SI Appendix

Appendix 1: Data Sources, Calculations, and Simulations

This appendix describes the forest inventory data used to parameterize the PPA, and how these data were used to generate observed 100-year dynamics and observed successional status of tree species. It then describes the PPA model simulations, the calculations performed on the results of these simulations, and the calculation, for each species, of the metrics $\hat{Z}_j^*$ and $H_{20,j}$.

Data sources. Three different forest inventory data sets were used: FIA pre-1999, FIA post-1999, and FHM. All three data sets were collected by the USDA Forest Service and were publicly available at the time the data were downloaded.

The USDA Forest Inventory and Analysis (FIA) data has been collected for several decades (see (1, 2), and appendices in (3)). The design and implementation of the inventory was changed in 1999. We used one FIA data set from before 1999 (hereafter pre-1999), and one from after 1999 (hereafter post-1999). In both cases the inventory consisted of tree-level and plot-level data taken from a large network of permanent sample plots distributed across the US. The pre-1999 FIA data contained measurements from two surveys separated by an average of ~12 years (the remeasurement interval varied among the three states, and varied alightly among plots within a state: average survey dates for the three states were: Mn 1978 - 1990; Mi 1980 - 1993; Wi 1983 - 1996). Therefore, in the pre-1999 FIA the changes in diameter at breast height (dbh) of individual trees, or the mortality of individual trees, could be observed. Accordingly, we used the pre-1999 data to parameterize the growth and mortality parameters of the PPA (see Appendix 2). The post-1999 data at the time of our analysis did not yet include remeasurement data, but, unlike the pre-1999 FIA data, did include observations of height for individual trees, along with their dbh. Accordingly, we used the post-1999 FIA data to parameterize the height allometry component of the PPA: height allometry is defined here as the function that predicts the height of a tree from its dbh (see Appendix 2).

For both data sets, we selected all plots within the three states MI, MN and WI. From the pre-1999 data we discarded plots which had been harvested between the two survey intervals, and any plots that were not remeasured. We grouped the remaining plots, according to the FIA physiographic class (hereafter, ‘soil type’), into five groups: xeric, xero-mesic, mesic, hydro-mesic, and hydric (pre-1999 physiographic codes 3, 4, 5, 6, 7 respectively). There were relatively few xeric plots, so these were not included in the analysis. In the pre-1999 data at the tree level, we discarded trees that had a recorded dbh of zero at the time of the first survey: these were either saplings that had dbh below 1 inch at the first survey (‘ingrowth’ trees) or larger trees that grew sufficiently during the survey interval to be included in the variable radius plot sampling (‘ongrowth’ trees). Within the remaining data for each soil type, we extracted the eight species with the largest number of individuals in the data. The identity of these eight species varied among soil types. Within each soil type, we discarded all data from species other than these eight. The resulting sample sizes, for each soil and model component, are shown in Table S1.1.

Due to changes in the FIA soil classification scheme, we could not stratify the pre-1999 (growth and mortality) and post-1999 (height allometry) data into the same soil types. Therefore, we used the xeric/xero-mesic post-1999 FIA data to parameterize the height allometry on xero-mesic soils; the post-1999 mesic data for the height allometry on mesic soils; and the post-1999 hydro-mesic/hydric data for the height allometry on both hydro-mesic and hydric soils. The sample sizes for height allometry, on each soil, are given in Table S1.1.

The USDA Forest Health Monitoring (FHM) data is similar in form to the FIA, but includes a larger suite of measurements relevant to issues of forest health (1, 2). The FHM design changed in 1999, when it was subsumed by the FIA. The pre-1999 FHM data provided, for trees with dbh > 5 inches (12.7 cm), two measures of crown projection diameter (see Appendix 2). The FHM dataset is much smaller than the FIA, so we used the same data for crown allometry to parameterize crown-dh allometry on all soil types. From the pre-1999 FHM data, we extracted all available dbh and crown radius data from the three US Lake States (MI, MN, and WI) for the species of interest on each soil type.

Calculation of Observations. For comparison with PPA model predictions we calculated the observed 100-year dynamics of stand basal-area, 100-year dynamics of basal area within each of two successional guilds, and the diameter size distribution of 100-year old stands; the observed successional status of each species on each soil; the 100-year dynamics of the basal area of each species on each soil, and the species composition in 100-year-old stands on each soil (Figs. 1, S1 – S3).

Most of these calculations were based on $b_{j,s,a}$ ($\mathrm{m}^2\ \mathrm{ha}^{-1}$), defined as the average basal area of species j in stands of soil type s and age class a:

$$b_{j,s,a} = \frac{\sum_{i \in S(j,s,a)} (1/10000)\pi(dbh_i/2)^2 w(i)}{N(s,a)} \tag{S1.1}$$

where the set $S(j,s,a)$ contains all trees *i* of species *j*, in stands of soil type *s* and age class *a*; dbh_i is the diameter at breast height (cm) of tree *i* at the time of the second survey; $w(i)$ is the 'area expansion factor (ha^{-1}) of tree *i* (i.e., the inverse of the area on which *i* is sampled; see appendices in (3)); and $N(s,a)$ is the number of inventory plots with soil type *s* and age class *a*. A list of the $N(s,a)$ values is given in Table S1.2. The factor 1/10000 converts basal area from cm^2 to m^2.

We also calculated $b_{tot,s,a}$, the average stand basal area (i.e., basal area of all species combined) on soil *s* in age class *a*:

$$b_{tot,s,a} = \frac{\sum_{i \in Qall(s,a)} (1/10000)\pi(dbh_i)^2 w(i)}{N(s,a)} \tag{S1.2}$$

where $N(s,a)$ is the number of inventory plots with soil type *s* and age class *a*; and the set $Q_{all}(s,a)$ contains all trees *i* in plots with soil type *s* and age class *a*.

Age class in the above calculations is based on the 'stand age' reported in the FIA data for each plot. The FIA defines stand age as the average age of canopy trees. For comparison between model simulation and observations, we used this same definition of stand age in the model simulations (see below). This index of stand age should typically underestimate the time since the last stand-replacing disturbance (or the time since re-forestation). However, this bias should have little impact on our results, because we restricted our analysis to stand ages < 100 years. However, for chronosequences calculated over longer periods (multiple centuries), we would expect the FIA stand age to approach an equilibrium value, such that the FIA age would become much smaller than the true chronological age of the stand.

Values of $b_{j,s,a}$ were calculated for each of the eight most common species on each of the four soil types, for 11 age classes (0-110 years old) in 10-year increments. Plotting $b_{j,s,a}$ vs. age class reveals a chronosequence of the average dynamics of the basal area of species j in stands with soil type s. These plots are shown for selected species in Figure S3. Importantly, the chronosequences are calculated by averaging together all data within a large region: it is therefore possible that the chronosequences represent a sum of separate signals from different kinds of environments (within the broad soil type classifications used by the FIA). Also, it is important to bear in mind that the chronosequences are calculated from a single survey taken at one time, by comparing stands of different ages. This 'space-for-time' substitution approach (4) implicitly assumes that the dynamics have remained constant over time, so that older plots at a given time are informative about the future state of younger plots. This stationarity assumption is probably invalid for the Lake States (see discussion in main text), which can lead to mismatches between predicted and observed dynamics, even if the model correctly captures the current dynamics.

Observed Successional Status. We define the observed successional status of each species j on each soil s from the Spearman Rank correlation between $b_{j,s,a}$ (S1.1) and age class a. Species with a positive coefficient were assigned an observed successional status of *late*; and species with a negative coefficient were assigned an observed successional status of *early*. We also assigned a statistical significance to the *early* or *late* classification for each species, according to whether the Spearman Rank correlation was significant at $P < 0.05$.

Observed Basal Area vs. Stand Age. Given $b_{j,s,a}$ for each species *j* in stands with soil type *s* and age class *a*, and the successional status of each species on each soil, we calculated $b_{early,s,a}$, defined as the basal area of all early-successional species combined in stands with soil type *s* and age class *a*; and likewise for $b_{late,s,a}$. This was done by simply summing $b_{j,s,a}$ for all species (among the eight most common) observed to be early-successional, and then for all species observed to be late-successional:

$$b_{early,s,a} = C_s \sum_{j \in J(early,s)} b_{j,s,a}$$

$$b_{late,s,a} = C_s \sum_{j \in J(late,s)} b_{j,s,a} \qquad \text{(S1.3)}$$

where the set $J(early, s)$ contains all species *j* that are observed to be early successional on soil *s*, and similarly for $J(late, s)$; and $C_{s,a}$ is the correction factor (S1.4; see below) for soil *s* and stand age *a*.

Correction Factor for Observed Basal Area. The above calculations for observed basal area consider only the eight most common species on each soil. Unlike our PPA analyses, where these species comprise the entire forest community, these species comprise only part of the FIA data. Therefore, relative to the above calculations (S1.3), the PPA should predict too much basal area, on average, for these species. To account for this bias we calculated

$$C_{s,a} = \frac{\sum_{i \in Q_{all}(s,a)} (1/10000)\pi(dbh_i)^2 w(i)}{\sum_{i \in Q_8(s,a)} (1/10000)\pi(dbh_i)^2 w(i)} \qquad \text{(S1.4)}$$

where the set $Q_8(s,a)$ contains all trees *i* of the eight most common species in plots with soil type *s* and age class *a*; and the set $Q_{all}(s,a)$ contains all trees *i* of all species in plots with soil type *s* and age class *a*.

Observed Species Composition of 100-Year-Old Stands. For comparison with the PPA predictions, we define the observed species composition of 100-year-old stands as $b_{j,s,100}$ for the eight most common species on soil type *s*. To compare predictions and observations on an equal basis, the observed $b_{j,s,100}$ values were adjusted with the correction factor (S1.4): $b_{j,s,100} \to C_{s,a} b_{j,s,100}$.

Observed Diameter Distribution. The average density of trees in dbh class *d* in plots with soil type *s* and stand age class *a* is

$$v_{s,d,a} = \frac{\sum_{i \in Q_{all}(s,d,a)} w(i)}{N(s,a)} \qquad \text{(S1.5)}$$

where the set $Q_{all}(s,d,a)$ contains all trees *i* in dbh class *d* on plots with soil type *s* and stand age class *a*. We calculated $v_{s,d,a}$ for $d = 1, 2, 3, \ldots 15$ where $d = 1$ means $0 < dbh_i < 4$ cm, $d = 2$ means $4 \le dbh_i < 8$ cm, and so on.

PPA Simulations. The special case of the PPA considered in this paper includes seven species-specific parameters (G_D, G_L, μ_D, μ_L, ϕ, α, and β) for each of the eight most common species on each soil type. We define $\boldsymbol{\theta}$ as the vector of 7 × 8 = 56 species-specific parameters on a given soil type. We used numerical methods in a Bayesian framework to generate, for each soil type, a large sample of vectors $\boldsymbol{\theta}$ from $p(\boldsymbol{\theta} \mid \mathbf{X})$, the joint probability distribution of $\boldsymbol{\theta}_s$ given the data, $\mathbf{X}$ (Appendix 2). To propagate uncertainty in $\boldsymbol{\theta}$ through the PPA simulations of forest dynamics, we drew one $\boldsymbol{\theta}$ at random for each of 50 PPA simulations on each soil type. We did not propagate uncertainty in the fecundity parameter F (which is not species-specific in the special case of the PPA considered in this paper), because the procedure we used to estimate F returned a single value per soil type (Appendix 2). Thus, each of the 50 PPA simulations per soil type had different values for the elements of $\boldsymbol{\theta}$ but the same value for F.

The PPA simulations generated a set of predicted basal areas $b_{j,s,a,k}^{(pred)}$ for species j, soil type s, stand age class a, and simulation k (1, 2, 3 … 50). The simulations also generated a set of predicted densities $v_{s,d,a,k}^{(pred)}$ for soil type s, dbh class d, stand age class a, and simulation k. From these sets of predictions, we calculated means and intervals for the model predictions. For example, the mean of $v_{s,d=1,a=11}^{(pred)}$ is

$$v_{s,d=1,a=11}^{(pred,mean)} = (1/50)\sum_{k=1}^{50} \sum_{i \in Q(s,d=1,a=11,k)} w(i) \tag{S1.6}$$

where the set $Q(s, d=1, a=11, k)$ contains all model cohorts i (see below) from simulation k, soil type s, dbh class 1, and stand age class 11. To obtain 68% intervals for a given prediction, we calculated the range of the central 34 values from the 50 simulations.

Using this approach, we calculated from the simulations the predicted means and central 68% intervals for the same metrics that we extracted from the data (e.g., stand basal area vs. stand age; basal area vs. stand age for the early- and late-successional guilds; dbh-class distribution in 100-year-old stands; basal area vs. stand age for particular species). For consistency with the FIA (see above), we defined stand age in the PPA simulations as the average age of canopy trees: at each iteration of each PPA simulation, we calculated stand age as the average age of the trees in the canopy. Because FIA data do not include trees with dbh < 2.54 cm, we did not include these trees in the PPA stand-age calculations.

Initial Condition for Cohorts. Just as we drew a random parameter vector $\boldsymbol{\theta}$ for each PPA simulation to propagate uncertainty in the species-specific parameters (see above), we also assigned the initial condition of each simulation at random from the regional pool of young FIA plots in order to propagate uncertainty in the state of young stands (which reflects processes such as seed dispersal, germination, seedling survivorship, and how these interact with different types of disturbance). Specifically, the procedure to determine the initial condition for each of the 50 PPA simulations on soil type s was as follows: (i) create an empty stand for the PPA model; (ii) draw a plot q at random from the young (stand age < 20 years) pre-1999 FIA data on soil type s; (iii) add to the initial condition a cohort i (see below) for each tree i in plot q; (iv) repeat steps ii-iii, sampling with replacement, until 50 plots have been added; (v) divide the spatial density, $w(i)$, of each cohort i by 50. Thus, for *each* of the 50 simulations, the initial condition was the sum of 50 young plots, drawn at random from the appropriate soil type.

We simulated the dynamics of tree cohorts (defined by species identity and dbh) rather than individual trees. This is computationally much more efficient than simulating each individual, but leads to identical results in the large-population limit (and nearly the same results for even modest-sized populations; see (5)). Each cohort was initialized with the species identity, dbh and spatial density of the corresponding tree in the FIA data (steps ii-iii above).

The average initial condition reflects the average condition in young FIA plots on a given soil type; but, around this average, there was stochastic variation in the initial condition among the 50 simulations per soil type, as a result of the random selection of the particular plots entering into the initial condition. And, because the sampling of plots for the initial condition was done randomly from all across the region, it is possible that, in reality, no single young stand would have a species composition and structure very close to the average initial condition in the PPA simulations.

Implementation of PPA Simulations. The PPA is described in detail in (5). Each simulation consisted of a number of iterations, beginning with the initial condition, and ending when the stand age (defined above) reached 100 years. Each iteration consisted of three steps, explained in detail below: (i) calculate Z^*; (ii) apply growth and mortality to each cohort; and (iii) add new cohorts through reproduction.

Calculate Z^*. Reference (5) describes in detail the procedure for calculating Z^* for the flat-top model assumed in this present work. Z^* calculations for more general cases of the PPA (e.g., curved crowns with species-specific shapes) are described in reference (6). The flat-top Z^* can be calculated as follows: (i) calculate the total crown area of the tallest cohort *i*: $w(i)\pi(\phi_j dbh_i)^2$, where *j* is the species identity of cohort *i*; (ii) calculate the crown area of the next tallest cohort, and add this area to the previously calculated area; (iii) repeat step ii until the total crown area exceeds the ground area; (iv) Z^* is the height of the trees in the last cohort added.

Apply growth and mortality to each cohort. Given the value for Z^*, the following transformations are applied to each cohort *i* (the subscripts *j* indicates the species to which *i* belongs):

$$w(i) \rightarrow \begin{cases} (1-\mu_{L,j})w(i) & \text{if height of cohort } i \geq Z^* \\ (1-\mu_{D,j})w(i) & \text{if height of cohort } i < Z^* \end{cases} \qquad \text{(mortality)} \qquad \text{(S1.7)}$$

$$dbh_i \rightarrow \begin{cases} dbh_i + G_{L,j} & \text{if height cohort of } i \geq Z^* \\ dbh_i + G_{D,j} & \text{if height cohort of } i < Z^*. \end{cases} \qquad \text{(growth)} \qquad \text{(S1.8)}$$

After these transformations, a new height and crown area is assigned to each cohort *i* according to the new value for dbh_i, and according to the allometric parameters α_j, β_j and ϕ_j for species *j* of cohort *i*.

Add new cohorts through reproduction. New recruits (i.e., cohorts *i* with $dbh_i = 0$) are added at each iteration. One new cohort is added per species per iteration. The spatial density $w(i)$ for the new cohort of species *j* reflects the representation of j in the canopy (understory trees are assumed to be incapable of reproduction in this special case of the PPA: see (7, 8)). Here a choice must be made regarding the spatial scale over which to measure this representation. Does recruitment depend primarily on the average representation within the stand itself, or over the landscape? In the simulations presented in this paper, we used the average taken over all plots on the correct soil type within the region. Crucially, however, reproduction has very little effect – in the sense that the results are extremely similar even if all reproduction is set to zero – on the predictions for stand basal area vs. stand age, the dynamics of succession, and the species composition of old stands. Reproduction does have an important signature on the predicted diameter distribution of old plots, because the densities within the smaller size classes depend on the rate of arrival, and subsequent growth and mortality, of small trees. Therefore, the diameter distributions in Figure S1 should be viewed with some caution, given the choice to use reproduction dependent on the regional average species composition of the canopy.

Given an average regional canopy representation (m^2 ha^{-1}) for species *j* of A_j, the new cohort of species *j* created in each iteration is assigned a density $w(i) = FA_j$ and $dbh_i = 0$. In subsequent iterations, these cohorts are treated like any other, according to eqns. S1.7-S1.8.

Metrics for Successional Performance: H_{20} and $\hat{Z}^*$. In addition to implementing simulations of the PPA, we used the PPA parameters to calculate, for each species on each soil, metrics for early- and late-successional performance, and for different components of late-successional performance. The metric for early-successional performance is $H_{20,j}$, the height of a 20-year-old tree of species *j* that has never been shaded. The metric for late-successional performance is $\hat{Z}_j^*$, the height of canopy closure (Z^*) in an equilibrium monoculture of species *j*. In the special case of the PPA considered here, in which the understory environments of all closed-canopy forests on a given soil type are considered identical (i.e., $G_{D,j}$ and $\mu_{D,j}$ are assumed constant for species *j* on a given soil type), the late-successional dominant is the species *j* with the largest value of $\hat{Z}_j^*$ (7).

From the sample of parameter vectors **θ** on each soil type, we selected 1000 at random, denoted $\boldsymbol{\theta}_k$ for $k = 1, 2, 3 \ldots 1000$. For each *k*, we calculated four metrics for each species *j*:

$$H_{20,j,k} = \alpha_{j,k}[20G_{L,j,k}]^{\beta_{j,k}} \tag{S1.9}$$

$$\hat{Z}_{j,k}^* = \alpha_{j,k}(G_{D,j,k} / \mu_{D,j,k})^{\beta_{j,k}}[\ln(2\pi\phi_{j,k}^2 F G_{L,j,k}^2 \mu_{L,j,k}^{-3})]^{\beta_{j,k}} \tag{S1.10}$$

$$Y_{understory,j,k} = (G_{D,j,k} / \mu_{D,j,k})^{\beta_{j,k}} \tag{S1.11}$$

$$Y_{canopy,j,k} = [\ln(2\pi\phi_{j,k}^2 F G_{L,j,k}^2 \mu_{L,j,k}^{-3})]^{\beta_{j,k}} \tag{S1.12}$$

where $Y_{understory,j,k}$ and $Y_{canopy,j,k}$ are the understory and canopy components, respectively of late-successional performance ($\hat{Z}_{j,k}^*$).

The above calculations produced 1000 values for each of the four metrics, for each of the eight species on each soil type. From these values, we extracted the mean, and central 68% intervals. Thus, like the PPA model simulations described above, the calculation of the early- and late-successional metrics included a propagation of parameter uncertainty.

References for Appendix 1

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Appendix 2: Parameter Estimation

The special case of the PPA model considered in this paper requires, for each soil type, a single fecundity parameter F and seven species-specific parameters for each of the eight most common species j (Table S2.1). Thus, the model requires 7 × 8 = 56 species-specific parameters (the vector $\boldsymbol{\theta}$) for each soil type. We used the Metropolis-Hastings Markov chain Monte Carlo (MCMC) algorithm in a Bayesian context to generate samples from $p(\boldsymbol{\theta} \mid \mathbf{X})$, the posterior distribution of $\boldsymbol{\theta}$ given the data $\mathbf{X}$ (1, 2). We used a separate procedure to estimate F for each soil type (see below).

The posterior density, $p(\boldsymbol{\theta} \mid \mathbf{X})$, is proportional to the product of the likelihood and the prior (3): $p(\boldsymbol{\theta} \mid \mathbf{X}) \propto p(\mathbf{X} \mid \boldsymbol{\theta}) \times p(\boldsymbol{\theta})$, where $p(\mathbf{X} \mid \boldsymbol{\theta})$ is the likelihood of the inventory dataset (see Appendix 1, DATA SOURCES) conditional on a particular value of $\boldsymbol{\theta}$, and $p(\boldsymbol{\theta})$ is the prior probability density of $\boldsymbol{\theta}$. We used uniform priors on a finite range (Table S2.1), so that $p(\boldsymbol{\theta}) = C$, where C is a constant. This choice of prior is completely noninformative on the scale of $\boldsymbol{\theta}$. With uniform priors, $p(\boldsymbol{\theta} \mid \mathbf{X}) \propto p(\mathbf{X} \mid \boldsymbol{\theta})$; i.e., the analysis depends only on the likelihood. Given the large sample sizes in our analysis, the posterior means should be similar to the maximum likelihood estimates (3).

For convenience, we work with the log-likelihood, $\ell(\mathbf{X} \mid \boldsymbol{\theta}) \equiv \log[p(\mathbf{X} \mid \boldsymbol{\theta})]$, which includes terms for growth, mortality, height allometry, and crown allometry:

$$\begin{aligned} \ell(\mathbf{X} \mid \boldsymbol{\theta}) = \quad & \ell(\mathbf{X}_{growth} \mid \mathbf{G_L}, \mathbf{G_D}, \boldsymbol{\sigma}_{GL}, \boldsymbol{\sigma}_{GD}) + \ell(\mathbf{X}_{mortality} \mid \boldsymbol{\mu}_\mathbf{L}, \boldsymbol{\mu}_\mathbf{D}) \\ & + \ell(\mathbf{X}_{height} \mid \boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\sigma}_{height}) + \ell(\mathbf{X}_{crown} \mid \quad , \boldsymbol{\sigma}_{crown}) \qquad \text{(S2.1)} \end{aligned}$$

where $\mathbf{X}_{growth}$ is the inventory data for growth (for a particular soil type), and similarly for $\mathbf{X}_{mortality}$, $\mathbf{X}_{height}$ and $\mathbf{X}_{crown}$; and $\mathbf{G_L}$ is the vector of $G_{L,j}$ parameters over all species j included in the estimation, and similarly for understory growth ($\mathbf{G_D}$), canopy and understory mortality ($\boldsymbol{\mu}_{\mathbf{L}}, \boldsymbol{\mu}_{\mathbf{D}}$), height allometry (**α**, **β**) and crown allometry ( ). The **σ** terms are vectors of species-specific parameters describing unexplained variation in growth, height, and crown radius (see below). Each term in eq. S2.1 is described in the next section, along with details of the data sources and data selection criteria.

Growth. The special case of the PPA considered here requires two growth parameters for each species *j*: annual diameter at breast height (dbh) growth rates $G_{L,j}$ and $G_{D,j}$ for canopy and understory trees, respectively. To estimate these parameters from FIA data, we assumed that individual dbh growth rates are normally distributed with means $G_{L,j}$ and $G_{D,j}$ and standard deviations $\sigma_{L,j}$ and $\sigma_{D,j}$ for canopy and understory trees, respectively. The parameters $\sigma_{L,j}$ and $\sigma_{D,j}$ describe the magnitude of the unexplained variation in growth. We assume that the growth rates exhibited by the individual trees within any group are independent. Under these assumptions we have

$$\ell(\mathbf{X}_{growth} \mid \mathbf{G}_{\mathbf{L}}, \mathbf{G}_{\mathbf{D}}, \boldsymbol{\sigma}_{GL}, \boldsymbol{\sigma}_{GD}) =$$

$$\sum_{j=1}^{8} \sum_{i \in \mathbf{X}_{growth,j}} \ln\left\{P_i N(\Delta D_i \mid G_{L,j}, \sigma_{GL,j}) + (1 - P_i) N(\Delta D_i \mid G_{D,j}, \sigma_{GD,j})\right\} \qquad \text{(S2.2)}$$

where ΔD_i is the observed annual dbh growth rate for tree *i* (see below); $N(\Delta D_i \mid G_{L,j}, \sigma_{GL,j})$ is the normal probability density for ΔD_i with mean $G_{L,j}$ and standard deviation $\sigma_{GL,j}$; and P_i is the probability that tree *i* was in the canopy at the start of the time interval over which growth was measured. Eq. S2.2 sums over the eight most common species *j* on a given soil type.

If the FIA had provided observations of crown class (trees in the understory vs. canopy) for the time of the first survey (the initial plot measurement), we could have assigned $P_i = 1$ or $P_i = 0$ for each tree *i* (assuming no errors in FIA crown-class assignments). However, crown class was only given for the time of the second survey (the plot remeasurement), and more importantly, was not given at all for trees that died (see below), necessitating the probabilistic approach in eq. S2.2.

To calculate P_i, we used FIA crown-class data reported for the second survey to calculate P_i for each species *j*, conditional on the prediction of canopy status (in or out of the canopy) given by the model structure and parameter values in reference (4) applied to the second survey. [Note that ref 4 employed two different parameter estimation schemes for the crown shape parameters, from which we employed the 'single axis fit' parameters here]. That is, we applied the model from (4) to generate a value of Z^* for each plot *q* at the time of the second survey, and then assigned a predicted canopy status $U_i^{(pred)}$ for the time of the second survey (1= canopy, 0 = understory) to each tree *i* in *q* ($U_i^{(pred)}$ = 1 if tree *i* is taller than Z^*, and 0 otherwise). We then compared the observed canopy status $U_i^{(obs)}$ of the trees in *q* at the time of the second survey with the predictions $U_i^{(pred)}$ to give the conditional probability:

$$P_{i,t} = \begin{cases} \gamma_{1,j} & \text{if } U_{i,t}^{(pred)} = 1 \\ \gamma_{0,j} & \text{if } U_{i,t}^{(pred)} = 0 \end{cases} \qquad \text{(S2.3)}$$

where *t* refers to the time of the survey (1 = first survey; 2 = second survey), and

$$\gamma_{1,j} = \frac{S[U_{i,2}^{(obs)} = 1 \text{ and } U_{i,2}^{(pred)} = 1]}{S[U_{i,2}^{(pred)} = 1]}$$

$$\gamma_{0,j} = \frac{S[U_{i,2}^{(obs)} = 1 \text{ and } U_{i,2}^{(pred)} = 0]}{S[U_{i,2}^{(pred)} = 0]} \qquad \text{(S2.4)}$$

where $S[]$ denotes the number of trees i that match the criteria contained in []. Typical values of $\gamma_{1,j}$ and $\gamma_{0,j}$ were 0.90 and 0.20 respectively, showing that the model and parameter values from (4) gave quite accurate predictions of canopy status for individual trees. Nonetheless, we found that the error rates (i.e., 0.10 and 0.20) were sufficient to produce substantial differences in the estimates for the PPA parameters, compared to the estimates given by treating the canopy status predictions as perfect (i.e., assuming $\gamma_{1,j}$ = 1 and $\gamma_{0,j}$ = 0). Note that, unlike the analysis in (4), the special case of the PPA presented in the main text used a simplified ‘flat-top’ canopy model (where crowns are flat discs with radius proportional to stem diameter); the parameters for this flat-top model (see HEIGHT ALLOMETRY and CROWN ALLOMETRY, below) were estimated separately from those in (4). Thus, the model and parameter estimates from (4) were used only to generate the conditional probability for canopy status in eq. S2.2.

Data sources and selection criteria. The inventory data $\mathbf{X}_{growth}$ were taken from remeasured FIA plots in the Lake States for which the second survey occurred in the mid 1990s; i.e., prior to 1999, when the design of the FIA was changed (5, 6). Plots placed in plantation forests were not included. The pre-1999 data give, for each tree *i*, dbh from the first and second surveys: $D_{i,1}$ and $D_{i,2}$. From these values, we calculated an average annual dbh growth rate for *i*:

$$\Delta D_i = [D_{i,2} - D_{i,1}] / t_i \qquad \text{(S2.5)}$$

where t_i is the time between the two surveys for tree *i* (average value 12.2-12.5 years, depending on soil type).

The set $\mathbf{X}_{growth,j}$ (i.e., the trees *i* included in the growth likelihood for species *j*) included only those trees *i* of species *j* satisfying the following criteria: *i* belongs to a plot in MI, WI, or MN on the relevant soil type (referred to as 'physiographic class' in the FIA) that was not harvested between the two surveys; and *i* was recorded as being alive at both surveys.

Mortality. The special case of the PPA considered here requires two mortality parameters for each species *j*: $\mu_{L,j}$ and $\mu_{D,j}$, which are annual mortality probabilities for trees in the canopy and understory, respectively. During an interval of *t* years, trees of species *j* that begin the interval as canopy and understory trees, respectively, of species *j* die with probabilities $1-(1-\mu_{L,j})^t$ and $1-(1-\mu_{D,j})^t$. We assume that mortality events suffered by the trees within any group are independent, such that

$$\ell(\mathbf{X}_{mortality} \mid \boldsymbol{\mu}_\mathbf{L}, \boldsymbol{\mu}_\mathbf{D}) =$$

$$\sum_{j=1}^{8} \sum_{i \in \mathbf{X}_{mort,j}} \ln\Big\{ M_i \big[(1-P_i)(1-(1-\mu_{D,j})^{t_i}) + P_i(1-(1-\mu_{L,j})^{t_i}) \big] + (1-M_i)\big[(1-P_i)(1-\mu_{D,j})^{t_i} + P_i(1-\mu_{L,j})^{t_i}\big]\Big\} \tag{S2.6}$$

where $M_i = 1$ if tree *i* was observed to have died during the remeasurement interval, and 0 otherwise; and P_i is the probability that tree *i* was in the canopy at the start of the time interval, as explained for GROWTH above. Eq. S2.6 sums over the eight most common species *j* on a given soil type.

Data sources and selection criteria. The selection criteria for $\mathbf{X}_{mort,j}$ were the same as those for $\mathbf{X}_{growth,j}$ (see above), except that $\mathbf{X}_{mort,j}$ included trees that were alive or dead (from non-harvest causes) at the time of the second survey, whereas $\mathbf{X}_{growth,j}$ only included trees that survived the remeasurement interval.

Height Allometry. The special case of the PPA considered here requires two height-dbh allometric parameters, α_j and β_j, for each species j. To estimate these parameters from FIA data, we assumed, based on visual inspection of the data, that the standard deviation of individual height increases linearly with mean predicted height. Thus, the log-likelihood for the height data is:

$$\ell(\mathbf{X}_{height} \mid \boldsymbol{\alpha}, \boldsymbol{\beta}_{\mathbf{D}}, \boldsymbol{\sigma}_{height}) = \sum_{j=1}^{8} \sum_{i \in \mathbf{X}_{height,j}} \ln\left\{N(h_i \mid dbh_i, \alpha_j, \beta_j, \sigma_{height,j})\right\} \qquad \text{(S2.7)}$$

where $N(\cdot)$ is the normal probability density for tree i with observed height h_i (m) and diameter dbh_i (cm), with mean $z_i = \alpha_j dbh_i^{\beta_j}$ and standard deviation $\sigma_{height,j} z_i$.

Data sources and selection criteria. The dataset $\mathbf{X}_{height,j}$ included only those trees i of species j satisfying these three criteria: i is from the post-1999 FIA data (which, unlike the pre-1999 FIA, includes individual height measurements, but currently lacks remeasurement data for most of the U.S.) from MI, WI, or MN with plots placed in plantation forests discarded. i is a live tree with a measured height; i belongs to a plot with the relevant soil type that did not include any trees classified as harvested.

Crown Allometry. The special case of the PPA considered here assumes crown radius to be proportional to dbh and the crown to be a flat disc. Thus, crown allometry requires only one parameter, the coefficient of proportionality ϕ_j. For parameter estimation, we assume a normal distribution of unexplained variation in the crown radius of trees of a given dbh, with mean zero and standard deviation $\sigma_{crown,j}$. Thus, the log-likelihood for the crown radius data is

$$\ell(\mathbf{X}_{crown} \mid \quad , \boldsymbol{\sigma}_{crown}) = \sum_{j=1}^{8} \sum_{i \in \mathbf{X}_{crown,j}} \ln\left\{ N(r_i \mid \phi_j, dbh_i, \sigma_{crown,j}) \right\} \qquad \text{(S2.8)}$$

where r_i is the observed crown radius (m) for tree *i* (see below), dbh_i is the dbh (cm) for tree *i*, and $N(r_i \mid \phi_j, dbh_i, \sigma_{crown,j})$ is the normal probability density of r_i with mean $\phi_j dbh_j$ and standard deviation $\sigma_{crown,j}$.

For each tree with crown diameter information (trees over 5 inches dbh in the pre-1999 FHM data: see reference 4), we calculated a value for observed crown radius r_i (m) from $cdia_{i,1}$ (the maximum crown diameter) and $cdia_{i,2}$ (crown diameter measured at 90º to $cdia_{i,1}$). We first calculated observed crown area a_i (m^2) assuming an elliptical shape:

$$a_i = \pi(cdia_{i,1}/2)(cdia_{i,2}/2) \qquad \text{(S2.9)}$$

and then calculated r_i (m) as $\sqrt{(a_i / \pi)}$. Thus, r_i is the radius of a circle with the same area as the ellipse defined by $cdia_{i,1}$ and $cdia_{i,2}$.

Data sources and selection criteria. The dataset $\mathbf{X}_{crown,j}$ included trees *i* of species *j* satisfying the following criteria: *i* is from the pre-1999 FHM from MI, WI, or MN with plots from plantation forests discarded; *i* has species identity *j*; *i* belongs to a plot with the relevant soil type that was not harvested between the two survey dates; $cdia_1$ and $cdia_2$ were available for *i*.

Parameter Ranges and Reparameterization. We allowed wide ranges on each parameter, encompassing all reasonable values (see Table S2.1). To speed convergence of the MCMC algorithm, we reparameterized the growth and mortality parameters as follows. We reparameterized mortality as

$$\rho_{L,j} = 1/\mu_{L,j}$$

$$\rho_{D,j} = 1/\mu_{D,j} \qquad \text{(S2.10)}$$

and estimated values for $\rho_{L,j}$ and $\rho_{D,j}$ rather than $\mu_{L,j}$ and $\mu_{D,j}$, for each species *j*. For both growth and mortality, we estimated understory rates as a function of canopy rates:

$$\rho_{D,j} = \Omega_{\rho,j}\rho_{L,j}$$

$$G_{D,j} = \Omega_{G,j}G_{L,j} \qquad \text{(S2.11)}$$

where $0 < \Omega_{\rho,j} < 1$ and $0 < \Omega_{G,j} < 1$. Thus, for each species *j*, we estimated four growth and mortality parameters (as in the original parameterization): $\rho_{L,j}$, $\Omega_{\rho,j}$, $G_{L,j}$, and $\Omega_{G,j}$. We reparameterized height allometry as

$$height = \alpha_j^{20}(dbh/20)^{\beta_j}, \qquad \text{(S2.12)}$$

where $\alpha_j^{20} \equiv \alpha_j\ 20^{\beta_j}$, and we estimated α_j^{20} rather than α_j. We emphasize that the reparameterizations were employed for convenience only. Preliminary analyses without these reparameterizations yielded similar results.

MCMC Sampling. We used the Metropolis-Hastings MCMC algorithm to sample from the joint posterior distribution of the parameters (1, 2). The definition of the Metropolis-

Hastings MCMC algorithm leaves a great deal of freedom in the definition of (for example) the functional forms and the proposal distributions used to alter parameter values, and the choice of how many parameter values to alter at each MCMC step. These choices can have important effects on the efficiency and stability of the algorithm. For this analysis we used a custom algorithm that we have found useful in a variety of parameter estimation problems (e.g., 4, 7, 8). We have found that this algorithm, which conforms to the requirements for the Metropolis-Hastings MCMC algorithm to converge to the correct posterior distribution, is robust to the problem of local (non-global) maxima and converges quickly. In this algorithm, at each MCM step, changes are proposed to randomly selected parameters, where the number of parameters to be changed varies from one to the total number of parameters. Proposal distributions for each parameter (table S2.1) are tuned during an initial 'burn-in' period (in this case, 30,000 MCMC steps) to achieve an approximate Metropolis-Hastings acceptance rate of 0.25. This tuning is accomplished by iteratively adjusting the standard deviations of the normal random variables that define the proposal distributions (table S2.1). The standard deviations are fixed at the end of the burn-in period. We used different proposal distributions for parameters bounded between 0 and infinity, and parameters bounded between 0 and 1 (table S2.1), and we did not explicitly include any prior information in the metropolis criterion. Thus we used non-informative priors with different forms for the noninformative priors on each parameter (uniform over logarithm of values, uniform over untransformed values, respectively: see reference 7). Following the burn-in period, we recorded a posterior sample (i.e., the current values of all model parameters) every 100th MCMC step for 30,000 steps. We saved these samples for error propagation in the calculation of analytical metrics (such as $\hat{Z}_j^*$), and in model simulations (see Appendix 1).

Fecundity. The special case of the PPA used here requires only one reproductive parameter, fecundity (F): the number of size-zero individuals produced per unit exposed crown area per unit time (9-11). Unlike the other parameters in the PPA model, it is problematic to estimate F directly from FIA (or FHM) data, because the FIA only includes stems with dbh ≥ 1 inch (2.54 cm). Such trees can be seen appearing in the data as they traverse the 1 inch threshold through growth (so-called 'ingrowth'). But there are few such saplings in the data, and more importantly, there could be a substantial time lag between germination (when dbh = 0) and appearance in the FIA (when dbh ≥ 1 inch). To estimate F properly, it would be necessary to know (or estimate) the representation of each species in the canopy at the time of seed production, and the canopy status (canopy vs. understory) of each ingrowth sapling during its previous history. Given these complications, we did not attempt to estimate F directly. Instead, we first reduced the dimensionality of the problem by assuming that all species share the same value for F. Then, for each soil type, we determined the value of F (while propagating uncertainty in the other model parameters; see below) such that the average predicted density of trees with dbh between 4-8 cm in 100-year old stands was equal to the density observed. Specifically, we implemented 30 PPA simulations (prior to the 50 simulations described in Appendix 1) to determine the value of F that would result in the observed density of 4-8 cm dbh trees. In each of these simulations, we selected a value for F at random from a uniform (0, 0.03) distribution, and assigned all other parameter values by drawing at random from the MCMC samples described above. We then plotted the 30 pairs of predicted density of 4-8 cm dbh trees vs. F. Visual inspection of this plot suggested a linear relationship, which we determined using linear regression separately for each soil type. The regression yielded an estimated relationship between F and the predicted density of 4-8 cm dbh trees, which we then used to solve for the F that would result in the observed density.

Therefore, unlike all other parameters, F was estimated from the same data that was used to compare model predictions with observations. This can be seen in the comparison of predicted vs. observed size distributions in Figure S1, where the model prediction for the density of trees with 4-8 cm dbh appears perfect: this match is a necessary outcome of the way F was estimated. However, importantly, because F was shared across species, F constituted only one parameter, compared to $7 \times 8 = 56$ parameters estimated from short-term data independent from the long-term data against which model predictions were compared. Moreover: (i) the value of F was parameterized to match only a single value, from a single kind of metric, rather than to maximize the overall fit of observations to data – this was done deliberately to maximize the independence of the other comparisons of predictions vs. observations, including the rest of the size distribution; (ii) it is simple to show analytically that F is less important than the other parameters in determining the outcome of interspecific competition (9); (iii) to confirm the preceding result, we implemented an ensemble of 50 models simulations with F set to zero. We found that the predictions for basal area vs. stand age and for successional dynamics were almost completely insensitive to this change, showing that these predictions are dominated by the growth and mortality of trees already in the initial condition (young plots). However, as expected, with F set to zero, the predictions for size distributions were very poor, because trees in small size classes were predicted to be absent; (iv) in contrast to PPA results obtained by assuming the same F for all species, implementing simulations with the other PPA parameters set equal between species gave poor predictions for basal area and very poor predictions for ecological succession and the species composition of old stands.

References for Appendix 2

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