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Survival of tree seedlings across space and time: estimates from long-term count data

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Summary

1 Tree diversity in forests may be maintained by variability in seedling recruitment. Although forest ecologists have emphasized the importance of canopy gaps in generating spatial variability that might promote tree regeneration, the effects of canopy gaps on seedling recruitment may be offset by dense forest understories.

2 Large annual fluctuations in recruitment processes, coupled with the long life of forest trees, can provide an alternative mechanism for maintaining tree diversity. Evaluating the relative importance of spatial vs. temporal variability in recruitment, however, requires estimates of seedling survival that are extensive on both scales.

3 Estimates of survival derived from conventional statistical methods require that individual seedlings are monitored through time, and are therefore often limited in extent. We demonstrate a relatively fast and easy alternative approach to measuring survival that uses repeated counts of individuals in quadrats.

4 Annual seedling counts were used to quantify both the effects of small canopy gaps and understorey shrubs on the survival of *Acer rubrum* (red maple) seedlings and the magnitude of residual spatial and temporal variability in seedling survival.

5 We found that a dense understorey had a greater effect on seedling survival than did canopy gaps. Our canopy gaps had only a slight positive effect on seedling survival, and their benefit was offset by a large negative effect of the understorey shrub *Rhododendron maximum*.

6 Annual fluctuations in recruitment processes were seven times greater than spatial variability across transects and the effect of individual years on seedling survival was larger than even that of understorey shrubs.

7 The long life span of trees coupled with large annual variability in recruitment success across species may maintain the diversity of forest trees through a storage effect.

Key-words: *Acer rubrum*, Bayesian statistics, canopy gaps, forest dynamics, *Rhododendron maximum*, seedling survival, spatial variability, storage effect, temporal variability, tree diversity

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Introduction

Competing explanations for patterns of tree diversity have alternately emphasized the role of spatial or temporal variability in tree regeneration (e.g. Grubb 1977; Pacala & Roughgarden 1982; Huston 1994; Kelly & Bowler 2002). Canopy gaps and resulting spatial variability in understorey light conditions have played a prominent role in explanations of forest diversity (Shugart 1984; Platt & Strong 1989; Botkin 1993). Light is a resource that limits tree seedling recruitment in many forest understories, and canopy gaps can raise light levels, leading to increased seedling recruitment and higher levels of species diversity (Pickett & White 1985; Canham 1988; Platt & Strong 1989; Pacala *et al.* 1994). Many forests support dense understories, however, that may compete with tree seedlings for resources such as light, limiting seedling recruitment even in canopy gaps (e.g. Veblen 1982; Yamamoto *et al.* 1995; HilleRisLambers

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& Clark 2003), and diminishing the efficacy of canopy gaps in promoting seedling recruitment. Variation in the density of forest understories across sites could lead to ambiguous evidence for the importance of canopy gaps in maintaining tree diversity (e.g. Beckage *et al.* 2000; Webb & Scanga 2001,Gutierrez *et al.* 2004).

Alternative explanations of tree diversity have emphasized the role of annual variability in seedling recruitment. Large annual variability in regeneration success that is weakly correlated across tree species (HilleRisLambers & Clark 2003; Clark *et al.* 2004), together with the stochastic timing of gap formation, could determine which species successfully capture canopy openings, rather than static competitive relationship between species (e.g. Runkle 1989). The long life spans of tree species relative to the scale of temporal variability may provide a buffer or storage effect that promotes species diversity by allowing tree species to persist through periods of low recruitment, when years of high fecundity or survivorship do not coincide with periods of gap formation, and thus maintain a positive long-term population growth rate (Chesson & Warner 1981; Warner & Chesson 1985).

Determining the relative importance of spatial and temporal variability in recruitment requires data on the regeneration success of tree seedlings across environmental conditions and years. Traditional techniques for measuring seedling survival require the monitoring of individual seedlings through time: seedlings are marked with unique identifiers that must be subsequently relocated in order to assess the status of each individual as alive or dead (Klein & Moeschberger 1999; Beckage & Clark 2003). This method is laborious and time-consuming, is prone to problems with lost seedling markers and is inefficient, as seedling mortality tends to be high, with most marked seedlings lost in the first year. These factors tend to limit the spatial and temporal extent of sampling. This is problematic because large sample sizes are required to characterize fully the range of variability in regeneration processes across space and time (Clark *et al.* 1999).

The characterization of seedling survival would be simplified if survivorship could be estimated directly from repeated counts of seedlings in permanently marked quadrats, without the need to mark and track individual seedlings. Lavine *et al.* (2002) developed a Bayesian method for estimating survival parameters from repeated count data that only requires data on numbers of individuals in age or size classes. We investigated the use of this methodology to estimate survival of *Acer rubrum* L. (red maple) seedlings in small overstorey gaps with or without dense understorey shrubs and to characterize the residual spatial and temporal variance in seedling survival. We specifically address the following questions. Do small canopy gaps increase seedling survival? Are the effects of canopy gaps on seedling survival mediated by understorey shrubs? Is the magnitude of temporal variability in seedling survival greater than that of spatial variability?

Materials and methods

FIELD METHODS

We characterized seedling survival in second-growth forests at the Coweeta Hydrologic Laboratory (35°03′ N, 83°27′ W), North Carolina, in the southern Appalachian mountains, USA. Elevation in the 1626-ha Coweeta Basin ranges from 675 m to 1592 m. Field sites were located in mixed oak forests, which are found at mid elevations and intermediate moisture levels. *Rhododendron maximum* L. is a common evergreen shrub in the Coweeta Basin that forms a dense subcanopy layer 3–7 m in height with stem densities of 5000–17 000 ha^{-1} (Baker & Van Lear 1998) and leaf area indices of approximately 4.8–6.6 (J. HilleRisLambers, unpublished data).

Twelve experimental gaps were created in two mixed-oak stands at 850 m and 1100 m elevation. Sites had a north-eastern aspect, and slopes ranged from 30% to 70%. Up to five canopy trees were girdled to produce gaps, with standing dead trees, of approximately 300 m^2 (expanded gap definition, Runkle 1981) and a gap diameter to canopy height ratio of approximately 0.95. Three of the six gaps at each elevation contained a dense, natural *Rhododendron* understorey. Twelve transects, consisting of 40 contiguous 1-m^2 quadrats, were established at the planned site of each gap prior to gap formation. Pretreatment data were collected and experimental canopy gaps were created by girdling trees in late summer 1993. Girdled trees remained standing for the duration of our study, although large branches began to fall in the fourth year. Following gap creation, the central quadrats of each transect were exposed to gap conditions and the outer quadrats were subtended by the surrounding canopy. The border between gap and canopy conditions was ambiguous, reflecting the irregular canopy shapes of bordering trees. Therefore, we estimated survivorship parameters using the seedling counts from the central 16 quadrats and eight quadrats from each end of the transect (i.e. omitting a 4-m transitional area on each side of the gap edges). The inner 16 quadrats were in the canopy gap treatment (post-gap formation only) whereas the outer 16 quadrats and all pre-gap quadrats were considered the closed canopy treatment.

Seedlings and saplings (< 1.5 m in height) of *A. rubrum* were censused along transects annually in July or August from 1993 to 1998. Seedlings that had germinated in the current growing season were recognized by the presence of cotyledons and lack of terminal bud scale scars and were classified as 'New'. All seedlings that had germinated prior to the census year were classified as > 1 year old ('Old' seedlings), although this group may include some vegetative reproduction. These age classes are natural groupings for estimating seedling survival because survival is initially low for newly germinated seedlings but relatively constant across the subsequent several years of life (Streng *et al.* 1989; Jones *et al.* 1994).

STATISTICAL METHODS

Seedling survival was modelled as a binomial process. The number of Old seedlings in year $y + 1$ in a given quadrat comprised the New and Old seedlings that survived from the previous year. We modelled this process as the sum of two binomials:

$$D_{y+1} \sim \text{Binomial}(N_y, S_n) + \text{Binomial}(D_y, S_d)$$

where D_{y+1} is the number of Old seedlings in year $y + 1$, D_y is the number of Old seedlings in year y and N_y is the number of New seedlings in year y. Our censuses were conducted annually, so S_n and S_d represent probabilities of seedlings surviving from year y to year $y + 1$ for New and Old seedlings, respectively. If we consider one quadrat across two censuses that span one year, the probability of observing D_{y+1} is:

$$P(D_{y+1} \mid D_y, N_y, S_d, S_n) = \sum_{X} \{\text{Binomial}(D_{y+1} - x \mid D_y, S_d)\ \text{Binomial}(x \mid N_y, S_n)\}$$

where x represents the number of surviving New seedlings from year y and the summation occurs across the set X of potential number of surviving new seedlings that could lead to D_{y+1} (see supplementary Appendix S1).

We sometimes observed that the number of Old seedlings in a quadrat in a given year (i.e. D_{y+1}) exceeded the total of New and Old seedlings observed in the previous year ($N_y + D_y$), indicating an error in the previous year's census. This discrepancy could result from the germination of some seedlings after the annual censuses were completed or from a failure to count all seedlings present in a quadrat (i.e. 'missed' seedlings). Seedling germination following completion of the annual census would result in an undercount of New seedlings (N_y) while 'missing' seedlings could potentially affect either age class. We believe, however, that counting errors (i.e. 'missed' seedlings) would primarily apply to the New seedling class (N_y) because they were generally shorter in stature (≤ 5 cm) than Old seedlings and more likely to be overlooked in the ground-layer vegetation. We accounted for this error by modelling the observed number of New seedlings, n_y, as a binomial process: $n_y \sim \text{Bin}(N_y, f)$, where N_y is the 'true' number of New seedlings present in the quadrat at the end of the growing season, and f is the probability of the census-taker finding each of the N_y seedlings. We assumed that the numbers of New seedlings were distributed as a Poisson random variable with rate parameter λ, which was allowed to vary across years and transects, as well as with gap/*Rhododendron* conditions, but which was constant across the 16 quadrats within the gap or canopy portion of a transect. The Poisson distribution is often used to model seedling densities (Clark *et al.* 1999; Keyes *et al.* 2001) and is particularly appropriate when sources of extra-Poisson variability are explicitly conditioned, as is the case in our analysis. The probability of observing D_{y+1} for one quadrat across two censuses is then

$$P(D_{y+1} \mid D_y, N_y, f, S_d, S_n, \lambda) = \sum_{X} \{\text{Binomial}(D_{y+1} - x \mid D_y, S_d)\ \text{Binomial}(x \mid N_y, S_n)\}\ \text{Binomial}(n_y \mid N_y, f)\,\text{Poisson}(N_y \mid \lambda)$$

We modelled fixed and random effects on the survival probability, S, of New and Old seedlings using a logit link, where $\text{logit}(\mathbf{S}) = \mathbf{F\beta} + \mathbf{T\beta}_t + \mathbf{U\beta}_y + \mathbf{I}_d\beta_d$. $\mathbf{F}$ is the design matrix for the fixed effects and $\boldsymbol{\beta}$ is the vector of estimated fixed effects. The vector $\boldsymbol{\beta}$ consists of the intercept (β_0), the effect of the understorey shrub *Rhododendron* (β_r), the effect of gaps (β_g) and the interaction of *Rhododendron* and canopy gaps (β_{gr}). $\mathbf{T}$ and $\mathbf{U}$ are the design matrices for the transect and year random effects, and $\boldsymbol{\beta}_t$ and $\boldsymbol{\beta}_y$ are the vectors of estimated transect and year random effects. $\mathbf{I}_d$ is a vector of indicator variables that take a value of 1 if a seedling is classified in the Old age class or 0 otherwise. β_d is the estimated effect of being in the Old age class on seedling survival. We treated $\boldsymbol{\beta}_t$ and $\boldsymbol{\beta}_y$ as random effects that were distributed as Normal(0, σ_t^2) and Normal(0, σ_y^2), respectively.

We adopted a Bayesian approach to model fitting that allowed the quantification of uncertainty in model parameters in the form of probability distributions (Gelman *et al.* 2003). A Bayesian analysis combines the observed data in the form of a likelihood function with prior evidence or beliefs represented by prior probability distributions to yield the posterior probability distribution of model parameters. The posterior probability distribution provides the basis for all inference through probability statements on model parameters. The explicit calculation of the posterior distribution is often intractable in complex models and an alternative approach is to simulate a large number of random samples from the posterior distribution using Markov Chain Monte Carlo simulation (MCMC; Gilks *et al.* 1996). In MCMC simulation, random samples are generated from the posterior distribution and these samples are summarized to make inferences about model parameters. We present the results of our analysis using both graphical plots and 95% credible intervals for each parameter of interest based on the samples generated from the posterior distribution. We describe our likelihood function, prior distributions and implementation of MCMC in Appendix S1. The computer code used to fit the model is available from the first author's website (www.uvm.edu/~bbeckage).

Results

The observed seedling densities for 1993–98 with respect to gaps and *Rhododendron* are shown in Fig. 1. Seedling survival was affected by the understorey shrub *Rhododendron*, canopy gaps and seedling age class. *Rhododendron* had a large but negative effect on survival (β_r, Table 1, Fig. 2a) with seedlings beneath *Rhododendron* being 0.41 times as likely to survive as

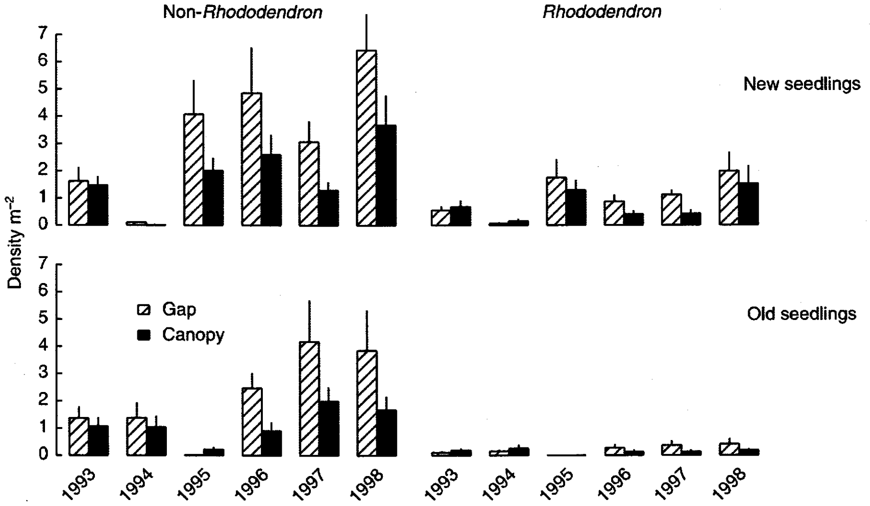

Fig. 1 Observed densities of New and Old seedlings in gap and closed canopy conditions with *Rhododendron* present or absent (plot means and standard errors).

Table 1 Means, medians and 95% credible intervals for parameter estimates. Model terms are defined in the Methods. Superscripts denote a particular component of a given vector

Term		Mean	Median	2.5%	97.5%	Odds ratio (mean)
Find probability	f	0.51	0.51	0.44	0.56	–
Intercept	β_o	−2.06	−2.02	−3.28	−1.01	–
Canopy gap	β_g	0.12	0.12	−0.10	0.34	1.13
Rhododendron	β_r	−0.88	−0.87	−1.29	−0.55	0.41
Rhododendron-gap interaction	β_{gr}	−0.25	−0.25	−0.64	0.14	0.78
Old age class	β_d	1.46	1.46	1.14	1.77	4.29
Transect random effect						
Variance	σ_t^2	0.05	0.04	0.01	0.18	–
	$\beta_t^{(1)}$	0.00	0.00	−0.25	0.25	1.00
	$\beta_t^{(2)}$	0.09	0.09	−0.14	0.33	1.09
	$\beta_t^{(3)}$	0.02	0.02	−0.23	0.28	1.02
	$\beta_t^{(4)}$	−0.12	−0.10	−0.60	0.26	0.89
	$\beta_t^{(5)}$	0.07	0.06	−0.23	0.41	1.07
Transects	$\beta_t^{(6)}$	0.20	0.18	−0.11	0.63	1.22
	$\beta_t^{(7)}$	−0.26	−0.25	−0.55	−0.03	0.77
	$\beta_t^{(8)}$	0.19	0.19	−0.02	0.41	1.21
	$\beta_t^{(9)}$	−0.02	−0.02	−0.26	0.19	0.98
	$\beta_t^{(10)}$	−0.26	−0.23	−0.73	0.07	0.77
	$\beta_t^{(11)}$	0.11	0.10	−0.20	0.48	1.12
	$\beta_t^{(12)}$	0.02	0.01	−0.28	0.34	1.02
Year random effect						
Variance	σ_y^2	2.66	1.72	0.48	10.43	–
	$\beta_y^{(1)}$	0.59	0.54	−0.38	1.87	1.80
	$\beta_y^{(2)}$	−1.84	−1.87	−2.94	−0.57	0.16
Years	$\beta_y^{(3)}$	0.81	0.76	−0.15	2.07	2.25
	$\beta_y^{(4)}$	1.00	0.94	0.05	2.30	2.71
	$\beta_y^{(5)}$	0.86	0.82	−0.10	2.14	2.37

seedlings in areas without the shrub. By contrast, the effect of canopy gaps on seedling survival was positive but relatively small (β_g, Table 1, Fig. 2a); seedlings in canopy gaps were slightly more likely (1.13 times) to survive than those beneath closed canopy, but the 95% credible interval included 0. The small effect size and overlap with 0 suggest that the gap effect was weak. The canopy gap–*Rhododendron* interaction was similarly weak: there was a tendency for seedlings in gaps with *Rhododendron* to be less likely (0.78 times) to survive than those in gaps lacking the shrub, but the 95% credible interval again contained 0 (β_{gr}, Table 1, Fig. 2a). The effect of seedling age class, however, was large, with Old seedlings nearly 4.3 times more likely to survive from one year to the next than were New seedlings (β_d, Table 1, Fig. 2a). In addition, we estimated that only about half of the New *A. rubrum* seedlings were found by the end of the growing season (f, Table 1).

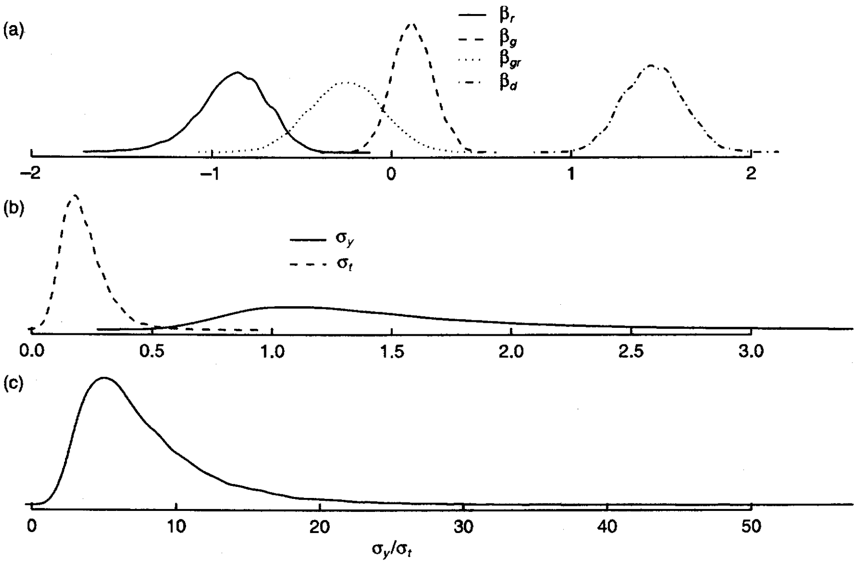

Fig. 2 Posterior distributions of selected model parameters and derived quantities: (a) the effect of canopy gaps (β_g), *Rhododendron* understories (β_r), the gap–*Rhododendron* interaction (β_{gr}) and seedling age class (effect of being an Old seedling, β_d) on *A. rubrum* seedling survival; (b) variability (standard deviation) in survival associated with years (σ_y) and transects (σ_t); and (c) the ratio of σ_y to σ_t. All posteriors have been smoothed using a gaussian kernel estimator.

Seedling survival was approximately seven times more variable across years than across transects ($\sigma_y = 1.6$ vs. $\sigma_t = 0.22$, Fig. 2b) with the 95% credible interval on this ratio ranging from 2.5 to 22.8 (Fig. 2c). The estimated transect random effects on seedling survival were relatively small, varying from −0.26 to 0.19 (Table 1). By contrast, the year random effect on survival ranged from −1.8 to 1.0, which was larger than any fixed effect except seedling age class (Table 1). The 95% credible interval included 0 for 11 of the 12 transect effects and for three of the five year effects, suggesting considerable uncertainty in these estimates.

We computed the posterior survival probabilities in all canopy gap–*Rhododendron* combinations for New and Old seedlings after removing year and transect effects, and these are shown on the untransformed probability scale in Fig. 3. Canopy gaps had only a weak effect on seedling survival, resulting in either slight decreases in median survival probability if *Rhododendron* was present or slight increases if *Rhododendron* was absent, i.e. a difference of approximately 0.02 in each case. *Rhododendron*, by contrast, had a strong and consistent negative effect on survival of both New and Old seedlings, regardless of canopy condition: median survival probabilities were decreased by the presence of the understorey shrub by up to 0.21 (Fig. 3). Survival probability was strongly dependent on age class: survival probability of Old seedlings was 0.13–0.25 higher than New seedlings across *Rhododendron* and canopy gap treatments.

Strong correlations were found between some model parameters. The total number of imputed new seedlings, *N*, was strongly and negatively correlated with the estimates of findability f ($\rho = -0.96$), indicating a tradeoff between the probability of finding a new seedling, f, and the imputed number of actual New seedlings present, *N*. Lower find probabilities resulted in larger numbers of imputed seedlings (Lavine *et al.* 2002). Transect and year effects were also often strongly correlated, as were σ_t^2 and σ_y^2 ($\rho = 0.90$).

Discussion

We estimated annual survival probabilities for both newly germinated and established *A. rubrum* seedlings using 6 years of seedling count data. We found that canopy gaps had only a slight positive influence on seedling survival whereas the understorey shrub *Rhododendron* had a large negative effect on survivorship. The presence of *Rhododendron* offset the beneficial effects of canopy gaps, supporting observations that forest understories are an important determinant of tree regeneration patterns (Clinton *et al.* 1994; Lorimer *et al.* 1994; George & Bazzaz 1999; Beckage *et al.* 2000; HilleRisLambers & Clark 2003). Light levels in our gaps increased modestly beginning in the year following gap creation, with the proportion of light reaching the understorey ranging from 11% in canopy gaps to 5% beneath closed canopy, both outside of *Rhododendron*, to 2% beneath *Rhododendron* where there was no measurable increase following gap creation (Beckage *et al.* 2000). Small canopy gaps have been postulated to promote tree regeneration and maintain forest diversity in temperate forests (e.g. Barden 1979; Runkle 1981), but we found little evidence of this in the seedling survival of *A. rubrum* in our 20-m-diameter canopy gaps. Although *A. rubrum* is considered shade-tolerant (Burns & Honkala 1990), tree species that are more tolerant of shade, such as beech or hemlock, might respond more strongly to gaps of this size and

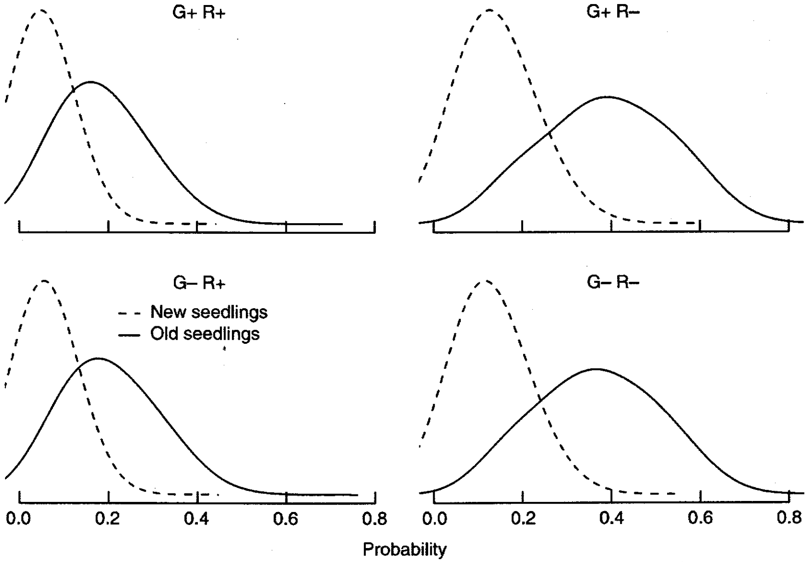

Fig. 3 Posterior distributions of seedling survival in all canopy gap–*Rhododendron* combinations for New (newly germinated) and Old seedlings on the untransformed probability scale. Parameters were estimated from 6 years of census data for *A. rubrum*. The posteriors have been smoothed using a gaussian kernel estimator. We refer to gap conditions as G+ (vs. canopy, G–) and to the presence of *Rhododendron* as R+ (vs. non *Rhododendron*, R–).

nature. The lack of a strong recruitment response to small canopy gaps, however, is consistent with other studies of forest regeneration (Busing & White 1997; Beckage *et al.* 2000; Webb & Scanga 2001; Beckage & Clark 2003). Temperate forests in this region of the United States are subjected to frequent and intense hurricane disturbances that cause extensive areas of large blowdowns (Greenberg & McNab 1998). We suggest that large canopy gaps, such as result from severe tropical disturbances, with corresponding disturbance to the forest understorey may be necessary to increase seedling survival and maintain the high levels of tree diversity observed in forests of this region.

Annual variability in seedling survival of *A. rubrum* was much larger than spatial variability in survival across transects. The effects of individual years on seedling survival were larger than even our strongest treatment effect, i.e. the presence of the shrub *Rhododendron* (Table 1). Large interannual variability in seedling survival may have been driven by variation in environmental variables such as precipitation. The strong negative effect on seedling survival in Year 2 (Table 1), for instance, may have resulted from an unusually dry spring that year. Red maple seedlings emerge from winter dormancy in April in this region and, in 1995, precipitation was only 24–50% of that received in April of the other years of our study. *Acer rubrum* seedlings are not tolerant of drought (Barton & Gleeson 1996; Beckage & Clark 2003), so this dry period would be expected to result in low seedling survival (as shown in Table 1, Fig. 1). Annual fluctuations in the establishment and survival of seedlings can also be caused by biological factors such as seed or seedling predator abundance or variable seed rain (Clark et al. 1998; Beckage & Clark 2005), as well as by other environmental variables besides precipitation.

Large annual fluctuations in recruitment processes can allow diverse tree species to capture vacant sites in different years rather than available sites being consistently dominated by the best competitor (Kelly & Bowler 2002). Our estimates of large annual variability in seedling survival are similar to other long-term studies that have consistently found large annual fluctuations in recruitment processes such as seed production (Clark *et al.* 2004), survival (Streng *et al.* 1989) and seedling establishment (Boerner & Brinkman 1996; Connell & Green 2000). Large annual fluctuations in seedling recruitment, together with periodic hurricane disturbances that create large canopy openings, could lead to the high diversity of overstorey trees observed in temperate forests of the southern Appalachian mountains (Whittaker 1956). Frequent large disturbances, recruitment limitation of most tree species in most years and large annual variability in recruitment that is only weakly correlated across species may together promote tree diversity through a storage effect (Clark *et al.* 1998, 2004; Hubbell *et al.* 1999; Kelly & Bowler 2002). Our results also emphasize the need for including multiple years of sampling as increased spatial coverage will not capture the large annual variability observed in long-term studies.

The use of seedling counts to estimate seedling survival can lead to better characterization of patterns of tree recruitment. The labour required to mark and track large numbers of seedlings over long time periods may contribute to the limited characterization of seedling survival using traditional statistical techniques (Clark *et al.* 1999). Our new statistical methodology relies on repeated seedling counts rather than long-term monitoring of individual seedlings, substantially reducing the field effort required to derive survival probabilities, and enabling ecologists to sample spatial and temporal variability more broadly. In addition, seedling survival can be estimated from already existing count data, provided that seedlings were censused within categories with similar survival (e.g. our New and Old seedlings). In the absence of extensive data on seedling recruitment, forest regeneration can be modelled using shorter-term studies (e.g. Ribbens *et al.* 1994) or projections of future forest composition based on relative densities of recruits (Runkle 1981; see also Acevedo *et al.* 1995). The former approach is likely to miss important variability in regeneration processes while the latter assumes that subsequent survival will not vary across species, an assumption that is unlikely to be true. Although our methodology may reduce effort in the field, there is a trade-off between ease of data collection and information content of the data – census data contain less information on seedling survival than do marked seedling data. Lavine *et al.* (2002) explored this trade-off using 100 simulated datasets and found that the ratio of information content of census seedling studies to marked seedling studies tends to 0 as new seedling survival approaches old seedling survival. Fortunately, this is unlikely to be the case for most species. In addition, the statistical analysis that we present differs from traditional survival analyses in that we model transition probabilities between years rather than time to death. The time to death approach allows for probability of mortality to change continuously as seedlings age, a characteristic that might be desirable in some situations.

Our analysis suggests that we found only half of the new seedlings that were present at the end of the growing season (i.e. $f = 0.51$). A low find probability could have resulted from several causes. First, *A. rubrum* seedlings may have germinated for an extended period over the growing season, so that many seedlings may not have emerged until after our annual censuses were completed in the beginning of July to mid August across years. This explanation receives only limited support from a study of *A. rubrum* germination showing that the timing of germination varied annually, with nearly 50% of seedlings emerging in July in some years (HilleRisLambers & Clark 2005). Second, New seedlings that were present at the time of the census may have been missed by census takers. Ground-layer vegetation can make it difficult to spot small seedlings, which predominately belong to the 'New' age class. Third, vegetative reproduction (root suckers) would be classified as Old seedlings based on their physical appearance, without ever having passed through a New seedling stage, resulting in a lowered find probability. Similarly, misidentification of seedling age, i.e. erroneously placing a New seedling in an Old seedling class, may also have occurred on occasion for seedlings that germinated early in the growing season. In reality, all of these errors probably contributed to some extent to our low find probability, but we do not have data to distinguish between their relative importance.

We assumed conditional independence between adjacent quadrats and did not model additional spatial structure in our seedling survival model. We initially explored the strength of spatial correlation between adjacent quadrats in our transects using a Gaussian random field model, which indicated that this additional model structure was not needed to account for spatial effects. This result was consistent with another investigation of spatial structure in seedling survival, which we conducted using a separate data set (from the same study area) and was presented in a more theoretical paper (Lavine *et al.* 2002), where we concluded that there was not a clear need to model spatial correlation in adjacent quadrats. Although the previous model and data did not include environmental information, such as gaps and *Rhododendron*, this additional information should only reduce residual spatial autocorrelation. While we assume in our current model that survival is equivalent across adjacent quadrats, after conditioning for the presence of *Rhododendron*, gap environment, year and plot, we could have included a quadrat-specific random effect to account for additional variability across quadrats. The random effects model could be structured so as to account for spatial correlation. This might be necessary in some situations where there is significant environmental variation that strongly affects seedling survival, varies over adjacent quadrats and is not specifically conditioned upon.

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References

Acevedo, M.F., Urban, D.L. & Arlan, M. (1995) Transition and gap models of forest dynamics. *Ecological Applications*, **5**, 1040–1055.

Baker, T.T. & Van Lear, D.H. (1998) Relations between density of rhododendron thickets and diversity of riparian forests. *Forest Ecology and Management*, **109**, 21–32.

Barden, L.S. (1979) Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the Southern Appalachians, Tennessee. *Oecologia*, **44**, 141–142.

Barton, A.M. & Gleeson, S.K. (1996) Ecophysiology of seedlings of oaks and red maple across a topographic gradient in eastern Kentucky. *Forest Science*, **42**, 335–342.

Beckage, B. & Clark, J.S. (2003) Seedling survival and growth of three southern Appalachian forest tree species: the role of spatial heterogeneity. *Ecology*, **84**, 1849–1861.

Beckage, B. & Clark, J.S. (2005) Does predation contribute to tree diversity? *Oecologia*, **143**, 458–469.

Beckage, B., Clark, J.S., Clinton, B.D. & Haines, B.L. (2000) A long-term study of tree seedling recruitment in Southern Appalachian forests: the effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research*, **30**, 1617–1631.

Boerner, R.E.J. & Brinkman, J.A. (1996) Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. *Bulletin of the Torrey Botanical Club*, **123**, 309–317.

Botkin, D.B. (1993) *Forest Dynamics: an Ecological Model.* Oxford University Press, Oxford.

Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America*, Vol. 2. *Hardwoods.* USDA, Washington, DC.

Busing, R.T. & White, P.S. (1997) Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos*, **78**, 562–568.

Canham, C.D. (1988) Growth and canopy architecture of shade tolerant trees: the response of *Acer saccharum* and *Fagus grandifolia* to canopy gaps. *Ecology*, **69**, 786–795.

Chesson, P.L. & Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, **117**, 923–943.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., MacLachlan, J., Mohan, J. & Wyckoff, P. (1999) Interpreting recruitment limitation in forests. *American Journal of Botany*, **86**, 1–16.

Clark, J.S., LaDeau, S. & Ibanez, I. (2004) Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs*, **74**, 415–442.

Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, **68**, 213–235.

Clinton, B.D., Boring, L.R. & Swank, W.T. (1994) Regeneration patterns in canopy gaps, mixed-oak forests of the southern Appalachians: influences of topographic position and evergreen understory. *American Midland Naturalist*, **132**, 308–319.

Connell, J.H. & Green, P.T. (2000) Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology*, **81**, 568–584.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2003) *Bayesian Data Analysis*. Chapman & Hall, New York.

George, L.O. & Bazzaz, F.A. (1999) The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. *Ecology*, **80**, 846–856.

Gilks, W.R., Richardson, S. & Spiegelhalter, D.J. (1996) *Markov Chain Monte Carlo in Practice*. Chapman & Hall, New York.

Greenberg, C.H. & McNab, W.H. (1998) Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. *Forest Ecology and Management*, **104**, 179–191.

Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.

Gutierrez, A.G., Armesto, J.J. & Aravena, J.C. (2004) Disturbance and regeneration dynamic of an old-growth North Patagonian rain forest in Chiloe Island, Chile. *Journal of Ecology*, **92**, 598–608.

HilleRisLambers, J. & Clark, J.S. (2003) Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. *Canadian Journal of Forest Research*, **33**, 783–795.

HilleRisLambers, J. & Clark, J.S. (2005) The benefits of seed banking for red maple (*Acer rubrum*): maximizing seedling recruitment. *Canadian Journal of Forest Research*, in press.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & Loo de Lao, S. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **283**, 554–557.

Huston, M. (1994) *Biological Diversity: the Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.

Jones, R.H., Sharitz, R.R., Dixon, P.M., Segal, D.S. & Schneider, R.L. (1994) Woody plant regeneration in four floodplain forests. *Ecological Monographs*, **64**, 345–367.

Kelly, C.K. & Bowler, M.G. (2002) Coexistence and relative abundance in forest trees. *Nature*, **417**, 437–440.

Keyes, C.R., Acker, S.A. & Greene, S.E. (2001) Overstory and shrub influences on seedling recruitment patterns in an old-growth ponderosa pine stand. *Northwest Science*, **75**, 204–210.

Klein, J.P. & Moeschberger, M.L. (1999) *Survival Analysis: Techniques for Censored and Truncated Data*. Springer-Verlag, New York.

Lavine, M., Beckage, B. & Clark, J.S. (2002) Statistical modeling of seedling mortality. *Journal of Agricultural, Biological, and Environmental Statistics*, **7**, 21–41.

Lorimer, C.G., Chapman, J.W. & Lambert, W.D. (1994) Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology*, **82**, 227–237.

Pacala, S.W., Canham, C.D., Silander, J.A. Jr & Kobe, R.K. (1994) Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research*, **24**, 2172–2183.

Pacala, S.W. & Roughgarden, J. (1982) Spatial heterogeneity and interspecific competition. *Theoretical Population Biology*, **31**, 92–113.

Pickett, S.T.A. & White, P.S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Inc., Orlando.

Platt, W.J. & Strong, D.R. (1989) Gaps in forest ecology. *Ecology*, **70**, 535.

Ribbens, E., Silander, J.A. Jr & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.

Runkle, J.R. (1981) Gap regeneration in some old-growth forests of the eastern United States. *Ecology*, **62**, 1041–1051.

Runkle, J.R. (1989) Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology*, **70**, 546–547.

Shugart, H.H. (1984) *A Theory of Forest Dynamics: the Ecological Implications of Forest Succession Models*. Springer-Verlag, Berlin.

Streng, D.R., Glitzenstein, J.S. & Harcombe, P.A. (1989) Woody seedling dynamics in an east Texas floodplain forest. *Ecological Monographs*, **59**, 177–204.

Veblen, T.T. (1982) Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. *Bulletin of the Torrey Botanical Club*, **109**, 474–487.

Warner, R.R. & Chesson, P.L. (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *American Naturalist*, **125**, 769–787.

Webb, S.L. & Scanga, S.E. (2001) Windstorm disturbance without patch dynamics: twelve years of change in a Minnesota forest. *Ecology*, **82**, 893–897.

Whittaker, R.H. (1956) Vegetation of the Great Smoky Mountains. *Ecological Monographs*, **26**, 1–80.

Yamamoto, S., Nishimura, N. & Matsui, K. (1995) Natural disturbance and tree species coexistence in an old-growth beech–dwarf bamboo forest, southwestern Japan. *Journal of Vegetation Science*, **6**, 875–886.

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Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com

Appendix S1 Full conditional distributions for MCMC sampling