386C - 1.247H_d - 3.125H_s - 0.140E + 0.034S + 0.661\cos(a) - 0.026\sin(a)$	6.828***	611.8
Reduced	$-4.333^{**} + 0.136N^{***} - 0.180N^{****} - 0.312B^{***} - 1.433H_d^{***} - 2.934H_s^{*}$	6.945***	582.1
Other species			
Full	$-10.354^{**} + 0.073N^{**} - 0.016N^{*} - 0.159B + 0.511C - 5.844H_d^{*} + 8.541H_s^{**} - 0.503E - 0.011S - 2.088\cos(a) - 0.746\sin(a)$	10.308***	703.4
Reduced	$-10.538^{***} + 0.108N^{***} - 0.106N^{****} - 5.797H_d^{***}$	10.727***	677.9

Tobit recruitment equations were estimated by maximum likelihood.
Significance levels: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table 8. Estimated parameters of the stem volume model.

	Model	R^2
Alaska cedars		
Full	$-0.4193^{***} + 1.5965D^{***} + 2.4582D^{2***} - 0.0047B + 0.0835C^{***} + 0.047H_d + 0.0911H_s^{***} + 0.0434E^{*} + 0.0028S + 0.0091\cos(a) + 0.0038\sin(a)$	0.95
Reduced	$-0.292^{***} + 1.6253D^{***} + 2.4015D^{2***} - 0.003B^{***} + 0.084C^{***}$	0.95
Boreal spruce		
Full	$-0.0362^{**} - 0.3256D^{**} + 6.2675D^{2***} + 0.0052B^{**} + 0.0013C + 0.0116H_d + 0.0035H_s - 0.0971E^{***} - 0.0006S + 0.005\cos(a) + 0.0093\sin(a)^{**}$	0.94
Reduced	$-0.0123^{***} - 0.2632D^{***} + 6.1993D^{2***} - 0.1153E^{***} + 0.0067\sin(a)^{***}$	0.94
Other species		
Full	$-0.1833^{***} + 0.4255D^{***} + 4.8037D^{2***} + 0.015B^{***} + 0.0347C^{***} - 0.0281H_d^{*} + 0.0361H_s^{***} - 0.0891E^{***} + 0.0032S^{*} - 0.0004\cos(a) + 0.0115\sin(a)^{*}$	0.93
Reduced	$-0.1322^{***} + 0.3291D^{***} + 4.969D^{2***} + 0.0276H_d^{*} + 0.0167\sin(a)^{*}$	0.92

Stem volume equations were estimated by ordinary least squares. Independent and response variables are ln + 1 transformed. sin(*a*) and cos(*a*) are ln + 2 transformed. Species-specific volume equations are from 13 published sources, as documented in Barrett and Christensen (2011). R^2 is an adjusted value.
Significance levels: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

only those explanatory variables that contributed significantly to the goodness of fit as determined through hierarchical partitioning (HP) and met the expected biological response. To avoid compromised type I error rates and severe artifacts commonly associated with model selection procedures, HP (Mac Nally 2000) was used for the screening of explanatory variables by decomposing the goodness of fit of this model through incremental partitioning to determine the average independent contribution of each variable. The HP analysis was conducted with the hier.part package of the R program (Mac Nally and Walsh 2004).

The accuracy of the present model was evaluated through short-term prediction errors. A short-term prediction error was defined as the difference between the observed and the predicted stand states on 293 independent validation plots. Predicted stand states were obtained by setting the stand states of the initial inventory as the initial states and applying Equation 2 iteratively over the elapsed period between the two inventories. For comparison, we also calculated prediction errors of the FVS model (Keyser 2008) on the same validation plots. FIA data were imported into the FVS using the procedures outlined by Shaw (2008), and predictions were estimated for each plot using its database extension software (Crookston et al. 2003).

Spatial Autocorrelation

Large-scale spatial trends are common ecological phenomena that often cause spatial autocorrelation in biotic and abiotic variables (Legendre 1993). In coastal Alaska, for example, Farr and Harris (1979) confirmed a latitudinal effect on the site index, and Harris and Farr (1974) showed that average stand height and total stand volume was correlated with elevation. Barnes (1962) traced inaccuracies in a yield table to uncontrolled geographic locations. McClellan and Biles (2003) reported that the current prognosis growth-and-yield model is subject to unrealistic results because of its recruitment function that predicts a uniform mixture of Sitka spruce and western hemlock recruitment everywhere in the region. Because the coastal Alaska region is composed of two distinct parts—southeast and southcentral Alaska (Viereck and Little 1975), and each area has distinctive climatic conditions and species composition (see

Table 9. Estimated parameters of the stem biomass model.

	Model	R^2
Alaska cedars		
Full	$0.638^{***} + 17.302D^{***} - 10.925D^{2***} - 0.018B + 0.162C^{***} + 0.404H_d^{***} + 0.621H_s^{***} + 0.318E^{***} - 0.002S + 0.013\cos(a) - 0.029\sin(a)$	0.95
Reduced	$1.447^{***} + 17.509D^{***} - 11.318D^{2***} + 0.162C^{***} - 0.014\sin(a)^{**}$	0.95
Boreal spruce		
Full	$1.068^{***} + 25.220D^{***} - 28.061D^{2***} + 0.093B^{***} - 0.091C^{***} - 0.096H_d^{*} + 0.014H_s - 1.074E^{***} - 0.018S^{**} + 0.024\cos(a) + 0.053\sin(a)^{*}$	0.91
Reduced	$0.991^{***} + 24.841D^{***} - 27.496D^{2***} + 0.066B^{***} - 1.172E^{***} + 0.084\sin(a)^{***}$	0.90
Other species		
Full	$0.603^{***} + 24.717D^{***} - 24.418D^{2***} + 0.094B^{***} + 0.259C^{***} - 0.394H_d^{***} + 0.167H_s^{***} - 0.363E^{***} + 0.017S^{**} + 0.005\cos(a) - 0.003\sin(a)$	0.92
Reduced	$0.664^{***} + 24.215D^{***} - 23.616D^{2***} + 0.252C^{***}$	0.91

Independent and response variables are ln + 1 transformed. sin(a) and cos(a) are ln + 2 transformed. Species-specific volume equations are from 13 published sources, as documented in Barrett and Christensen (2011). R^2 is an adjusted value.
Significance levels: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Introduction), testing for spatial autocorrelation is an important step in examining the accuracy of the matrix model presented here.

A key hypothesis, then, behind this matrix model was that when physiographic factors such as aspect, elevation, and slope are controlled for adequately, the models' predictions would exhibit no spatial autocorrelation. Spatial autocorrelation was tested via an analysis of annual prediction errors, $\boldsymbol{\varepsilon}$, of Equation 2 using the validation data set errors. If large-scale spatial trends were accounted for, $\boldsymbol{\varepsilon}$ should be spatially independent. If not, it could imply that spatially dependent factors, such as soil attributes, temperature, or precipitation, were not appropriately controlled (Bivand et al. 2008). Annual prediction error was calculated by taking the difference of observed and predicted total basal area B, by species and dividing it by the remeasurement interval.

We used three nonparametric tests, viz, variograms and envelopes, Moran's I, and Geary's C, to test for spatial autocorrelation. Empirical variograms and envelopes based on permutations were estimated using the geoR package in R (Ribeiro and Diggle 2010). Permutation tests of Moran's I and Geary's C statistics were estimated using the spdep package in R (Bivand et al. 2010). Spatial autocorrelation of the annual prediction error was significant if there was agreement between the tests.

Results

Parameter Estimates

Parameter estimates for the full and reduced diameter growth models are presented in Table 5, and the accompanying contribution of each variable to the goodness of fit of the model is presented in Table 10. Trees on more productive sites and steeper slopes grew faster, regardless of species. Diameter growth was negatively associated with stand basal area, except for mountain hemlock, for which basal area was insignificant for diameter growth. In general, site productivity contributed most to the goodness of fit. Structural and species diversity effects on diameter growth varied highly but were generally found to be significant with the HP method.

The parsimonious mortality models, in general, consisted of fewer variables than the parsimonious diameter growth models (Table 6). Mortality of western hemlock was found to be independent of any explanatory variable and was therefore set as a constant. The mortality of Alaskan cedars was only subject to a positive effect of slope, and the mortality of other nonmajor species was only subject to a positive effect of basal area and structural diversity.

Recruitment of all the species was consistently higher if there were more trees of that species (N) on the stand, and basal area (B) reduced recruitment of western hemlock, Sitka spruce, and boreal spruce but was insignificant for the other species (Table 7). In general, N and N^2 contributed considerably (70−90%) to the goodness of fit of recruitment of all the species, whereas the contribution of all other variables was inconsistent (Table 10). The Bayesian information criterion (BIC) was reported for the diameter growth models (Table 5), mortality models (Table 6), and recruitment models (Table 7) as a model selection criterion, because BIC features a greater penalty for the number of parameters in the model.

Table 10. Independent contribution of each explanatory variable to the goodness of fit of the response variables.

	Western hemlock	Mountain hemlock	Sitka spruce	Alaskan cedars	Boreal spruce	Other species
			(%)			
Diameter growth						
D	2.6***	2.4***	2.4***	5.9***	5.6***	0.9*
D^2	1.6***	2.4***	1.4***	5.7***	7.1***	0.7
B	5.4***	1.3	28.2***	7.6***	15.5***	6.5***
C	49.9***	2.4**	34.1***	32.2***	28.8***	34.7***
H_d	20.2***	18.3***	29.7***	6.4***	7.0***	29.2***
H_s	10.0***	54.6***	0.4*	13.0***	0.5	24.4***
E	1.5***	3.4***	0.9***	16.7***	9.1***	0.2
S	1.7***	11.9***	1.2***	6.8***	2.4**	2.7***
cos(a)	0.3	1.0	0.9***	4.2***	17.1***	0.5
sin(a)	6.8***	2.2	0.8	1.4	6.9***	0.2
Mortality						
D	15.9	0.6	18.3*	8.3	20.0***	2.1
D^2	8.8	0.7	6.2	4.1	13.8***	2.9
B	9.6	52.5***	18.8**	4.6	4.7	40.6***
C	14.4	0.9	4.8	9.8	0.70.8	
H_d	0.8	9.7*	13.4	15.8	2.4	32.4***
H_s	7.1	31.8***	0.8	7.3	0.1	2.2
E	22.8	1.8	20.9**	1.8	1.5	2.1
S	5.5	1.3	13.7	46.9**	48.0***	3.3
cos(a)	1.7	0.6	2.0	0.4	8.5*	2.6
sin(a)	13.3	0.2	1.0	0.9	0.4	11.1
Recruitment						
N	52.5***	50.4***	39.1***	57.8***	63.7***	33.1***
N^2	18.4***	39.8***	42.6***	22.8***	27.4***	57.4***
B	4.1***	−1.1	3.1***	−0.5	4.8***	1.5
C	12.6***	2.1**	4.7***	3.0**	−1.2	−0.2
H_d	1.7	−1.3	9.4***	0.2	6.2***	6.0***
H_s	1.9	−1.5	1.0	16.7***	1.2*	0.0
E	1.7	10.7***	0.4	−0.1	−1.4	0.1
S	2.5*	1.7**	−0.1	−0.7	0.5	−0.1
cos(a)	2.3*	−1.5	−0.9	−1.3	−1.4	−0.1
sin(a)	2.2	0.8	0.7	2.1	0.3	2.4

Significance levels: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

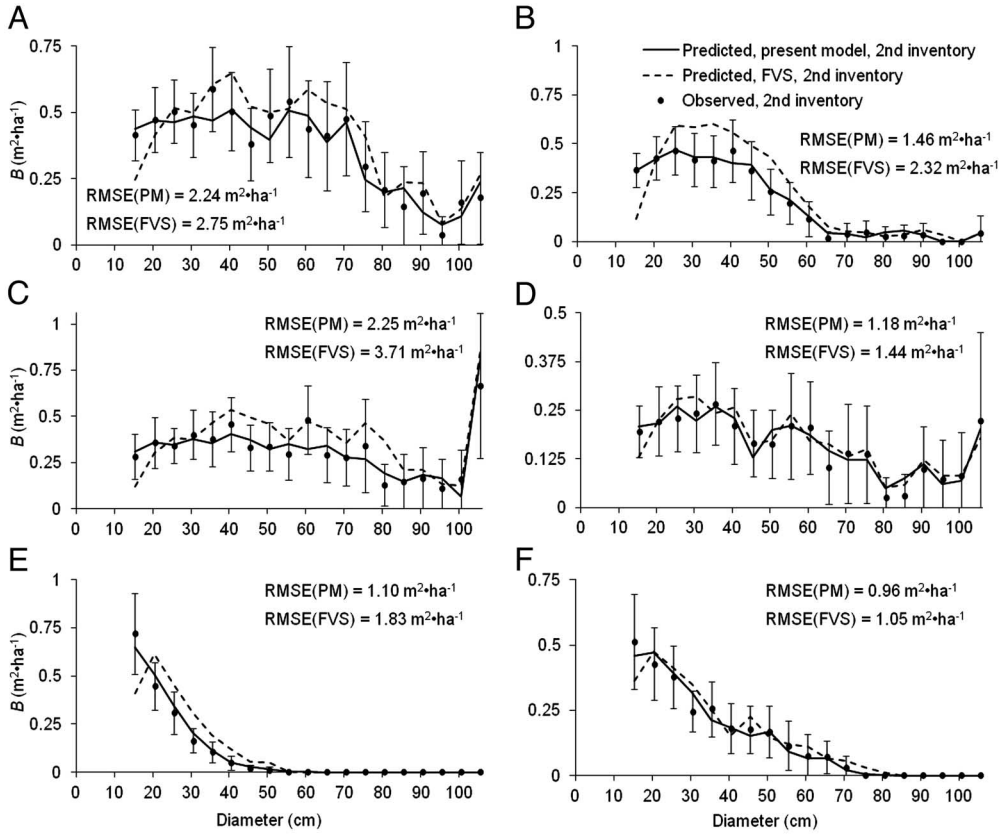

Figure 2. Average predicted and observed stand states at the second inventory for the present model (PM) and the FVS on the 293 postsample validation plots, with the 95% confidence interval of the observed mean, for western hemlock (A), mountain hemlock (B), Sitka spruce (C), Alaska cedars (D), black spruce and white spruce (E), and other species (F). The RMSE for each species group was also provided for a comparison between the present model and the FVS.

Parameter estimates for the full and reduced volume and biomass models are presented in Tables 8 and 9. The coefficient of determination was greater than 90% for all the models, suggesting that the models explained a large amount of the variability. Diameter and diameter squared were the most important variables and contributed more than 99% to the goodness of fit of stem volume and biomass models. Site productivity (*C*), although providing much less to the overall goodness of fit of each model, had consistent positive effects on volume and biomass in the reduced models.

Prediction Errors

Short-term prediction errors were calculated using the 293 postsample validation plots in terms of basal area by diameter class and species predicted by the present model, and all fell within the 95% confidence intervals of the observed mean and had an overall root mean square error (RMSE) of 4.48 $m^2 \cdot ha^{-1}$ (Figure 2). In general, the stand state at the second inventory predicted by the present model was close to the observed stand state, and there was no systematic under- or overestimation. Most prediction errors occurred in the smallest size classes, and the model was more accurate for large trees.

In comparison, some predictions made by the FVS fell outside the 95% confidence intervals of the observed mean. The FVS underestimated the basal area of the smallest trees and systematically overestimated the basal area of trees larger than 20 cm in diameter (Figure 2). Overall, the present model (RMSE = 4.48 $m^2 \cdot ha^{-1}$) reduced the RMSE by 36% from the FVS (RMSE = 6.98 $m^2 \cdot ha^{-1}$), and the present model was also evidently more accurate for all the species groups than the FVS (Figure 2).

Residual Spatial Autocorrelation

Annual prediction errors from the present model and the FVS were analyzed with three metrics: empirical variograms and tests of Moran's I and Geary's C. The present model was generally free of spatial autocorrelation according to the three metrics, except that Moran's I value indicated that prediction errors for mountain hemlock were spatially dependent (Figure 3). In contrast, both Moran's I and Geary's C values indicated that the FVS was subject to strong spatial autocorrelation for mountain hemlock, Sitka spruce, and boreal spruce, and variogram plots also displayed the presence of spatial autocorrelation in mountain hemlock and Sitka spruce, because the variograms of both species fell outside of their empirical envelopes.

Ecological Inference

As a result of numerous confounding factors, ecological inference from empirical forest dynamics models is admittedly a difficult task (Monserud 2003, Liang et al. 2005). For the dynamics components of this matrix model, namely diameter growth, mortality, and recruitment, the physiographic variables (*E*, *S*, and *a*) had mixed significance and effects (Tables 5–7) across species, which reinforces the ecological consensus that the influence of physiographic conditions varies by species (e.g., Stage and Salas 2007). The effects of tree

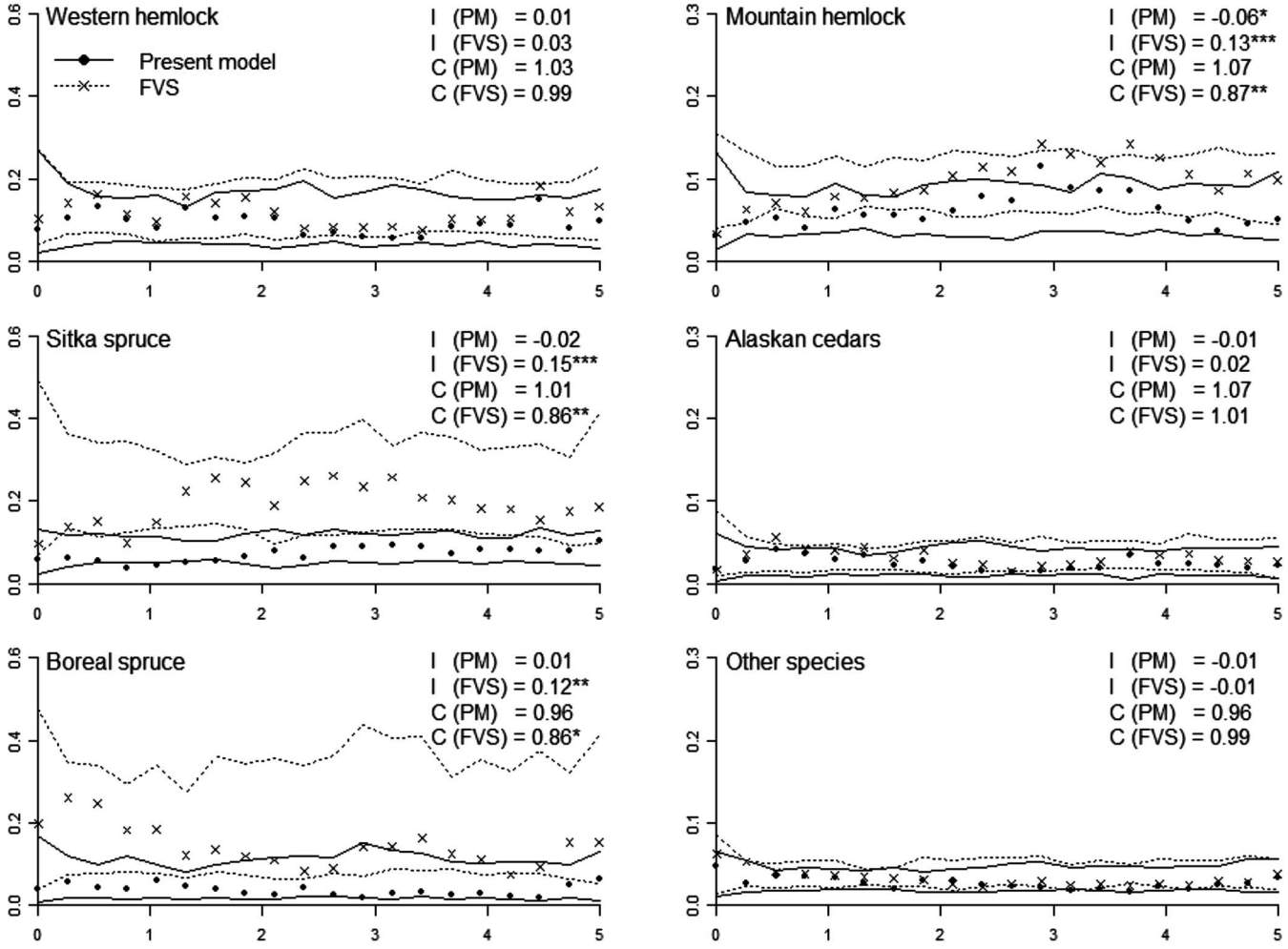

Figure 3. Empirical variograms and envelopes based on permutations of the annual prediction errors of the present model (PM) and the FVS. The vertical axis is the semivariance and the horizontal axis represents the distance between plots in WGS84 degrees. I and C represent calculated values of Moran's I and Geary's C, respectively.

species diversity (H_s) and tree size diversity (H_d) were also inconsistent across different species.

It is noteworthy that several key explanatory variables had significant and consistent effects in the present model. For diameter growth, site productivity (C) had a positive effect across all species, which suggests that secondary growth of all the tree species in Alaska coastal forest is governed by site productivity. Total stand basal area (B) was negatively affected for all species but mountain hemlock (Table 5), implying that secondary growth of most species slows down as stocking goes up; mountain hemlock may be an exception because of its occurrence in muskegs and near the treeline (Viereck and Little 1975), where the competition effect is less limiting than environmental constraints. Higher growth as slope increases is probably a result of better drainage, because flat areas often develop into bogs and muskegs, given the very high precipitation in southeast Alaska. Stand basal area (B) also had a negative impact on the recruitment of western hemlock, Sitka spruce, and boreal spruce, indicating that competition may hinder the recruitment of both shade-tolerant (western hemlock) and less shade-tolerant (Sitka spruce and white spruce) species, and the effect of stocking on recruitment was decided not only by shade tolerance but also by the size of the seed bank (represented by the total number of mature trees, N), site productivity (C), and physiographic conditions (Table 7).

Discussion and Conclusion

A density-dependent, size-specific, and species-specific matrix model was developed to study the dynamics of Alaska coastal forest. The present model was tested on 293 postsample validation plots, and the predicted stand states all fell within the 95% confidence intervals of the observed means. In comparison, the FVS-SEAPROG systematically underestimated stem density of small trees and overestimated stem density of large trees, and the present model is generally more accurate than the FVS with 36% percent less RMSE. Analysis of the present models' residuals revealed no spatial autocorrelation, which indicated that the model was able to adequately account for the effects of physiographic factors.

Differences between species groups are numerous and difficult to quantify, especially in large regions with many different climatic and physiographic conditions. Large- and fine-scale spatial patterning is known to cause problems in individual tree growth-and-yield models (Fox et al. 2007a, 2007b, Liang and Zhou 2010), but our results support the finding by Liang (2012) that if exogenous variables such as physiographic variables and site productivity are appropriately

accounted for, the matrix growth model predictions can be a stationary process. Spatial autocorrelation in a growth model's prediction errors, by species, would inform us that the prediction errors are generally more similar at shorter distances than further apart, implying either that a model did not account for a variable (e.g., localized climatic conditions) or that an error was introduced (e.g., recruitment of species in a region where it is not present). The present model illustrates that the inclusion of physiographic variables in nonspatial models, applied via a matrix growth model, can control for these large- and micro-scale spatial variations in regions having numerous varied climate conditions, consisting of a mixture of tree species that reach the extent of their range, while still being able to provide an adequate level of prediction accuracy.

Users should be aware of the limitations of the present models. There is no distinction between forest types and old- or young-growth stands, and a number of species had to be grouped because of data availability and model complexity issues. Long-term predictions can be unstable because of the recruitment equations of the present models, e.g., predicting white spruce regeneration in a western hemlock-Sitka spruce forest. Although the error of annual predicted recruitment is negligible, it can aggregate over time and confound predictions in long-term projection. It is recommended that simulation results over 100 years be made cautiously. Predictions are limited to trees $>$12.7 cm (5 in.) at dbh, and it is recommended that users define their management objectives before using the present model if they want to know about growth of trees $<$12.7 cm.

As interest in the region changes from old-growth to young-growth timber management (Alexander et al. 2010), there is an increasing need for a model that can accurately predict the management effects of both clearcutting and ATC systems (McClellan 2005). Land managers and forest researchers interested in the use of silvicultural systems (i.e., partial cutting and thinning) to achieve structural old-growth characteristics or to harvest biomass and biofuel should find the present model useful, because it was calibrated with an unbiased, representative data set that includes old-growth, young-growth, productive, nonproductive, even-aged, and multi-aged stands, and the simple structure and associated computer simulation programs under development will make model application an easy and quick process. To this end, we have completed a simulation package entitled fgmod with R language (R Core Team 2013) to facilitate the application and development of matrix growth-and-yield models to forestry data.[1]

Endnote

1. This package is being uploaded to the Comprehensive R Archive Network (CRAN, cran.rstudio.com/) and the corresponding author's website (jiliang.forestry.wvu.edu/home). A copy of this package can also be obtained by contacting the corresponding author.

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