Differences in tree species presence within harvest gap regeneration in two expanding-gap silvicultural treatments in the Acadian Forest

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Introduction

Within the last 25 years silvicultural systems designed to emulate the compositional and structural outcomes of natural disturbance have been suggested as a way to successfully manage for multiple uses including biodiversity and commodity production(Lindenmayer and Franklin 2002; North and Keeton 2008). Additionally, the retention of vertical structure and biological legacies in the form of reserve trees is a critical element in the ecological forestry 'toolbox,' and is universally recognized as an efficient means of providing multiple ecological functions in forests worldwide (Gustafsson et al. 2012; Lindenmayer et al. 2012). Based on the gap-dynamics disturbance regime typical of the Northern Forest (Fraver et al. 2009), the Acadian Forest Ecosystem Project (AFERP) was initiated in 1994 to test these ecological forestry concepts using three experimental replications of two expanding-gap regeneration systems with structural retention and unharvested controls (Seymour et al. 2002; Seymour 2005). At the time of establishment, it was postulated that such systems can sustain productivity for commodity harvests and recruit regeneration of desirable species mixtures while also promoting greater ecosystem complexity and resilience than is maintained under simpler, commodity-driven silvicultural systems (Puettmann et al. 2009; Messier et al. 2013).

The AFERP experiment consists of two silvicultural treatments based on traditional German expanding-gap (femelschlag) techniques, modified such that the designed disturbance emulates as far as feasible the spatial and temporal patterns of the natural disturbance regime common to the Acadian ecoregion. Two treatments, a large, quickly expanding gap treatment and small slowly expanding gap treatment are tested against an unharvested control in three replications for each condition. In the 20:10 femelschlag (FS) treatment, 20% of the stand on an areal basis is removed each decade through the creation of 0.2 ha gaps or expansions on those gaps, with a 10 year regeneration window and a 50-year rest period following the first five cycles. In the 10:10 group selection (GS) treatment, 10% of the total stand area is harvested per cutting cycle through the creation of 0.1 ha gaps or expansions, with a 20 year regeneration window and no rest period. Both cutting treatments reserve 10% of basal area in permanent retention, and up to an additional 20% of basal area until the next gap expansion if additional overwood is required to secure regeneration in the gap. Initial harvesting of the three replicates of each silvicultural treatment occurred in 1994, 1995, and 1996, with the second entries occurring from 2004-2006.

Testing broader theories regarding the effect and role of these silvicultural systems in the managed forest landscape requires accurate and detailed information regarding the regeneration dynamics across the range of growing conditions that exists in these treated stands. After nearly twenty years, regeneration composition data from the permanent plot network in the AFERP experiment currently exists only at a relatively coarse scale. Preliminary work has assessed the impact of harvest spatial pattern on stand growth (Arseneault et al. 2011; Arseneault and Saunders 2012) and the overall spatial distribution of regeneration throughout these stands (Olson and Wagner 2011). No study to date has assessed the regeneration dynamics specifically within the harvest gap environment, however, despite the fact that harvest gaps now make up to 20-40% of total stand area and exhibit high variability in regeneration composition and structure both between individual harvest gaps and more broadly between silvicultural treatments.

code	name
ABBA	Abies balsaea
ACPE	Acer pensylvanicum
ACRU	Acer rubrum
ACSA	Acer saccharum
ALIN	Alnus incana
BEAL	Betual alleghaniensis
BEPO	Betula populifolia
FAGR	Fagus grandifolia
FRAM	Fraxinus americana
OSVI	Ostrya virginiana
PIGL	Picea glauca
PIRE	Pinus resinosa
PIRU	Picea rubens
PIST	Pinus strobus
POGR	Populus grandidentata
POTR	Populus tremuloides
PRSE	Prunus serotina
QURU	Quercus rubrum
THOC	Thuja occidentalis
TSCA	Tsuga canadensis

Table 1: Species codes

This study contributes to the understanding of the differences in regeneration composition between stands treated in each of the two expanding-gap regeneration systems employed in the AFERP experiment by examining presence/absence of species within the regeneraion and sapling layers within harvest gaps. At the time that the experiment was initiated, it was hypothesized that the large-gap femelschlag (FS) treatment should include regeneration of some shade-intolerant and mid-tolerant species while the small-gap group selection (GS) treatment should favor shade-tolerant species and exclude intolerants. To test this hypoth-

esis, we collected species presence/absence information on 91 plots in the large gap treatment and 27 plots on the small gap treatment, then for each species found across the experiment estimated 95% HD intervals of difference in presence probability between the two treatments using Bayesian estimation procedures.
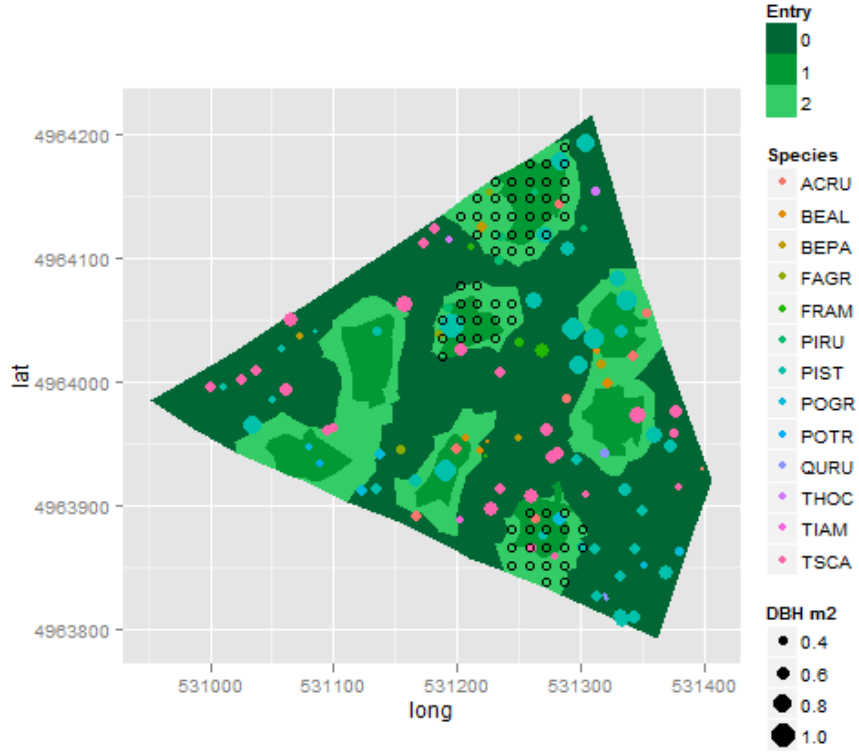

Figure 1: Example layout of harvest gaps, retention trees, and sampling plot network in each of the femelschlag (FS) treatment

Methods

Field Methods

During the summer of 2013 harvest gaps centered on three of the initial entries in each of the three replications of the two expanding-gap treatments were randomly chosen in which to sample regeneration composition and structure. A systematic
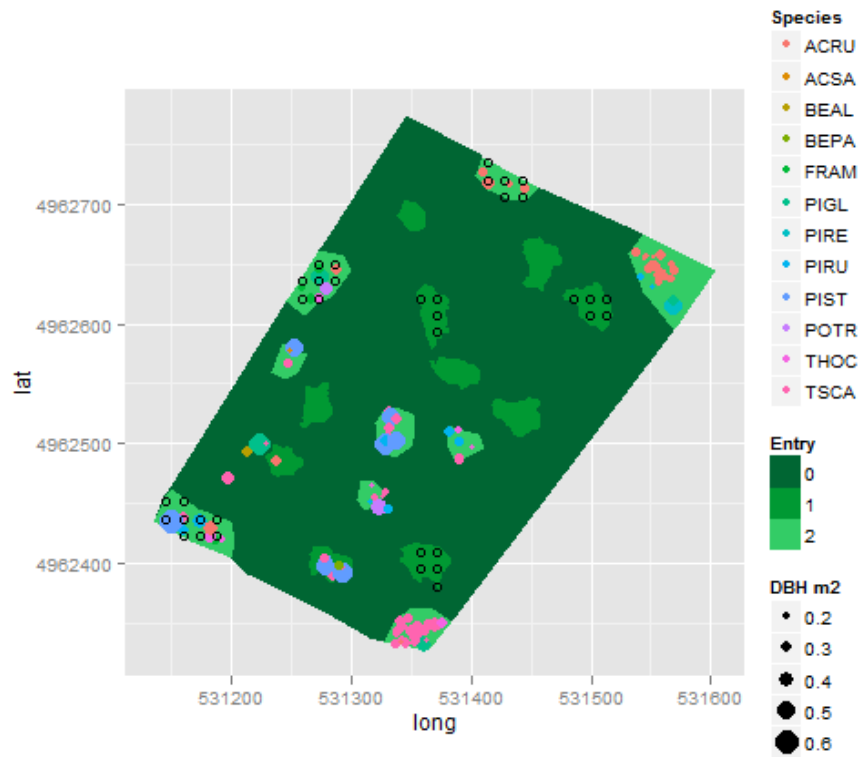
Figure 2: Example layout of harvest gaps, retention trees, and sampling plot network in each of the group selection (GS) treatment

random sample network of circular 0.002 hectare plots was laid out at 14.14 meter grid spacing, capturing approximately 10% of total harvest gap areas in each of the two treatments. Gap layout with retention trees and sample plot network are displayed in Figure 1. At each sample plot, height, diameter, crown length, and social position was recorded for each of the four tallest individuals of every species present on the plot. In this analysis, these data were transformed to simple presence/absence information for each species on each sample plot.

Analysis

Data analysis was accomplished using RStudio 0.97.551 calling R version 3.0.2 (2013-09-25) (Team 2013) and JAGS 3.4.0 (Plummer 2003) via the R2jags library (Su and Yajima 2013). Data visualization and presentation were accomplished using the knitr (Xie 2013), xtable (Dahl 2013), and ggplot2 (Wickham 2009) libraries.

To analyze regeneration data, species presence was modeled using a hierarchical Bayesian framework in which:

$$p(\theta_{i,j}, \mu_i, \kappa_i | y_{i,j,k}) = \frac{p(y_{i,j,k} | \theta_{i,j}, \mu_i, \kappa_i) p(\theta_{i,j}, \mu_i, \kappa_i)}{p(y_{i,j,k})}$$

Individual presence/absence response $y_{i,j,k}$ for each of the $j = 1, 2, ..., 20$ species on each of $k = n_i$ sample plots within each of the $i = 1, 2$ treatments was modeled as a Bernoulli trial with presence probability $theta_{i,j}$ such that $y_{i,j,k} \sim Bernoulli(\theta_{i,j}, 1 - \theta_{i,j})$. In this model, each of the $\theta_{i,j}$ parameters represents the probability of presence of species j in treatment i, and are themselves modeled as instances of a beta-distributed random variable such that $\theta_{i,j} \sim Beta(\alpha_i, \beta_i)$ where shape parameters α_i and β_i are dependent on mean presence probabilities among species μ_i and on precision of presence probabilites among species parameter κ_i for each of the i treatments such that $\alpha_i = \mu_i \kappa_i$ and $\beta_i = (1 - \mu_i)\kappa_i$. Prior distribution of mean presence among species for each of the i treatments μ_i was modeled as a Beta distribution with shape parameters $\alpha = 2$ and $\beta = 2$ such that $\mu \sim Beta(2, 2)$. Prior distribution of the precision parameters for each of the i treatments κ_i were modeled by a gamma distribution with shape parameter $\alpha = 1$ and rate parameter $\beta = 0.1$ such that $\kappa_i \sim \Gamma(1, 0.1)$.

The choice of prior distributions of μ and κ were selected to reflect weak beliefs regarding the mean and precision of species presence probabilities within each treatment. In particular, the selection of a flat prior on μ is unjustified given that each of the 20 species were detected at least once in the regeneration plots, and it is similarly implausible that even the most prevalent species were found on all plots. Because there are both relatively rare and relatively ubiquitous species within the sample, it also makes sense to use a prior distribution on μ centered on 0.5 without skewness, and with low probabilities for values close to zero and similarly low probabilities for values close to one. The prior distribution on κ

was similarly selected to reflect the potential wide range in possible values for each $\theta_{i,j}$.
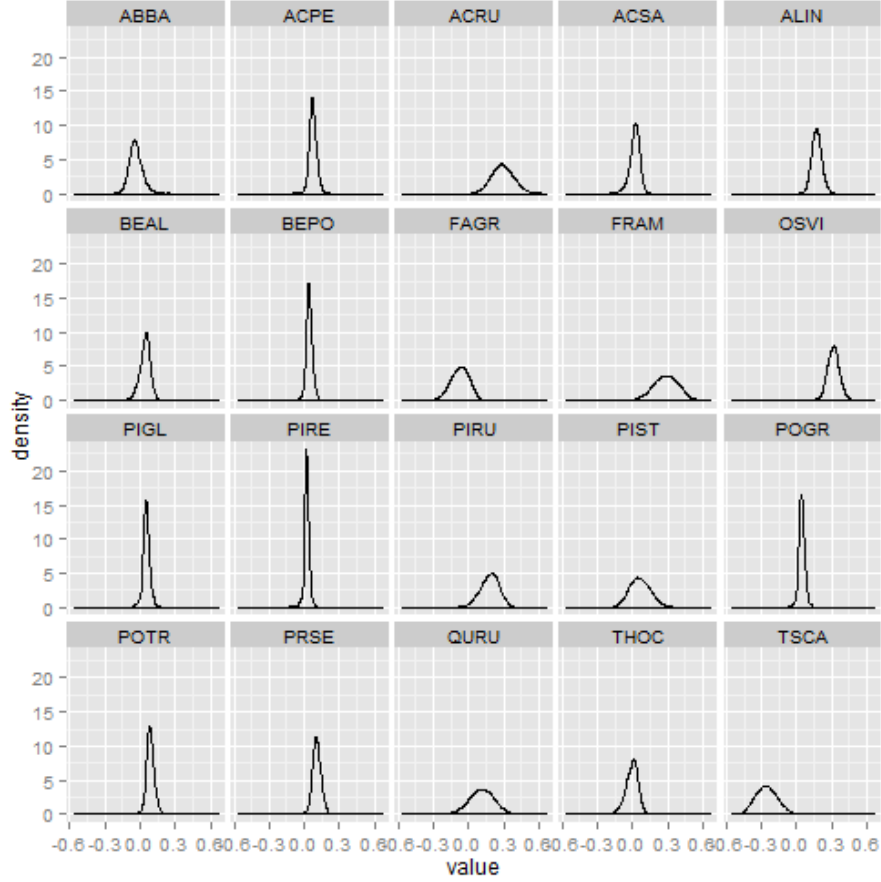
Figure 3: Posterior distribution of differences in within-gap species presence probability between large-gap and small-gap treatments

Following model specification, the a Markov Chain Monte Carlo algorithm was employed through the JAGS Gibbs sampler to generate samples from the posterior distribution of model parameters. In the MCMC process three sampling chains were used of 5000 total iterations with burnin period of 500 iterations and thinning rate of 4. In order to test the hypothesis that presence probability for species differ between the two silvicultural treatments, the posterior distribution and 95% highest density intervals of the difference in presence probability between the two treatments was calculated for each species.

Results

Inferences for $\theta_{i,j}$ parameters (presence probability given species and treatment) estimated from fitting the hierarchical Bayesian model, along with convergence diagnostics are presented in Table 1. Inferences for estimates of *mu* and *kappa* parameters along with convergence diagnostics are presented in Table 2. Posterior distributions of differences in species probability between the femelschlag and group selection treatments are presented in Figure 2, and 95% HD intervals are presented in Table 3. For species in which the 95% HD interval includes zero, there is at least a 95% probability that species presence probability on sample plots (and therefore stand-level stocking) differs between the two treatments.

Discussion

There were significant differences among species in response to gap size in terms of presence probabilities. The most shade tolerant species, Eastern hemlock (*Tsuga Canadensis*) had a higher presence probability in small gaps than in large gaps. By contrast, shade intolerant species such as white ash (*Fraxinus americana*), quaking aspen, (*Populus tremuloides*), and black cherry (*Prunus serotina*), and red maple (*Acer rubrum*) had higher presence probabilities in large gaps. Unexpectedly, shade tolerant understory trees such as hop hornbeam (*Ostrya virginiana*), speckled alder (*Alnus incana*), and striped maple (*Acer pensylvanicum*) had higher presence probabilities in the larger gap treatments, as well as the shade tolerant red spruce (*Picea Rubens*). One of the original hypotheses of the AFERP experiment was that small-gap treatments would result in regeneration of more shade-tolerant species whereas large-gap treatments would include regeneration of mid-tolerant and some intolerant species. This projection seems to be born out, at least in the context of this preliminary analysis.

Citations

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trt	species	mean	sd	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
FS	ABBA	0.90	0.03	0.83	0.88	0.90	0.92	0.95	1.00	1300.00
GS	ABBA	0.94	0.05	0.82	0.91	0.95	0.97	0.99	1.00	2200.00
FS	ACPE	0.08	0.03	0.04	0.06	0.08	0.10	0.14	1.00	3400.00
GS	ACPE	0.01	0.02	0.00	0.00	0.00	0.01	0.06	1.00	3400.00
FS	ACRU	0.91	0.03	0.84	0.89	0.91	0.93	0.96	1.00	3400.00
GS	ACRU	0.61	0.09	0.43	0.56	0.62	0.68	0.78	1.00	2800.00
FS	ACSA	0.06	0.02	0.02	0.04	0.06	0.08	0.12	1.00	3400.00
GS	ACSA	0.04	0.04	0.00	0.01	0.03	0.06	0.14	1.00	3400.00
FS	ALIN	0.18	0.04	0.11	0.15	0.18	0.20	0.26	1.00	3400.00
GS	ALIN	0.01	0.02	0.00	0.00	0.00	0.01	0.05	1.00	3400.00
FS	BEAL	0.08	0.03	0.04	0.06	0.08	0.10	0.15	1.00	2400.00
GS	BEAL	0.04	0.04	0.00	0.02	0.03	0.06	0.14	1.00	3300.00
FS	BEPO	0.05	0.02	0.02	0.03	0.05	0.06	0.10	1.00	1400.00
GS	BEPO	0.01	0.02	0.00	0.00	0.00	0.01	0.06	1.00	3400.00
FS	FAGR	0.11	0.03	0.06	0.09	0.11	0.13	0.19	1.00	3400.00
GS	FAGR	0.19	0.07	0.07	0.13	0.18	0.23	0.34	1.00	3400.00
FS	FRAM	0.68	0.05	0.58	0.65	0.69	0.72	0.77	1.00	3400.00
GS	FRAM	0.40	0.09	0.23	0.33	0.40	0.46	0.58	1.00	3400.00
FS	OSVI	0.32	0.05	0.23	0.29	0.32	0.35	0.42	1.00	2400.00
GS	OSVI	0.01	0.02	0.00	0.00	0.00	0.01	0.06	1.00	3100.00
FS	PIGL	0.06	0.03	0.02	0.04	0.06	0.07	0.12	1.00	3400.00
GS	PIGL	0.01	0.02	0.00	0.00	0.00	0.01	0.06	1.00	3400.00
FS	PIRE	0.03	0.02	0.01	0.02	0.03	0.04	0.07	1.00	3400.00
GS	PIRE	0.01	0.02	0.00	0.00	0.00	0.01	0.06	1.00	3400.00
FS	PIRU	0.33	0.05	0.24	0.30	0.33	0.36	0.43	1.00	3400.00
GS	PIRU	0.15	0.07	0.05	0.10	0.14	0.19	0.30	1.00	3100.00
FS	PIST	0.82	0.04	0.74	0.80	0.83	0.85	0.89	1.00	3400.00
GS	PIST	0.76	0.08	0.59	0.71	0.76	0.82	0.90	1.00	3400.00
FS	POGR	0.05	0.02	0.02	0.03	0.05	0.06	0.10	1.00	1200.00
GS	POGR	0.01	0.02	0.00	0.00	0.00	0.01	0.06	1.00	3400.00
FS	POTR	0.09	0.03	0.04	0.07	0.09	0.11	0.16	1.00	3400.00
GS	POTR	0.01	0.02	0.00	0.00	0.00	0.01	0.06	1.01	1100.00
FS	PRSE	0.11	0.03	0.06	0.09	0.11	0.14	0.19	1.00	3200.00
GS	PRSE	0.01	0.02	0.00	0.00	0.00	0.01	0.06	1.00	3400.00
FS	QURU	0.51	0.05	0.41	0.48	0.51	0.55	0.61	1.00	1800.00
GS	QURU	0.40	0.09	0.23	0.34	0.40	0.46	0.59	1.00	3400.00
FS	THOC	0.07	0.03	0.03	0.05	0.07	0.09	0.13	1.00	3400.00
GS	THOC	0.08	0.05	0.01	0.04	0.07	0.11	0.20	1.00	1700.00
FS	TSCA	0.50	0.05	0.40	0.47	0.50	0.54	0.60	1.00	3400.00
GS	TSCA	0.76	0.08	0.59	0.71	0.76	0.81	0.90	1.00	2000.00

Table 2: Convergence diagnostics and inferences based on estimates of species presence probabilities generated from MCMC fitting of hierarchical Bayesian model

	mean	sd	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
deviance	147.33	8.42	132.71	141.40	146.52	152.68	165.67	1.00	3400.00
kappa[FS]	1.98	0.55	1.07	1.58	1.93	2.31	3.23	1.00	3400.00
kappa[GS]	1.00	0.39	0.42	0.72	0.94	1.20	1.94	1.00	3400.00
mu[FS]	0.34	0.06	0.23	0.30	0.33	0.38	0.46	1.00	3400.00
mu[GS]	0.23	0.06	0.12	0.18	0.22	0.27	0.37	1.00	3000.00

Table 3: Convergence diagnostics and inferences based on posterior distributions of mean (mu) and precision (kappa) parameters

species	lower	upper
ABBA	-0.13	0.09
ACPE	0.01	0.14
ACRU	0.12	0.49
ACSA	-0.09	0.09
ALIN	0.09	0.26
BEAL	-0.07	0.12
BEPO	-0.01	0.10
FAGR	-0.24	0.07
FRAM	0.08	0.47
OSVI	0.21	0.41
PIGL	-0.01	0.12
PIRE	-0.03	0.07
PIRU	0.01	0.33
PIST	-0.10	0.25
POGR	-0.01	0.10
POTR	0.02	0.16
PRSE	0.04	0.18
QURU	-0.10	0.31
THOC	-0.13	0.08
TSCA	-0.43	-0.07

Table 4: 95% Highest Density Intervals of difference in within-gap species presence probability between the large-gap and small gap treatments