ARTICLE

Recovery trends and predictions of Fraser fir (*Abies fraseri*) dynamics in the Southern Appalachian Mountains

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Abstract: The endemic Fraser fir (*Abies fraseri* (Pursh) Poir.) is found in only seven montane regions in the southern Appalachians above ca. 1500 m elevation. Due to widespread insect-caused mortality from the invasive balsam woolly adelgid (*Adelges piceae* Ratzeburg), as well as possible impacts from climate change and atmospheric pollution, the future of Fraser fir populations remains uncertain. Long-term monitoring programs have been in place since the 1980s, and here we present the first predictive population models for endemic Fraser fir populations using the inventory data from Great Smoky Mountains National Park, which contains 74% of extant Fraser fir forests. Using two kinds of population data (understory density counts and overstory census data), we model Fraser fir population dynamics on five different mountaintops as a stage-structured matrix model with transition parameters estimated using hierarchical Bayesian inference. We predict robust recovery over the next several decades for some Fraser fir populations, particularly where mature overstory fir has persisted throughout the last two decades, and continued decline for populations at the lowest elevations. Fraser fir densities are already low at these lower elevations, suggesting that this population is vulnerable to local extirpation.

Key words: Bayesian hierarchical modeling, stage-structured matrix model, balsam woolly adelgid; *Abies fraseri*.

Résumé : Le sapin de Fraser (*Abies fraseri* (Pursh) Poir.), une espèce endémique, est présent seulement dans sept régions montagneuses du sud des Appalaches à une altitude supérieure à environ 1500 m. L'avenir du sapin de Fraser demeure incertain à cause de la mortalité répandue causée par un insecte invasif, le puceron lanigère du sapin (*Adelges piceae* Ratzeburg), ainsi que des impacts potentiels du changement climatique et de la pollution atmosphérique. Des programmes de surveillance à long terme sont en place depuis les années 1980 et nous présentons ici les premiers modèles prédictifs de population pour les populations endémiques de sapin de Fraser à l'aide de données d'inventaire provenant du parc national des Great Smoky Mountains où l'on retrouve 74 % des forêts encore existantes de sapin de Fraser. En utilisant deux sortes de données de population (mesures de densité du sous-bois et données d'inventaire de l'étage dominant), nous avons modélisé la dynamique de population du sapin de Fraser sur le sommet de cinq montagnes différentes au moyen d'un modèle matriciel structuré en stades avec des paramètres de transition estimés par inférence bayésienne hiérarchique. Nous prédisons une forte récupération au cours de plusieurs des prochaines décennies pour certaines populations, particulièrement celles où un étage dominant de sapin de Fraser mature a persisté pendant les deux dernières décennies, ainsi que la poursuite du dépérissement dans les populations situées à plus basse altitude. La densité du sapin de Fraser est déjà faible à basse altitude, ce qui indique que cette population est sujette à une disparition locale. [Traduit par la Rédaction]

Mots-clés : modélisation bayésienne hiérarchique, modèle matriciel structuré en stades, puceron lanigère du sapin, *Abies fraseri*.

1. Introduction

The southern Appalachian spruce–fir forest is a relict ecosystem found in only seven mountaintop populations ranging from Mount Rogers in southwestern Virginia to the Great Smoky Mountains of eastern Tennessee and western North Carolina (Whittaker 1956). Currently occupying only about 26 kha (Smith and Nicholas 2000), the red spruce (*Picea rubens* Sarg.) – Fraser fir (*Abies fraseri* (Pursh) Poir.) forests of the Southern Appalachians are currently listed as one of the most endangered ecosystems in the United States (Christensen et al. 1996). These forests are noted for their relatively high level of endemic species, especially within the pure fir stands found on the highest peaks (White 1984).

The current geographic distribution of Fraser fir covers about half of what it once did in the late 19th century (Dull et al. 1988). Logging and failed regeneration caused by site degradation dramatically reduced the range of Southern Appalachian spruce–fir

in the early 1900s (Pyle and Schafale 1988). Since the late 1950s, Fraser fir has experienced 67% mortality of adult trees throughout the species' range, with up to 91% mortality in some areas of Great Smoky Mountains National Park (GSMNP) (Dull et al. 1988). Impacts potentially contributing to this decline are numerous. One well-known factor is depredation from the invasive insect *Adelges piceae*, the balsam woolly adelgid (BWA). The insect feeds on the phloem of adult Fraser fir and causes reduction in water and sap conductance, which generally results in tree mortality within 2–5 years (Hollingsworth and Hain 1991). Additionally, acidic deposition associated with air pollution is high in the montane cloud forests of the southern Appalachians (Nodvin et al. 1995) and has been linked to increased foliar injury and early senescence, reduction in leaf chlorophyll content, decreased cold hardiness, and alterations in soil aluminum and nutrient availability (Borer et al. 2005; Jacobson et al. 1990; McLaughlin et al. 1990). Alterations to carbon balance and foliar respiration associated
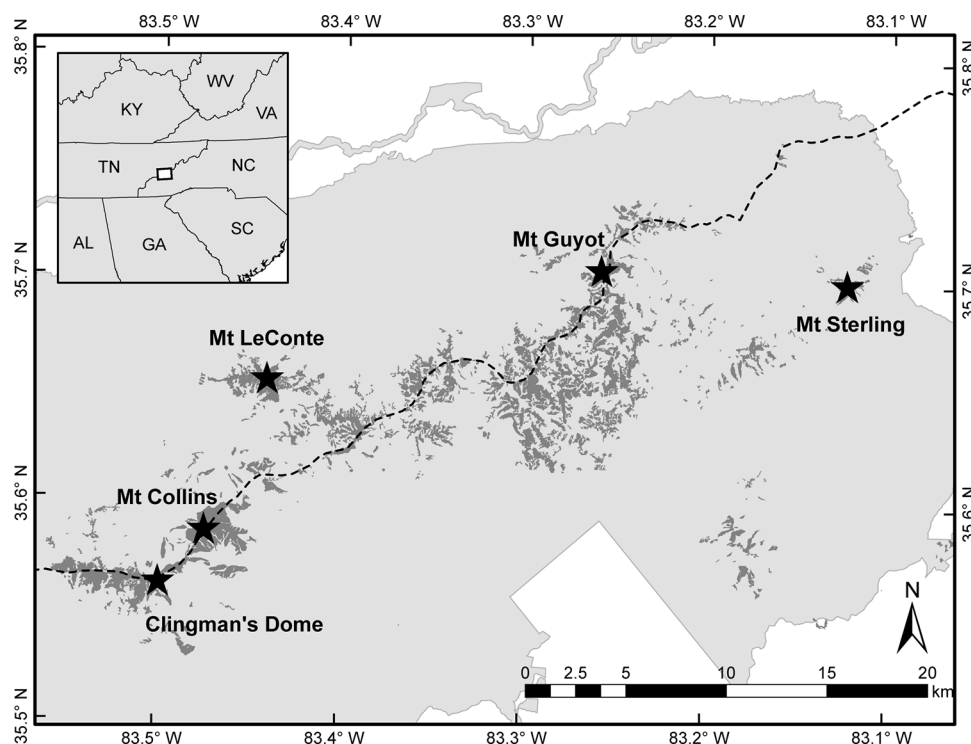
Fig. 1. Map of study area within Great Smoky Mountains National Park. Light grey shading denotes park boundary. Dark grey shading represents red spruce – Fraser fir forest cover provided as a GIS layer from the National Park Service. Stars denote the five mountains where monitoring plots are located.

with changing climate are another possible reason for reduced forest health, as suggested by Tjoelker et al. (1999) in work on boreal tree species.

In the face of these changes, the future of Fraser fir populations remains uncertain. The US Forest Service's 1988 regional assessment of spruce–fir forests using aerial photography was the last systematic inventory to document the total extent of high-elevation forests in the southern Appalachians but is limited to presence or absence data for this forest type at a single point in time. Several descriptive studies were done prior to the arrival of BWA (Oosting and Billings 1951; Whittaker 1956), and other studies document changes occurring during the infestation's initial outbreak (Busing et al. 1988, 1993; Dull et al. 1988).

Long-term monitoring programs were established during the 1980s throughout the range of Fraser fir. A number of studies have detailed forest dynamics over the past few decades at these sites (Jenkins 2003; Lusk et al. 2010; Mancusi 2004; McManamay et al. 2011; Moore et al. 2008) and generally describe juvenile and understory forests reaching the stem exclusion phase of stand development, indicating that recovery from disturbance is underway. In addition, Dale et al. (1991) generated paired Leslie matrix models for both Fraser fir and BWA to perform scenario analysis at different elevations. This study concluded that oscillations in BWA and fir populations with a cyclical pattern of mortality and recovery were likely but did not detail the length of this cycle. Additionally, because temperature ranges and amplitude affected the survival and fecundity of BWA, these factors had an indirect, but significant, impact on future Fraser fir populations. Finally, some predictive climate envelope modeling has also been performed on Fraser fir based on current species distributions (Potter et al. 2010) and suggests that suitable habitat will shrink by 2050 and then expand again by the end of the century. However, there are no predictive population models using the inventory data collected from monitoring efforts. By locating specific populations that are in decline, predictive population models could ben-

efit management and conservation of this endemic species by allowing managers to concentrate their efforts on these key populations.

In this paper, we describe past and current Fraser fir forest structure on five peaks in GSMNP. Additionally, we present the first predictive population models for Fraser fir in GSMNP: a set of stage-structured matrix models fit using Bayesian methods. We then use these models to generate predictions of Fraser fir stand density in 10-year increments until 2050, as well as confidence estimates around those predictions.

2. Methods

2.1. Study area

Fir populations were monitored by the National Park Service (NPS) in five high-elevation mountaintop sites in GSMNP. These five mountains encompass nearly the entire Fraser fir range in GSMNP: Mount Sterling, Mount Guyot, Mount LeConte, Mount Collins, and Clingmans Dome (Fig. 1). Thirty-seven long-term monitoring plots were established at these sites in 1990, with roughly eight plots on each mountain (exceptions being six plots on Mount Sterling and seven on Mount Guyot). Plots measure 400 m² and are situated at different aspects and elevations, ranging from 1722 m on Mount Sterling to 1999 m on Mount LeConte.

2.2. Data

Forest plots were measured over the summers of 1990 and 2000 by NPS staff and in 2010 by D. Kaylor and NPS staff. Species and diameter at breast height (dbh) were recorded for all adult trees (dbh > 5 cm) in each plot, which were also tagged. Total counts by species of seedlings (height < 1.37 m) and saplings (height > 1.37 m, dbh < 5 cm) were also recorded within twelve 1 × 1 m subplots and twelve 2 × 2 m subplots, respectively.

Fig. 2. Model schematic showing stages for seedlings (S), saplings (juveniles, J), nonreproductive adults (A), and reproductive adults (R). Between 10-year iterations, individuals may remain in their current stage (solid black arrows), transition to an older stage (dotted arrows), or die (gray arrows); additionally, reproductive adults may generate new individuals in the seedling or, less frequently, juvenile class (dashed arrows).
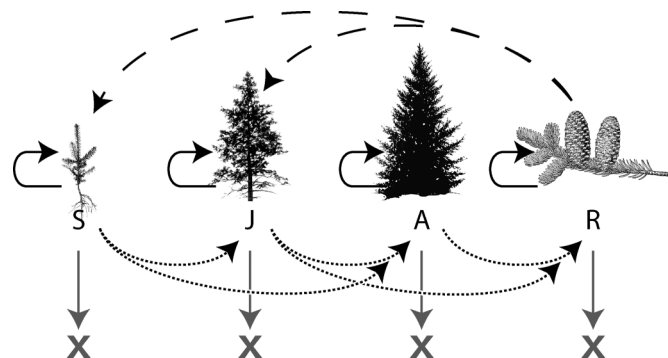
2.3. Past and current population size distributions

Data collected in 1990, 2000, and 2010 were used to generate both current live fir basal area and past and current size class distributions. The dbh for all seedlings was approximated as 0.5 cm (from an estimated range of 0–1 cm); similarly, the dbh for all saplings was set to 3.0 cm (estimated range of 1–5 cm). A kernel density estimator was applied to adult size data to estimate counts of adult trees in 1 cm increments. Error was estimated by means of a leave-one-out (jackknife) cross-validation over the plots for each mountain. Because seedlings are substantially more dense within plots than large overstory trees, data are reported on a log scale.

2.4. Population model

Population growth of Fraser fir on each mountaintop was modeled by a stage-structured matrix with transition parameters estimated using hierarchical Bayesian inference (Fig. 2). The fir population is divided into four stage classes (seedlings (S), saplings and juveniles (J), nonreproductive adults (A), and reproductive adults (R) defined as adult trees with dbh > 15 cm) and an additional 'stage' for dead stems (D) to account for the fate of all individuals over the study period. Over the two 10-year periods, individuals transitioned between stages. In the case of adult trees, these individual transitions were documented; in the case of saplings and juveniles, these transitions must be inferred from the aggregate count data. These stages, transitions, and recruitment rates define a matrix population model (Caswell 2001; Ellner and Guckenheimer 2006).

In the case when all transitions and recruitment events are recorded, those rates can be straightforwardly estimated from observed proportions. However, when only counts are available, those rates are not fully determined and the same data can be observed from different vital rates (Caswell 2001; Wood 1994). When given multiple observations with the goal of determining vital rates over all samples, multiple regression techniques (Lee et al. 1977; Lefkovitch 1965) and iterative methods (Lawless and McLeish 1984; MacRae 1977) are well established. However, these techniques provide point estimates only, and combining different types of data into the same model is challenging. A Bayesian approach can estimate model parameters using all of the available data. Additionally, it can provide uncertainty estimates around those parameters that can be propagated to functions of those parameters such as future population estimates (Gross et al. 2002).

Given that individuals may transition from stage to stage between observations, let m_{ij} represent the number of individuals that were in stage j at the beginning of a 10-year period and were then in stage i at the end of that period, including the cases in

which those individuals remain in the same stage (i.e., $i = j$). These values are multinomially distributed (Welton and Ades 2005) with parameters equal to the conditional probability of an individual ending in stage i given that it started in stage j:

$$[m_{Sj}, m_{Jj}, m_{Aj}, m_{Rj}, m_{Dj}] \sim \text{Multinomial}(p_{Sj}, p_{Jj}, p_{Aj}, p_{Rj}, p_{Dj})$$

It is these probabilities, p_{ij}, that define the matrix model. They are themselves given an uninformative prior distribution:

$$[p_{Sj}, p_{Jj}, p_{Aj}, p_{Rj}, p_{Dj}] \sim \text{Dirichlet}(1, 1, 1, 1, 1)$$

The Dirichlet is the conjugate prior to the multinomial and ensures that

$$p_{ij} \in [0, 1]$$

$$\Sigma_i p_{ij} = 1$$

These probabilities are combined with (unknown) reproductive rates, b_{ij}, into a matrix, **G**, that defines a linear model of population growth:

$$\mathbf{G} = \begin{bmatrix} p_{SS} & 0 & 0 & b_{SR} & 0 \\ p_{JS} & p_{JJ} & 0 & b_{JR} & 0 \\ p_{AS} & p_{AJ} & p_{AA} & 0 & 0 \\ 0 & p_{RJ} & p_{RA} & p_{RR} & 0 \\ p_{DS} & p_{DJ} & p_{DA} & p_{DR} & 1 \end{bmatrix}$$

The 'dead' stage is absorbing; individuals cannot transition into a different stage after dying. Reproductive adults can generate new seedlings and juveniles at rates equal to b_{SR} and b_{JR}, respectively. These reproductive rates must be non-negative but are not constrained in magnitude. Finally, some theoretically possible transitions in the model that are ecologically infeasible such as seedlings growing into reproductive adults in 10 years are defined to be zero.

Multiplying **G** with a vector representing the number of individuals in a population within each stage at a given time, v_t, generates an estimate of the stage structure at the end of a 10-year period, v_{t+1}:

$$v_{t+1} = \mathbf{G}v_t + \boldsymbol{\epsilon}$$

where $\boldsymbol{\epsilon}$ is a vector of normally distributed errors such that

$$\epsilon_i \sim \text{N}(0, \tau_i)$$

$$\tau_i \sim \text{Gamma}(1, 0.1)$$

and where τ_i is a precision for stage i, each of which is given a minimally informative prior distribution.

Because individual adult trees were tracked through time, the number of individuals that remain within the nonreproductive adult class (m_{AA}), remain within the reproductive class (m_{RR}), transition to reproductive adults from the nonreproductive class (m_{RA}), or transition from either adult stage to the dead stage (m_{DA}, m_{DR}) are known for each plot. Therefore, the distribution of the associated transition probabilities can be estimated directly from the multinomial distribution. However, distributions for reproductive rates and the transition proportions for seedlings and juveniles must be estimated indirectly from the linear model using the aggregate count data. The use of the Bayesian modeling

Table 1. Average basal area of Fraser fir ≥ 5 cm dbh and overstory density (with standard errors (SE) in parentheses) from 37 long-term monitoring plots on five peaks in Great Smoky Mountains National Park re-measured in 2010 and 2011.

Mountain	Elevation range (m)	No. of plots	Fir basal area (SE) ($m^2 \cdot ha^{-1}$)	Fir overstory density (SE) ($no. \cdot ha^{-1}$)
Clingmans Dome	1937–1993	8	18.4 (2.8)	2640 (530)
Mount LeConte	1892–1999	8	27.3 (5.7)	3200 (550)
Mount Collins	1821–1887	8	15.7 (2.9)	2750 (750)
Mount Guyot	1913–1990	7	13.7 (5.3)	2440 (700)
Mount Sterling	1722–1783	6	7.5 (2.1)	800 (180)

approach allows these data types to be seamlessly combined to estimate distributions of all probabilities simultaneously.

The total number of individuals in each stage in 1990, 2000, and 2010 were tallied for each plot, as were the number of known transitions. Plots on the same mountain were considered together to estimate shared parameters. Bayesian hierarchical modeling was used to sample from those parameter distributions using the Metropolis–Hastings algorithm (Hastings 1970) as implemented in OpenBUGS (Lunn et al. 2009). The algorithm was allowed to run for 100 000 burn-in iterations to converge; samples were taken over 20 000 additional iterations. Convergence was confirmed by scale reduction factors ($\hat{R}$) very near 1 ($|\hat{R} - 1| < 0.01$) for each monitored parameter (Gelman and Rubin 1992). For each of the five sets of parameter distributions sampled, five parallel chains with initial conditions selected from overdispersed distributions were aggregated for a total of 100 000 postconvergence samples. The OpenBUGS model specification is available as Appendix A.

Transition matrices of the same form as **G** were constructed from each of the 100 000 parameter samples drawn by OpenBUGS for each of the five mountains. Using each of these matrices, estimates of population structure were projected in 10-year increments from the observed stage-structured population totals on each mountain in 1990, 2000, and 2010. This provided likelihood distributions of population structure for each decade until 2050. In addition, by forecasting populations in 1990 and 2000 and comparing them with known counts in 2000 and 2010, the validity of the model was visually evaluated.

3. Results

3.1. Past and current stand structure

Stands at Clingmans Dome, Mount LeConte, and Mount Collins all showed recovery or increases in overstory fir over the last 20 years. At the time of the most recent measurements, these stands had the same average density of overstory fir —approximately 2000 stems·ha⁻¹ (Table 1). In terms of live fir basal area, average basal area was highest on Mount LeConte at 27.3 m²·ha⁻¹ (Table 1).

Fraser fir stands on Clingmans Dome showed the most consistency over the last two decades of any of the five peaks sampled (Fig. 3). Reproductive adults (>15 cm dbh) persisted over the last two decades, and in 2010, the forest structure had a fairly even mix of sizes, with a number of larger reproductive trees. Consistently high numbers of seedlings were present in all three sampling times. The large number of 5–10 cm dbh trees sampled in 2000 declined by an order of magnitude by 2010, but this is likely the result of these trees growing and moving to larger size classes, which is evidenced by an overall increase in the average number of stems per hectare in mature stems between these two years (Fig. 4).

Forest stands on Mount LeConte, Mount Collins, and Mount Guyot showed ongoing tree mortality but also recovery of overstory Fraser fir (Fig. 3). On Mount LeConte, a marked decline in seedling density occurred between 1990 and 2000. While there was a decline in average density of trees 8–15 cm dbh (shown in

the middle portion of the histogram in Fig. 3), this is coupled with an increase in trees of the largest size classes. On Mount Collins, mortality of overstory trees larger than 20 cm dbh occurred between 1990 and 2000. This is followed by dramatic recovery, as overstory fir (>5 cm dbh) more than doubled in the last decade (Fig. 4), though large trees > 30 cm dbh are not currently common as at many of the other sites. On Mount Guyot, the density of overstory trees < 20 cm dbh doubled between 1990 and 2000; however, many of the largest trees on this peak died over the last decade. This trade-off means that the average density of overstory fir has remained relatively constant since 1990 at about 1000 trees·ha⁻¹.

At Mount Sterling sites over the last two decades, we see a decline in seedlings and saplings by an order of magnitude. Although recruitment from the understory nearly doubled the average overstory fir density from 1990 to 2000, this site had the least dense coverage of overstory fir at about 500 trees·ha⁻¹. Our data also showed very little increase in larger, reproductive adults (>15 cm dbh) over the monitoring period.

3.2. Population model

Although data from all size classes were used to generate the population model, results for overstory and understory size classes are presented separately for ease of interpretation. As expected for a valid model, the majority of observed data points are within the 95% prediction intervals generated by the model.

While stands on Clingmans Dome already show the most complexity as far as live fir size distributions, our population model predicts a further increase in average overstory tree density by 2020. Current live standing overstory Fraser fir density is approximately 2000 trees·ha⁻¹. We predict that this will nearly double by 2020 and then level out, with densities at least as equal to current levels by 2050 (Fig. 4). For understory size classes, we predict that live fir density will stay relatively constant, with a slight increase over time indicating continued reproduction (Fig. 5).

By contrast, model results for Mount LeConte predict that overstory Fraser fir densities will stay at a relatively consistent level at about 2500 adult trees·ha⁻¹ (Fig. 4). For understory stems, this level will decline by 2020, likely due to stem exclusion of smaller trees. However, as on Clingmans Dome, we predict a slight increase over time indicating continued Fraser fir reproduction (Fig. 5).

Though stands on Mount Collins increased in overstory fir dramatically over the last decade, this average density is predicted to decline in the next 20 years. By 2040, the predicted average live overstory Fraser fir densities will reach that suggested by applying the model to the 1990 data (Fig. 4). By contrast, understory fir is expected to remain fairly constant through mid-century (Fig. 5).

On Mount Guyot, which has had a relatively constant density of adult trees in the overstory at around 1000 trees·ha⁻¹, our model predicts an increase by another 500 overstory trees·ha⁻¹ by 2020. This increase will be followed by a slow decline, with levels returning to what they were in 1990 by 2050 (Fig. 4). Understory stems also will continue to decline (Fig. 5).

Lastly, for Fraser fir populations on Mount Sterling, our model predicts no increase in overstory fir densities but a steady decline reaching below 1990 levels by 2050 (Fig. 4). We predict a steady average density of understory stems at around 250 individuals·ha⁻¹ (Fig. 5).

4. Discussion

Pre-adelgid forest census data collected in GSMNP in the 1930s suggest that Fraser fir forests were fairly uniform across peaks within the park, with an estimated average Fraser fir basal area of 40.7 m²·ha⁻¹ and an average total basal area of 55.9 m²·ha⁻¹ (Busing et al. 1993). Average Fraser fir basal areas measured in the present study are considerably lower than these estimates; average total basal area (which includes red spruce and hardwood

Fig. 3. Size class histograms for five populations of Fraser fir in Great Smoky Mountains National Park: Clingmans Dome (CD), Mount LeConte (LC), Mount Collins (MC), Mount Guyot (MG), and Mount Sterling (MS). Charts show 1 cm dbh size classes in 1990 (right), 2000 (center), and 2010 (left) reported on a log scale. The gray region is the area between the minimum and maximum estimations from jack-knifed cross-validation and represents uncertainty due to sampling; the dark line is the mean for all plots.
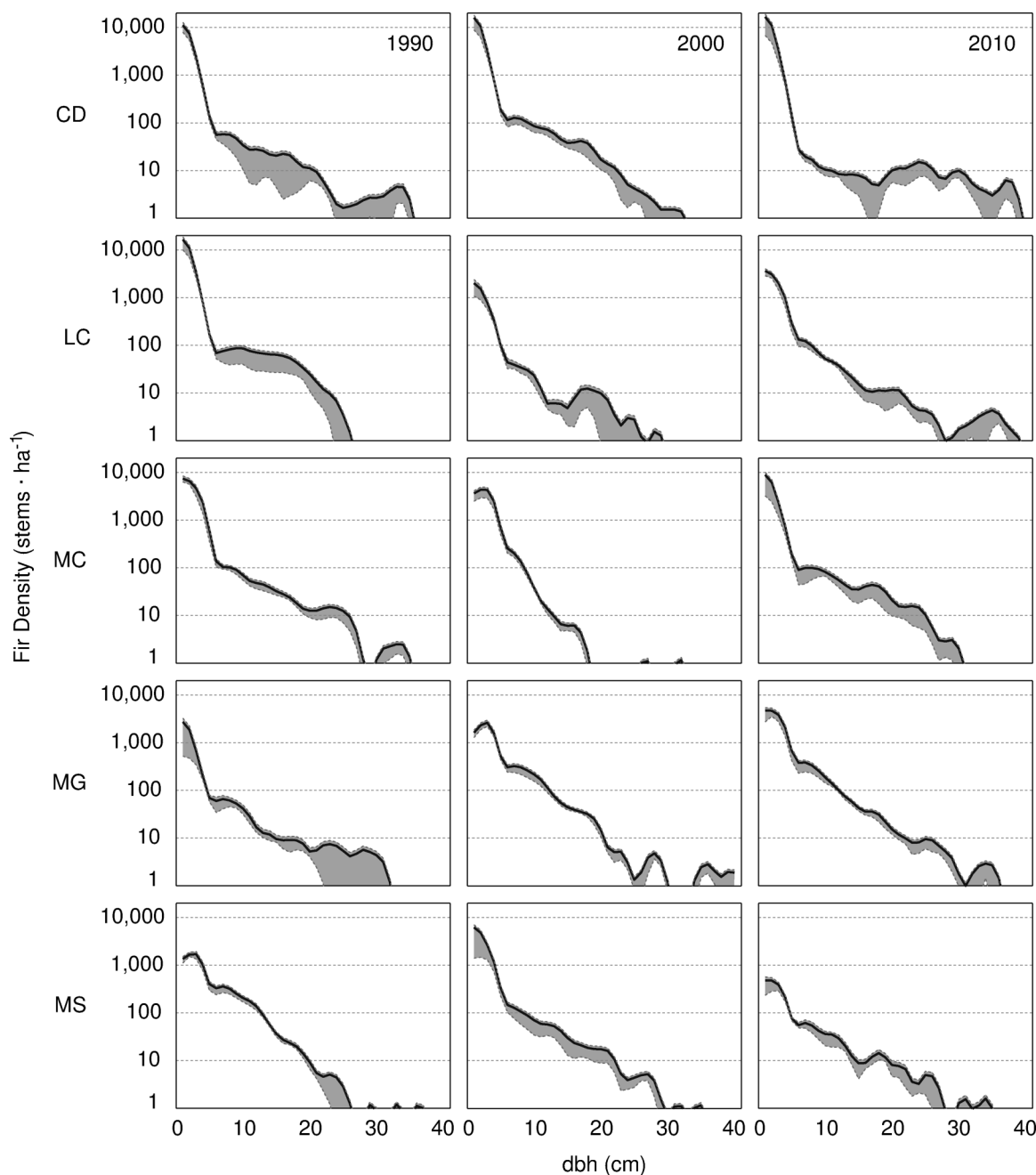
species) is 37.9 m²·ha⁻¹ (Franklin and Kaylor 2014), also much lower than measured in the 1930s. Additionally, stands at Clingmans Dome, Mount LeConte, and Mount Collins all show recovery or increases in overstory fir density over the last 20 years. When considering these most recent inventory data, there is no evidence to support the elimination of Fraser fir as suggested by Smith (1995) and Smith and Nicholas (1998), based on earlier inventories. In addition to recovery in GSMNP detailed in this study, Fraser fir forest recovery is also underway on Roan Mountain (White et al. 2012) and in the Black Mountains (Lusk et al. 2010; McManamay et al. 2011).

While overstory forest inventory data are often used to monitor forest recovery, seedling production and the transition rates be-

tween life stages are essential components in predicting future forest dynamics. The dramatic declines in seedling density, which are most extreme on Mount LeConte and Mount Sterling over the two decades of monitoring (Fig. 3), have been previously noted (Mancusi 2004; Smith and Nicholas 2000; Smith 1995). These declines in seedlings may have been caused by increased forest floor insolation (Smith and Nicholas 2000), understory competition (Mancusi 2004; Smith and Nicholas 2000; Smith 1995), or lowered seed production or viability (Fedde 1973; Nicholas 1992). It is only by considering seedling abundance within the context of longer term population dynamics that this dataset becomes useful in predicting the restoration and maintenance of a viable fir overstory (Clark et al. 1999). Our models are dynamic over multiple life

Fig. 4. Bayesian population model predictions for overstory adult (>5 cm dbh) Fraser fir on five mountains in Great Smoky Mountains: Clingmans Dome (CD), Mount LeConte (LC), Mount Collins (MC), Mount Guyot (MG), and Mount Sterling (MS). Open circles represent measured densities, and solid dots are projected means. Light gray dotted lines represent the 95% prediction interval of the model as applied to the initial measurements in 1990, dark grey dotted lines are the same bounds as applied to 2000 data, and solid lines are the same for 2010 data.
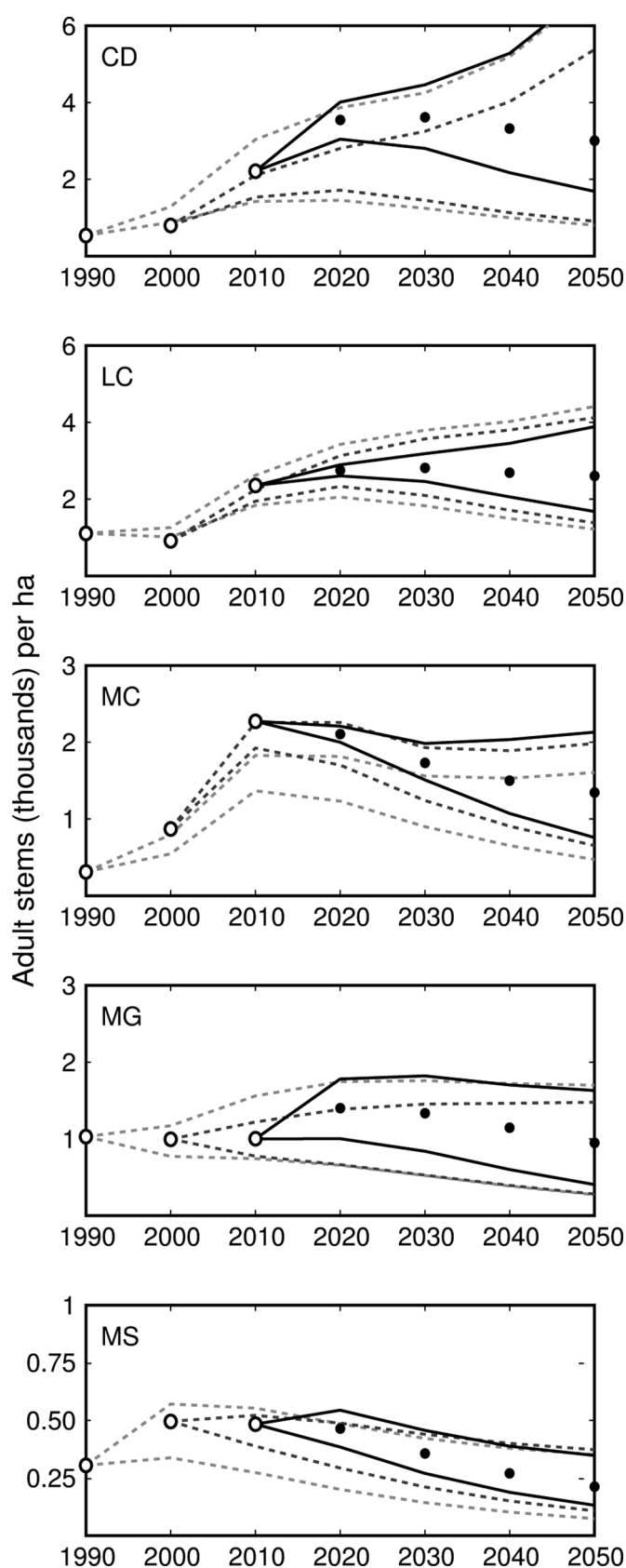

stages and account for misperceptions that can arise when focusing on a single life stage or transition. While many individual plots show large reductions in seedling densities over the last two decades, we predict relatively stable overstory fir populations and continued reproduction on Mount LeConte and Clingmans Dome. As has been noted in earlier surveys in GSMNP (Stehn et al. 2013; Jenkins 2003; Smith and Nicholas 2000), Fraser fir regeneration is patchy and has been linked to disturbance history, elevation, and soil nutrient content (Stehn et al. 2013); this patchiness is exhibited in the uncertainty estimates in our model.

However, our model does predict a steady decline in the Fraser fir population on Mount Sterling, the lowest elevation mountain in our study. These predictions are consistent with previous estimates of future suitable habitat for Fraser fir using a multitemporal spatial clustering method of climate envelope modeling (Potter et al. 2010), which showed a pattern of suitable habitat contraction by 2050 and slight expansion by 2100. Additionally, Delcourt and Delcourt (1998) hypothesize that a 3 °C increase in mean July temperatures will raise the lower bound of Fraser fir's habitat 480 m in elevation by 2100 CE. The continued decline of Fraser fir on Mount Sterling may be evidence of habitat suitability shifts caused by long-term environmental changes. Additionally, it may also indicate that differences in annual temperature range and amplitude at lower elevations benefit insect survival and dispersal as suggested by Dale et al. 1991.

The method that we present here differs widely from other approaches such as niche modeling, which uses current presence–absence data of a species and current and future environmental site parameters to predict the future extent of the species of interest (Godsoe 2010; Elith and Leathwick 2009; Peterson 2003). These models are biased by historical land use change, which limits the current geographic coverage of species. Further, the spatial resolution of predictions generated by niche models is limited by the spatial resolution of available environmental data. Additionally, they are not able to incorporate past population dynamics or generate predictions of differing densities, which is a strength of the approach that we have used.

The predictive population model that we present here assumes that no changes will occur in current and chronic stress factors. Because the population data and transition rates on each mountain incorporate individual-tree response to multiple environmental parameters (acidic deposition, climate, BWA-induced mortality, and others), these are implied in the model and are a source of variability and uncertainty. If, however, these factors change in the future, then our model cannot anticipate or account for the effects that this would have on future population dynamics. Further, the model assumes that the population will not change in its response to ongoing stresses. However, the gene pool may undergo future changes due to selective pressure and (or) limited and isolated populations.

Although matrix models similar to the one presented in this study often rely on eigenvalue analysis to determine the eventual fate of the population (Caswell 2001; Ellner and Guckenheimer 2006), the long-term dynamics of the Fraser fir forests in the Smoky Mountains are complex and deeply uncertain. Simple linear models such as the one constructed here cannot generate reliable predic-

tions centuries into the future. Therefore our analysis focuses on the relatively short-term transient dynamics of these populations that is enabled by using the distribution-generating tools of Bayesian methods.

Fig. 5. Bayesian population model predictions for understory seedlings and saplings (<5 cm dbh) Fraser fir on five mountains in Great Smoky Mountains: Clingmans Dome (CD), Mount LeConte (LC), Mount Collins (MC), Mount Guyot (MG), and Mount Sterling (MS). Open circles represent measured densities, and solid dots are projected means. Light gray dotted lines represent the 95% prediction interval of the model as applied to the initial measurements in 1990, dark grey dotted lines are the same bounds as applied to 2000 data, and solid lines are the same for 2010 data.

The comparison of model predictions of populations in 1990 and 2000 and known counts in 2000 and 2010 provides a visual estimate of model validity. Overall, our model accurately predicts observed data within a 95% prediction interval of the models applied to the 1990 data, with notable exceptions being the 2010 overstory fir density for Mount Collins (Fig. 4) and the 2000 understory density on Mount Sterling. For Mount Collins, this is likely due to the ongoing overstory mortality between 1990 and 2000 and release of smaller size classes into the overstory (Fig. 3). Alternatively, it may be that fir populations at Mount Collins are too unstable to model using our approach or that there are differing population trajectories occurring in different plots across this site. However, when 95% prediction intervals are applied to the 2000 data, we clearly see that observed data are on the upper bound of our predicted intervals for both 2000 and 2010. For the Mount Sterling understory, this unexpected spike in the seedling and sapling size class is caused by seedling increases in a single plot. Such spikes in seedling densities are not uncommon following canopy removal but are often followed by self-thinning, as our data demonstrate. Additionally, observed seedling densities at Mount Sterling are currently within the 95% prediction intervals so we believe our model predictions to be accurate.

Two important factors influencing the future of Fraser fir are the severity and timing of future BWA-induced mortality. Frequent and severe mortality events would cause a dramatic departure of this forest type from pre-BWA conditions, while infrequent or milder mortality events may yield a forest that is quite similar to pre-BWA forests with stable populations of Fraser fir. The emergence of a two-aged forest with cyclical BWA outbreaks and overstory fir mortality followed by a regeneration period has been hypothesized (Dale et al. 1991; Eagar 1984; Mancusi 2004; Smith and Nicholas 1998, 2000). We do not yet see evidence of this pattern in these long-term monitoring plots across mountains, which suggests a patchy forest structure that has also been noted in the Black Mountains (McManamay et al. 2011). Forests experienced widespread fir death at the summit on Mount Sterling in 1970–1972, on Mount Guyot in 1980–1982, on Mount LeConte in 1982–1984, on Mount Collins in 1985–1987, and on Clingmans Dome in 1990–1992 (Smith and Nicholas 2000). The generation time of Fraser fir is roughly 15 years from seedling to the onset of reproductive maturity (Beck 1990), and even the most recently infested site surpasses this period. Trees greater than 4 cm dbh are susceptible to BWA-induced mortality (Eagar 1984), which is sooner than the onset of reproduction.

While the exact timing of future mortality events is unknown, forest structural complexity may provide some resilience to large infrequent disturbances. Stands in which a number of large trees persisted through the infestation such as those on Clingmans Dome may recover more quickly due to the presence of reproductive trees. Other stands with very little overstory persistence are limited by the survival and maturation of trees present in the understory at initial disturbance. This creates a mosaic-like structure of stands in different stages of regeneration, which has been previously noted (Jenkins 2003; Smith and Nicholas 2000; McManamay et al. 2011). Because BWA feeds on mature fir and a contiguous, dense overstory of large, mature fir no longer exists, this structural complexity may provide some resilience to future BWA mortality.
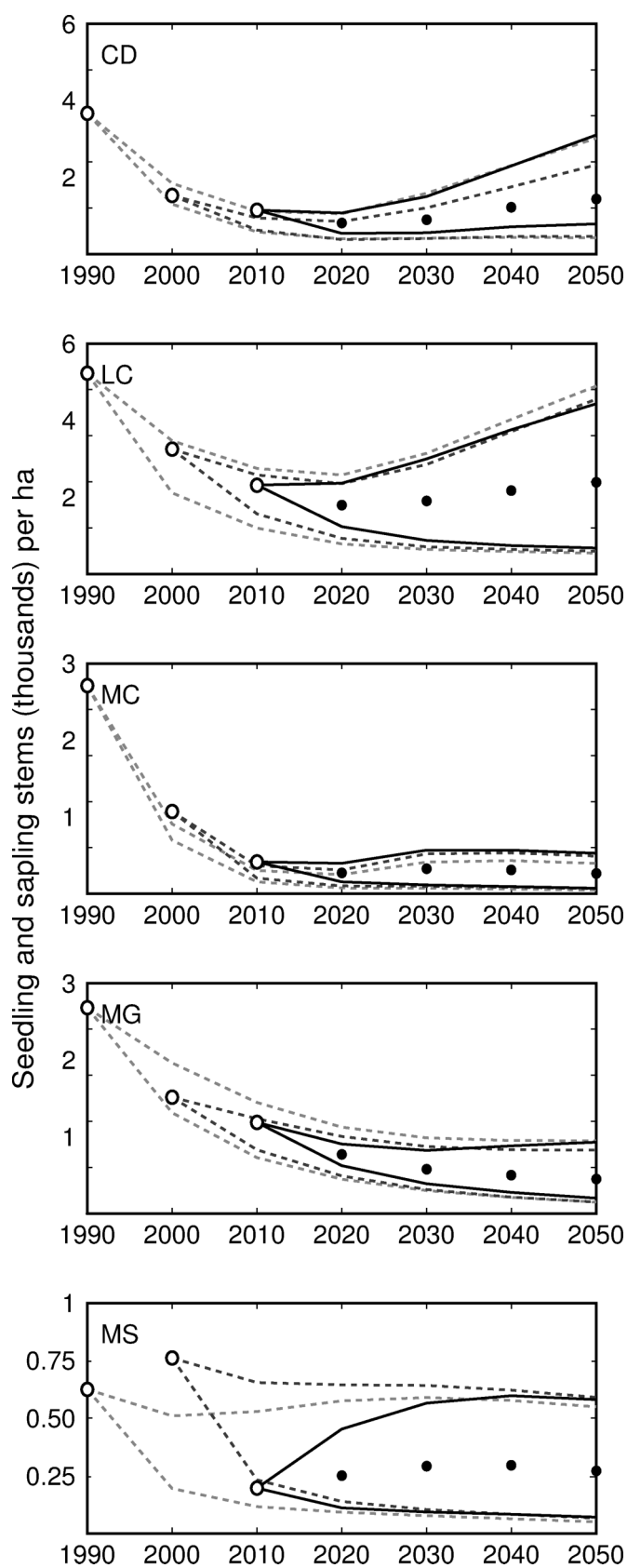
When comparing projected future populations between mountains, clear differences between them emerge. While proximal causes for these differences in outcomes are likely the aforementioned differences in forest structure, there are a number of possible

reasons for the persistence of mature trees and the differences in regeneration and mortality rates at different sites. Genetic differences between populations in response to environmental stresses are likely. Individual trees can show a tremendous ability to acclimate to a changing environment, with the magnitude and variability of this response dependent on species (Tjoelker et al. 1999), provenance (Bigras 2000), elevation (Ledig and Fryer 1972), and other factors. In a study of red spruce (a species co-dominant with Fraser fir) acclimation and adaptation to elevated temperatures (Hagen 2006), seedlings grown from seeds collected at one of four sites in GSMNP showed a significantly different response to an increase in growth temperature, suggesting that individuals capable of thriving under predicted temperatures may exist within local populations. The longevity, vigor, and fecundity of trees are determined, at least in some part, by tree physiological parameters such as photosynthetic rates, water use efficiency, and the size of nonstructural carbohydrate pools, which likely differ between trees in different locations. In addition, environmental factors such as temperature, precipitation, and soil chemistry differ across elevations and aspects. Additionally, recent work has highlighted the importance of cloud water and cloud immersion on Fraser fir physiology (Berry and Smith 2013; Reinhardt and Smith 2008). It is possible that cloud immersion differs across the study area and may account for some of the variation between predicted populations. It is clear that an understanding of the important environmental factors that affect individual-tree physiology is needed before long-term predictions of population dynamics can be made.

5. Conclusions

We present the first predictive model for Fraser fir populations in GSMNP. We predict robust recovery of select Fraser fir populations for at least the next several decades, as well as continued decline for populations on a number of mountains, notably those at the lowest elevations. Our data suggest that forest structural complexity may provide some resilience to large infrequent disturbances such as BWA infestation. Stands in which a number of large trees persisted through the infestation may recover more quickly due to the presence of reproductive trees. This suggests that management strategies that protect a selection of robust and reproductively mature individuals will improve recovery of Fraser fir populations through further mortality events. Further, our findings highlight vulnerable populations that would benefit from limiting human impacts on successful reproduction and recruitment and may also be appropriate sites for Fraser fir plantings.

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Appendix A

```
model {
# get survival and transition rates of adults from Panel Data
# sumA[i] and sumR[i] are the same as A0[i] and R0[i], except that
# samples with A0[i]==0 or R0[i]==0 are removed since those are
# not allowed as parameters to dmulti or dbinom
for (i in 1:NUM_ADULT_SAMP){
sumA[i] <-sum(A2ARD[i,1:3]);
A2ARD[i,1:3] ~ dmulti(Pa[1:3], sumA[i])
}
for (i in 1:NUM_REPROD_SAMP) {
R2R[i] ~dbin(Prr, sumR[i])
}
# get other transition probabilities from aggregate data
for (i in 1:NUM_SAMPLES) {
# Define the transition model
S1_mu[i] <- Pss*S0[i] + Bsr*R0[i]
J1_mu[i] <- Pjj*J0[i] + Pjs*S0[i] + Bjr*R0[i]
A1_mu[i] <- Paa*A0[i] + Paj*J0[i] + Pas*S0[i]
R1_mu[i] <- Prr*R0[i] + Pra*A0[i] + Prj*J0[i]
# Same as putting a noise term on the above equations
S1[i] ~ dnorm(S1_mu[i], tau_S)
J1[i] ~ dnorm(J1_mu[i], tau_J)
A1[i] ~ dnorm(A1_mu[i], tau_A)
R1[i] ~ dnorm(R1_mu[i], tau_R)
}
# Uninformative prior on precision of normal distribution
tau_S ~ dgamma(1, 0.1)
tau_J ~ dgamma(1, 0.1)
tau_A ~ dgamma(1, 0.1)
tau_R ~ dgamma(1, 0.1)
# Probabilties of moving from Seedlngs
Ps[1:4] ~ ddirch(alpha4[])
Pss <- Ps[1]
Pjs <- Ps[2]
Pas <- Ps[3]
# Probabilties of moving from Juveniles
Pj[1:4] ~ ddirch(alpha4[])
Pjj <- Pj[1]
Paj <- Pj[2]
Prj <- Pj[3]
# Probabilties of moving from Adults
Pa[1:3] ~ ddirch(alpha3[])
Paa <- Pa[1]
Pra <- Pa[2]
# Probability of staying in Reproduct Adult
# This reduces to Binomial from Multinomal since only two options
# and so has a beta distribution.
Prr ~ dbeta(1,1)
# Uninformative Prior on Reproductive rates
# But constrain Bjr to be somewhat realistic given
# seedling recruitment and survival rates
Bsr ~ dgamma(1,0.1)
Bjr ~ dgamma(mu_pjr,0.1)
mu_pjr <-Bsr*Pjs/Pss/10
#Construct transition Matrix
G[1,1] <- Pss; G[1,2] <- 0; G[1,3] <- 0; G[1,4] <- Bsr
G[2,1] <- Pjs; G[2,2] <- Pjj; G[2,3] <- 0; G[2,4] <- Bjr
G[3,1] <- Pas; G[3,2] <- Paj; G[3,3] <- Paa; G[3,4] <- 0
G[4,1] <- 0; G[4,2] <- Prj; G[4,3] <- Pra; G[4,4] <- Prr
# Calculuate Eigenvalue for ease of monitoring
# Eigenvalues are unused in analyses.
y[1:4] <- eigen.vals(G[,])
z <- ranked(y[1:4],4)
}
```