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## Does predation contribute to tree diversity?

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**Abstract** Seed and seedling predation may differentially affect competitively superior tree species to increase the relative recruitment success of poor competitors and contribute to the coexistence of tree species. We examined the effect of seed and seedling predation on the seedling recruitment of three tree species, *Acer rubrum* (red maple), *Liriodendron tulipifera* (yellow poplar), and *Quercus rubra* (northern red oak), over three years by manipulating seed and seedling exposure to predators under contrasting microsite conditions of shrub cover, leaf litter, and overstory canopy. Species rankings of seedling emergence were constant across microsites, regardless of exposure to seed predators, but varied across years. *A. rubrum* had the highest emergence probabilities across microsites in 1997, but *Q. rubra* had the highest emergence probabilities in 1999. Predators decreased seedling survival uniformly across species, but did not affect relative growth rates (RGRs). *Q. rubra* had the highest seedling survivorship across microsites, while *L. tulipifera* had the highest RGRs. Our results suggest that annual variability in recruitment success contributes more to seedling diversity than differential predation across microsites. We synthesized our results from separate seedling emergence and survival experiments to project seedling bank composition. With equal fecundity assumed across species, *Q. rubra* dominated the seedling bank, capturing 90% of the regeneration sites on average, followed by *A. rubrum* (8% of sites) and *L. tulipifera* (2% of sites). When seed abundance was weighted by species-specific fecundity, seedling bank composition was more diverse; *L. tulipifera* captured

62% of the regeneration sites, followed by *A. rubrum* (21% of sites) and *Q. rubra* (17% of sites). Tradeoffs between seedling performance and fecundity may promote the diversity of seedling regeneration by increasing the probability of inferior competitors capturing regeneration sites.

**Keywords** Canopy gaps · Seed predation · Seedling predation · Species coexistence

### Introduction

The recruitment of forest trees is mediated by animals that consume or prey on tree seeds or seedlings. Predation can exert a strong influence on tree recruitment and forest dynamics by mediating pre-emptive competition for regeneration microsites and altering competitive relationships among species (Hulme 1996). Predation may alter the composition of tree regeneration because seed and seedling loss to predators can be high (> 80% of seed production; Janzen 1971; Steele and Smallwood 1994; Tanaka 1995) and predators can display strong species preferences (Plucinski and Hunter 2001). Predation that differentially affects competitively superior species can promote species diversity by preventing competitive displacement of inferior competitors (Connell 1971; Caswell 1978; Pacala and Crawley 1992; Huston 1994). For example, seedlings of large-seeded tree species have a competitive advantage over small-seeded species because of greater energy reserves for seedling establishment (Foster and Janson 1985; Bonfil 1998). Predators, however, may differentially select large-seeded species because of their higher energy rewards, offsetting this competitive advantage and favoring smaller-seeded species (Condit et al. 1992).

Predation intensity is also influenced by microsite conditions that affect seed findability and predator foraging patterns (Manson and Stiles 1998). Leaf litter, for example, can make seeds more difficult for predators to

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find, decreasing the strength of predation effects (Myster and Pickett 1993; Cintra 1997). Leaf litter also influences moisture balance and seedling access to mineral soil (Molofsky and Augspurger 1992), so that the summed effect of leaf litter on recruitment success is unclear. Similarly, the foraging behavior of seed and seedling predators is affected by overstory condition and shrub cover (Buckner and Shure 1985; Whitmore and Brown 1996). Canopy gaps result in elevated light levels that benefit seedlings, but also influence predation intensity (Buckner and Shure 1985; Schupp et al. 1989; Whitmore and Brown 1996; Abe et al. 2001). The interaction of predation with microsite conditions determines final recruitment success and may create spatial variability in regeneration niches that promotes species coexistence (Grubb 1977).

We examined the potential of seed and seedling predation to contribute to the coexistence of three co-occurring tree species, *Acer rubrum* L (red maple), *Liriodendron tulipifera* L (yellow poplar), and *Quercus rubra* L (northern red oak), in deciduous forests of southeastern North America. Regeneration niches were defined by the intensity of predation (exposed to/protected from predation), crossed with overstory condition (gap/closed canopy), understory condition (understory shrub layer present/absent), and litter (present/absent). Seeds and seedlings of all three species were planted in replicated, experimental microsites defined by the factorial combination of these treatments. Seedling emergence, growth, and survival were monitored for 3 years to determine if differential predation across microsites provided sufficient heterogeneity to promote species coexistence. We specifically asked the question: Does each species outperform the others in some regeneration niche as measured by seedling emergence, survival, or growth? If regeneration microsites are contributing to the coexistence of these three species, we expect each species to clearly be the best performer in a subset of our treatments.

Microsites, however, may favor one life-history stage while negatively affecting another. Microsite conditions that benefit tree seeds, for example, can have negative effects on seedlings, leading to different and even contrasting effects on seeds and seedlings (Schupp 1995). Predictions of tree regeneration must account for discordant microsite effects on tree recruitment processes (Jordano and Herrera 1995). We therefore integrated the results from our separate experiments on seed and seedling predation and calculated the expected composition of seedling regeneration, i.e., the seedling bank, across two life-history stages, seed germination and seedling survival. We used these results to address a second question: Do our experimental regeneration niches promote the species diversity of the seedling bank?

## Materials and methods

Our study was conducted in second-growth, mixed-oak forests at the Coweeta Hydrologic Laboratory (35°03'N

degrees latitude, 83°27'W, elevation 675–1,592 m), North Carolina, USA. Mixed-oak forest is a widespread forest type in this region and is found at mid-elevations and at moisture levels intermediate between those of cove hardwoods and oak-pine ridges (Whittaker 1956). Average monthly temperatures at Coweeta range from 3°C in January to 19°C in July. Average annual precipitation is 1,800 mm and is distributed evenly throughout the year.

The shrub *Rhododendron maximum* L. is common in the forest understory at Coweeta (Swank and Crossley 1988). *R. maximum* forms a dense subcanopy layer 3–7 m in height, with stem densities between 5,000 and 17,000 per ha (Baker and Van Lear 1998), leaf area indices (LAI) ranging from approximately 4.8 to 6.6 (Janneke HilleRisLambers, unpublished data), and diameters typically ranging from 4 to 7 cm diameter at breast height (dbh) but sometimes greater than 10 cm dbh (B. Beckage, unpublished data). *Gaylussaccia bacata* (Wang.) K. Koch, an ericaceous shrub typically under 1 m in height, is common in areas lacking *R. maximum*.

We choose *A. rubrum*, *L. tulipifera*, and *Q. rubra* as focal tree species because they comprise a large component of deciduous forests in southeastern North America, co-occur within our study sites, and represent both a range of life-history traits and susceptibility to predators. *L. tulipifera* is shade intolerant, *Q. rubra* is intermediately shade tolerant, and *A. rubrum* is tolerant of shade (Beckage and Clark 2003). The seeds of *Q. rubra* are also an order of magnitude larger than those of *L. tulipifera* or *A. rubrum* (364 mg vs. 40 mg or 33 mg, respectively; Beckage and Clark 2003). The seeds and seedlings of *Q. rubra* and the seeds of *A. rubrum* are known to be preyed on by small mammals that consume their seeds and clip seedlings at their base (Ostfeld and Canham 1993; Steele and Smallwood 1994; Tanaka 1995; Ostfeld et al. 1997). We confirmed the importance of small mammals as predators using snap traps baited with seeds of these tree species, which consistently yielded white-footed mice (*Peromyscus leucopus*) and red-backed voles (*Clethrionomys gapperi*). These small mammals were also the likely seedling predators as deer densities are low in the Coweeta basin (Josh Laerm, University of Georgia, personal communication).

Twelve experimental gaps were created by girdling up to five canopy trees in the summer of 1993, creating intermediate-sized gaps of approximately 300 m<sup>2</sup> (expanded gap definition, Runkle 1981) with a gap diameter to canopy height ratio of approximately 0.95. The gaps were created in two mixed oak stands that bracket the elevation range of this community, referred to as low (850 m) and high elevation (1,100 m) sites. Sites had a northeast aspect, and slopes ranged from 30% to 50% (high elevation) and from 45% to 70% (low elevation). Three of the six plots at each elevation had a dense *R. maximum* understory, while three plots lacked *R. maximum*. Separate seed and seedling predation experiments were conducted within the twelve

experimental gaps and adjacent canopy controls. We refer to each gap-canopy pair as a plot.

### Seed predation

We examined the effect of seed predation on recruitment by comparing seedling emergence from a given quantity of seeds that were either exposed to or protected from predators. We limited predator access to seeds using metal enclosures and assumed that the difference in seedling emergence within versus outside of enclosures was due to predation. Seed predators, however, may remove seeds to caches, where they can later germinate, rather than consuming them, and this would result in underestimates of seed to seedling transition probabilities. We typically observed the remains of seeds that had been predated, however, suggesting that caching was not prevalent.

Seeds were protected from predators by wire cages or 'enclosures' constructed of 6 mm, galvanized hardware cloth (dimensions: 35 cm long×35 cm wide×25 cm high). The boxes were completely closed and staked to the ground. The design was initially tested and resulted in no seed loss in contrast to adjacent, unprotected quadrats. Unprotected controls were placed adjacent to each enclosure. An additional set of unprotected control plots was installed to monitor background levels of seedling emergence. Seeds were not added to these plots. Few seedlings appeared in these control plots, indicating that seedlings in our experimental quadrats were from seeds we placed in the treatments.

Litter was removed from half of each quadrat in the Protection treatment. A hardware cloth divider, 5 cm in height, separated the litter and cleared portions of the quadrat. The placement of the seeds relative to the litter layer reflected natural patterns of dispersal. *L. tulipifera* and *A. rubrum* seeds were placed on top of the litter as they are dispersed after leaf fall. *Q. rubra* acorns were placed beneath the litter as they are dispersed before and during leaf fall. Annual litterfall is approximately 300–400 g/m<sup>2</sup> (Hansen 2000; Bonito et al. 2003).

Seed predation experiments were conducted separately for each species, allowing the seed predation experiments to be initiated during the natural dispersal period of each species. *A. rubrum* and *L. tulipifera* seeds were placed out in the late spring, whereas *Q. rubra* acorns were placed out in the fall or early winter. The number of seeds used in each replication was chosen to reflect expected seed viability and to be within the natural range of observed seed densities so as to avoid artificial effects from either attracting or saturating predators. The quantity was fixed for a particular species in a specific year, but varied across years. We used either 15 or 30 seeds for *A. rubrum* and 5 or 6 acorns for *Q. rubra*. We initially used 100 seeds for *L. tulipifera* because of its low viability (5–20%, Burns and Honkala 1990). Counting out such large numbers of seeds was impractical, so we subsequently used a

fixed weight of seed. This complicated the analysis as discussed below.

Seedling emergence was periodically censused on a monthly/bimonthly basis through the natural period of germination, e.g., early to mid-summer. We did not follow potential transitions into and out of the seed bank. This was not a concern for *Q. rubra*, which does not have a seed bank (Burns and Honkala 1990). Similarly, most *A. rubrum* seeds (~95%) germinate within 10 days of seedfall but environmental conditions can sometimes cause seeds to germinate the following year (Abott 1974; Farmer and Cunningham 1981; Burns and Honkala 1990). When this occurred, we monitored *A. rubrum* seedling emergence for a second year (see [Materials and methods](#)). *L. tulipifera* seeds, however, can move into and remain in the seedbank for up to 4–7 years (Burns and Honkala 1990).

We repeated the seed predation experiments for three years: 1997, 1998, and 1999 for *Q. rubra* and *A. rubrum* but for only two years for *L. tulipifera* (1997 and 1999). In each year, the enclosures and plots were relocated within the gap or closed canopy portion of the plots. Seeds of *A. rubrum* and *L. tulipifera* failed to germinate in some years. This occurred for *A. rubrum* in 1998 and seedlings subsequently emerged the following spring. In subsequent analyses, these delayed individuals are associated with 1998. Seedlings of all three species emerged together in 1999 and our comparisons of seedling emergence across species are based on this year.

### Seedling predation

We examined the impact of predation on seedling survival and growth by manipulating predator access to seedlings using wire enclosures. The enclosures were 2 m long, 1 m wide, 1.1 m high, and buried 15 cm into the ground. They were constructed of 6 mm galvanized hardware cloth. The enclosures were open above, but had 36 cm of aluminum flashing at the top of the walls to prevent rodents from climbing inside. The enclosures were buried into the ground to a depth of 15 cm, to prevent rodents from burrowing into the protected plots, which also could have increased below-ground resources inside the plots by severing roots (Beckage and Clark 2003). We controlled for this effect by burying thin strips of hardware cloth around the perimeter of the unprotected control plots, so that seedlings in the controls would experience a similar reduction in below-ground competition. Within each enclosure or control, we planted sixteen 1st-year seedlings of *A. rubrum*, ten 1st-year seedlings of *L. tulipifera*, and ten 1st-year seedlings of *Q. rubra* for a total of 36 seedlings per enclosure or control and 1,728 seedlings altogether. We measured the initial height of each seedling prior to planting. We repeated this experimental design in the gap and canopy portions of each plot.

The seedling predation experiment was installed in two parts: the low elevation plots were completed in the

summer of 1996 and all seedlings were planted in the last week of August 1996. The upper elevation experiment was installed in the summer of 1997 with all seedlings planted in mid-July 1997. The low elevation plots were subsequently surveyed in the last week of August 1997, 1998, and 1999 while the high elevation plots were surveyed on the latter two dates only. Therefore, the effect of elevation is confounded with the year and so we do not estimate an ‘Elevation’ effect for seedling survival. During each survey, a seedling was recorded as either alive or dead. Seedling heights in all plots were re-measured in August 1999.

We quantified the understory light environment using hemispherical photographs taken over the center of each enclosure or control in the seedling predation experiment. Photographs were taken at a height of 1.4 m in August or September using a fisheye Nikkor 8 mm f2.8 lens (180° field of view) with a Kodak color slide film and a self-leveling gimbal. All photographs were taken with the magnetic north at the top of the image, allowing superposition of the solar track. Photographs were digitized and then analyzed using Hemiview canopy analysis software (Delta-T Devices, Cambridge, England). Global site factors (GSF), the proportion of direct and diffuse radiation received below the canopy as a fraction of that received above the canopy (Rich 1989), were calculated using meteorological data from the Coweeta basin. GSF values were used to compare gap and canopy light environments as well as the effect of *R. maximum* on light levels.

The use of enclosures to prevent predators from accessing seeds or seedlings could also have indirect effects on abiotic environmental variables such as light levels. Enclosures necessarily block some sky, lowering the levels of light available to seeds and seedlings at the forest floor. Since light can be a limiting resource in the forest understory, even in small gaps, this indirect effect would result in an underestimate of the positive effects of predator exclusion.

#### Analysis: seed predation

The number of emerged seedlings in the seed predation experiment was treated as a binomial process with emergence probability  $\theta$  given by:

$$\log\left(\frac{\theta}{1-\theta}\right) = \mathbf{X}\beta + \mathbf{Z}\omega$$

where  $\mathbf{X}$  is the fixed effects design matrix,  $\beta$  is the vector of fixed effect coefficients,  $\mathbf{Z}$  is the random effects design matrix, and  $\omega$  is the vector of coefficients associated with random effects. Fixed effects included Overstory, Understory, Litter, and Protection treatments as well as Elevation. The year was considered random and was modeled as Normal(0,  $\sigma_r^2$ ). The random year effect was omitted for *L. tulipifera*, which only produced seedlings in one year. We fit this model using Bayesian methods

and the WinBugs software (<http://www.mrc-bsu.cam.ac.uk>). Unknown parameters were assigned diffuse priors with one exception: in 1999, a fixed weight (20 g) of *L. tulipifera* seeds was placed in each treatment rather than a fixed number of seeds, so that the number of seeds in the binomial process was unknown. We constructed a prior distribution for this quantity by counting seeds in multiple 20-g samples.

We report parameter estimates of treatment effects and associated odds ratios. The odds ratio compares the odds of a seed producing a seedling with a particular treatment versus without it. We do not report odds ratios across species because species were analyzed separately. Parameter estimates are reported to be ‘significant’ if the Bayesian  $P$  value is  $\leq 0.05$  (Gelman et al. 1995).

#### Analysis: seedling predation

The analysis of seedling survival was based on the survival function,  $S(t)$ , which describes the probability that a seedling survives beyond age  $t$ . We compared seedling survival between microsites using the product-limit (Kaplan Meier) estimator of the survival function and the log rank test (Klein and Moeschberger 1999). We estimated the effects of individual treatments on seedling survival using a parametric survival model of the form

$$f(\text{seedling lifetime}) = \mathbf{X}\beta + \mathbf{Z}\omega + \sigma\varepsilon$$

where  $\mathbf{X}$ ,  $\beta$ ,  $\mathbf{Z}$ , and  $\omega$  are as defined above,  $f()$  is the model-dependent link function,  $\sigma$  is the scale parameter (scalar or vector), and  $\varepsilon$  is the error distribution (Klein and Moeschberger 1999). Fixed effects included Overstory, Understory, and Protection treatments, while plots were considered a random effect.

We selected the ‘best’ parametric model of seedling survival from the set of potential models that included six different error distributions, the experimental treatments and their interactions, and the random effect using a stepwise procedure that retained model terms based on Akaike’s Information Criterion (AIC). The error distribution selected in the final model was the loglogistic. This parametric model has a relative odds interpretation in addition to an accelerated time interpretation (Klein and Moeschberger 1999). We fit the final ‘best’ model using a Bayesian Markov Chain Monte Carlo (Gilks et al. 1996) sampler programed in Splus (Insightful, Seattle, Washington). We choose to estimate the model using Bayesian methods because posterior distributions easily allowed for sampling of survival times in our seedling bank simulation below. We report the parameter estimates, odds ratio, and accelerated time interpretations of treatments. The accelerated time interpretation is the factor by which time is accelerated by a treatment or an increase in a covariate.

## Seedling height growth

We analyzed the relative growth rate (RGR) for seedling height using a mixed linear model. The RGR for surviving seedlings was calculated as:

$$\text{RGR} = \frac{\log(H_T) - \log(H_0)}{T}$$

where  $H_T$  was the height of the seedling in the August 1999 census,  $H_0$  was the initial height of the seedling, and  $T$  was the elapsed time in days. Within each quadrat, a mean RGR was calculated across surviving seedlings of each species. A linear mixed model was fit to the mean RGRs with plots considered random. RGR data were necessarily unbalanced because mortality differed among plots and treatments, but the model fitting procedure was robust to unbalanced data (Pinheiro and Bates 2000). We tested differences among species RGRs within treatments by constructing contrasts (Steel et al. 1997).

We examined differences in light levels (i.e., GSF values) between overstory and understory environments using a mixed effects, linear model. The Box-Cox method indicated that neither a transformation of GSF nor RGR was required to normalize these data (Weisberg 1985).

## Seedling bank composition

We combined the differential effects of treatments on seedling emergence and survival to estimate the expected composition of the seedling bank. We made the simplifying assumptions that microsites represented by our treatments were equally abundant and that only a single seedling could occupy each regeneration site, i.e., quadrat. We initially assumed that seeds of each species were equally abundant and equally likely to reach a given microsite, but we relaxed this assumption in a second computation of seedling bank composition where seed abundance was made proportional to the fecundity of each species (in the ratio of 1:14:134 for *Q. rubrum*, *A. rubrum*, and *L. tulipifera*; Clark et al. 1998; Beckage et al. 2000). We estimated the expected seedling bank composition using the following algorithm: a seed of one species was randomly selected to occupy a regeneration site. The seed to seedling transition was simulated as a Bernoulli trial with the seed to seedling transition probability selected from the appropriate posterior distribution estimated from our 1999 empirical data. If no seedling was produced, then another seed was chosen at random and the process was repeated until a seedling occupied the regeneration site. The life of the seedling was projected from the fitted survival model. Once the seedling occupying a particular site died, this entire series of steps was repeated. We iterated this process for a large number of time steps (e.g., 1,000) to estimate the expected seedling bank composition.

## Results

Light levels were 4.7% (SE=1.2) higher in gaps than beneath closed canopy ( $P=0.003$ ). The understory shrub *R. maximum* lowered understory light levels by 5.3% (SE=1.8;  $P=0.017$ ) but there was no interaction between *R. maximum* and gaps ( $P=0.068$ ).

## Seedling emergence

*Quercus rubra* had the highest seedling emergence rate (16.8%) followed by *A. rubrum* (11.0%), and *L. tulipifera* (0.9%) (Table 1,  $P \leq 0.05$ ). Overall seedling emergence was 2.1, 3.3, and 2.9 times higher within exclosures relative to controls for *A. rubrum*, *L. tulipifera*, and *Q. rubra*, respectively, although the main Protection effect was significant only for *A. rubrum*, and *L. tulipifera* ( $P \leq 0.05$ ). Gaps did not directly affect seedling emergence of *A. rubrum*, *L. tulipifera*, or *Q. rubra* nor was there an interaction between gaps and predation ( $P > 0.05$ ). Leaf litter increased seedling emergence of *Q. rubra* ( $P \leq 0.05$ ), had no effect on *L. tulipifera* ( $P > 0.05$ ), and decreased emergence of *A. rubrum* ( $P \leq 0.05$ ). The effect of leaf litter on *A. rubrum*, however, depended on exposure to predators ( $P \leq 0.05$ ): seedling emergence was increased by litter removal if predators were excluded but was decreased otherwise, suggesting that litter makes seeds more difficult for predators to locate but also less likely to reach mineral soil to become established. *L. tulipifera* displayed a similar trend, although not statistically significant. The understory shrub *R. maximum* increased emergence of *L. tulipifera* ( $P \leq 0.05$ ) but its effect on *Q. rubra* and *A. rubrum* also depended on exposure to predators ( $P \leq 0.05$ ); seedling emergence was greater beneath *R. maximum* if predators were excluded, but was reduced beneath *R. maximum* if exposed to predators. The effect of exposure to predators on seedling emergence also depended on elevation for *L. tulipifera* and *Q. rubrum* ( $P \leq 0.05$ ). *L. tulipifera* emergence was greater at the lower elevation site in control plots ( $P \leq 0.05$ ) but was equivalent at both elevations when protected from predation ( $P > 0.05$ ), suggesting that greater predation intensity may have led to lowered abundance of *L. tulipifera* observed at higher elevations. In contrast, *Q. rubra* emergence was the same at both elevations when exposed to predators ( $P > 0.05$ ), but was 2.5 times greater at the high elevation site when protected from predators ( $P \leq 0.05$ ). This result also suggests that predation intensity is greater at the high elevation site.

Seedling emergence varied greatly across years (Fig. 1). *Q. rubra* was the only species to germinate in 1998 (*A. rubrum* seeds set out in 1998 actually emerged in 1999, see Materials and methods) and had the highest emergence rates in 1999. *A. rubrum* had higher emergence probabilities than *Q. rubra* in 1997. The large year effects, which were greater than or equal to treatment effects, and the high variance of the year random effect

**Table 1** Estimates of treatment effects on seedling emergence for *A. rubrum*, *L. tulipifera*, and *Q. rubra*

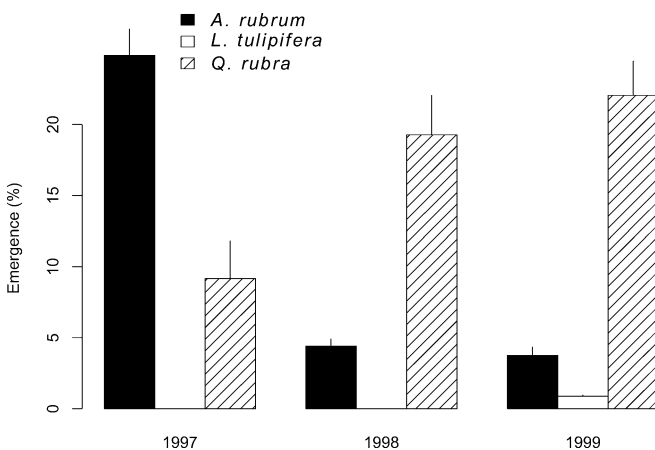
Parameter	<i>A. rubrum</i>		<i>L. tulipifera</i>		<i>Q. rubra</i>	
	Mean	Odds ratio	Mean	Odds ratio	Mean	Odds ratio
Intercept	-2.75 <sup>a</sup>	–	-5.55 <sup>a</sup>	–	-3.14 <sup>a</sup>	–
1997	1.50	4.50	–	–	-0.48	0.62
1998	-0.56	0.57	–	–	0.45	1.57
1999	-0.73	0.48	–	–	0.65	1.92
Litter	-0.39 <sup>a</sup>	0.68	-0.16	0.86	1.09 <sup>a</sup>	2.97
Protection	0.79 <sup>a</sup>	2.19	1.36 <sup>a</sup>	3.90	0.29	1.34
Protection:Elevation	0.14	1.15	0.88 <sup>a</sup>	2.41	1.19 <sup>a</sup>	3.29
Protection:Litter	-0.45 <sup>a</sup>	0.64	-0.38	0.69	-0.45	0.64
Overstory	0.16	1.17	-0.55	0.58	-0.53	0.59
Overstory:Protection	-0.07	0.93	0.20	1.22	0.27	1.31
Overstory:Litter	-0.20	0.82	0.04	1.04	0.21	1.24
Overstory:Understory	-0.02	0.98	0.08	1.08	0.31	1.37
Elevation	0.04	1.04	-0.76 <sup>a</sup>	0.47	0.38	1.47
Understory	-0.52 <sup>a</sup>	0.60	0.78	2.18	-0.45	0.64
Understory:Protection	0.62 <sup>a</sup>	1.87	-0.58	0.56	0.95 <sup>a</sup>	2.59
Understory:Litter	-0.01	0.99	0.31	1.37	-0.30	0.74
Variance across years	6.11	–	–	–	3.23	–

Protection estimates the effect of exclosures, Elevation estimates the effect of high elevation, Overstory estimates the effect of gaps, and Understory estimates the effect of *R. maximum*.

<sup>a</sup>Bayesian  $P \leq 0.05$ . The odds ratio is the ratio of the odds of a seedling emerging with a particular treatment versus without it.

(Table 1) indicate a large annual variability in the probability of successful transition from seed to seedling.

Rankings of species emergence probabilities were constant across most treatments within a year but not across years. *Q. rubra* had the highest seedling emergence rates in 15 of 16 treatments in 1999 (Fig. 2), with *A. rubrum* top ranked in the 16th treatment. *L. tulipifera* had low emergence rates across all treatment combinations. In contrast, *A. rubrum* had greater seedling emergence probabilities than *Q. rubra* in 15 of 16 microsites in 1997.



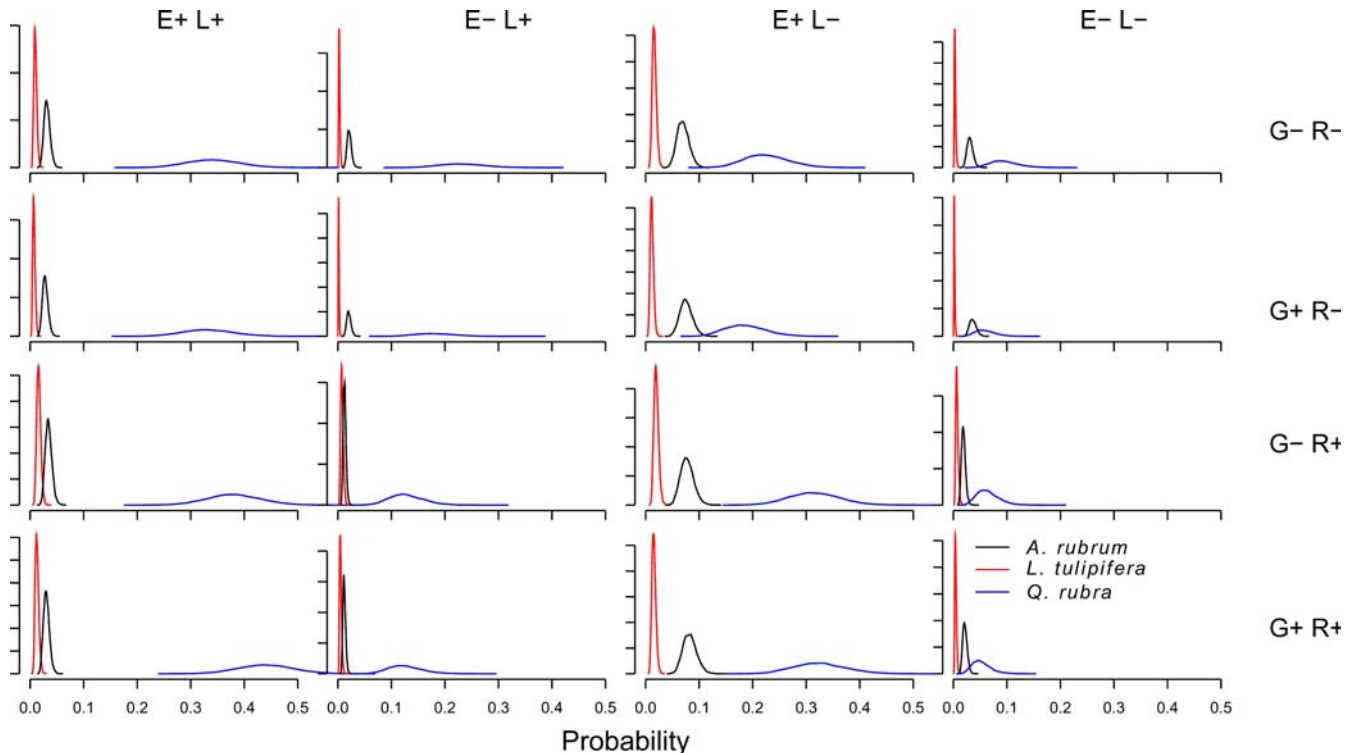
**Fig. 1** Seedling emergence in 1997, 1998, and 1999 for *A. rubrum*, *L. tulipifera*, and *Q. rubra* averaged over all other treatments (mean + SE). Annual variability in seedling emergence is underestimated because the *A. rubrum* seeds placed out in 1998 actually produced seedlings in 1999 (see [Materials and methods](#))

## Seedling survival

Seedling survival varied significantly among species (Table 2). *Q. rubra* had the highest survivorship (Fig. 3,  $P < 0.001$ ); the relative odds of a *Q. rubra* seedling surviving were approximately 11 times greater than for an *A. rubrum* seedling, whereas *A. rubrum* and *L. tulipifera* were not different ( $P = 0.65$ ). Exposure to seedling predators uniformly lowered the survival of all three species (Protection  $P = 0.01$ ; Species:Protection  $P = 0.52$ ); the odds of survival were 1.45 greater inside cages than in controls. Seedling survival was also uniformly lowered beneath closed canopy (Overstory  $P = 0.004$ ; Species:Overstory  $P = 0.42$ ); the relative odds of survival were 0.64 times less beneath closed canopy compared to gaps. *R. maximum* decreased seedling survival ( $P = 0.051$ ); the odds of seedling survival beneath *R. maximum* were 0.23 compared to areas lacking the shrub. A Species:Understory interaction ( $P < 0.001$ ) decreased *Q. rubra* survival beneath *R. maximum* and an Overstory:Understory interaction ( $P < 0.001$ ) reduced the survival of all three species beneath closed canopy in areas with *R. maximum*.

Spatial variability in seedling survival across plots was large with individual plot effects ranging from -1.67 to 0.93 (Table 2). The random effects were of the same magnitude as treatment effects, indicating substantial unaccounted for variability in seedling survival.

The species ranking of seedling survival did not change across treatments (Fig. 3). *Q. rubra* had the highest survival in six of the eight treatments. In the remaining two treatments, *Q. rubra*'s survival was not different from *L. tulipifera*'s but surpassed that of *A. rubrum* (log rank tests,  $P \leq 0.05$ ).



**Fig. 2** The posterior probability of a seed surviving to produce a seedling for *A. rubrum*, *L. tulipifera*, and *Q. rubra* under all 16 treatment combinations in the seed predation experiment (data for 1999). *Q. rubra* had the highest probability of seeds transitioning to seedlings in 15 of the 16 treatments. *A. rubrum* had the highest transition probability under conditions of closed canopy with

*R. maximum* present (i.e., G- R+). See [Materials and methods](#) for a description of how these probabilities were calculated. E+ Exclosure; E- no exclosure; L+ leaf litter present; L- leaf litter absent; G+ canopy gap; G- closed canopy; R+ understory shrub *R. maximum* present; R- understory shrub *R. maximum* absent

### Seedling height growth

Seedling RGRs for height varied greatly across species (Fig. 4,  $P < 0.001$ ), but there was neither a main effect of canopy gaps ( $P = 0.91$ ) nor predation ( $P = 0.30$ ) on seedling RGR. *L. tulipifera* had RGRs as much as 300% greater than *Q. rubra* and 379% greater than *A. rubrum*. *R. maximum* reduced growth rates through a Species:Understory interaction ( $P = 0.005$ ) that reduced *L. tulipifera*'s growth beneath *R. maximum* ( $P = 0.016$ ). However, *L. tulipifera*'s RGR was greater than that of *A. rubrum* and *Q. rubra* species in six of eight microsites, including all non-*R. maximum* treatments and gap treatments that contained *R. maximum* (Fig. 4,  $P \leq 0.05$ ).

### Seedling bank composition

When species were assumed to have equal fecundity, *Q. rubra* captured 90% of the regeneration sites, on average, while *A. rubrum* captured 8%, and *L. tulipifera* captured 2% of the sites. *L. tulipifera* had an approximately 1% probability of capturing no regeneration sites. When we considered differences in species fecundity, the relative abundance of species shifted dramatically: *L. tulipifera* captured 62% of the

regeneration sites, while *A. rubrum* captured 21% and *Q. rubra* captured 17% of the sites. No species were associated with particular treatments in either simulation, implying that regeneration niches do not contribute to the coexistence of these three species. Differential fecundity did offset differences in seedling performance, however, leading to a more diverse seedling bank.

### Discussion

We found little evidence that seed or seedling predation interacted with canopy gaps, understory shrubs, or leaf litter to promote the coexistence of *A. rubrum*, *L. tulipifera*, and *Q. rubra*. Species performance as measured by survival, growth, or emergence showed little tendency to change rank across treatments, allowing a single species to dominate all microsites. *Q. rubra* seedlings had consistently higher emergence probabilities than *A. rubrum* and *L. tulipifera* across treatments. Any seed caching by small mammals would be unlikely to qualitatively change this result because the species most likely to be cached by small mammals, *Q. rubra* (e.g., Steele and Smallwood 1994), already had the highest transition probabilities of the three study species and these probabilities would only

**Table 2** Parameter estimates for seedling survival model

	Value	SE	Bayesian <i>P</i> value	Odds ratio	Accelerated time
Intercept	6.69	0.29	< 0.001	NA	NA
Species: <i>L. tulipifera</i>	-0.05	0.12	0.65	0.93	1.05
Species: <i>Q. rubra</i>	1.73	0.17	< 0.001	10.81	0.18
Understory	-1.07	0.52	0.051	0.23	2.91
Protection	0.25	0.09	0.01	1.41	0.78
Overstory	-0.32	0.11	0.004	0.64	1.38
<i>L. tulipifera</i> :Understory	0.13	0.17	0.46	1.20	0.88
<i>Q. rubra</i> :Understory	-0.93	0.20	< 0.001	0.28	2.54
Overstory:Understory	-0.65	0.17	< 0.001	0.41	1.91
Random effects					
Plot 1	0.48	0.297	0.115	1.94	0.62
Plot 2	0.22	0.305	0.562	1.35	0.80
Plot 3	0.32	0.298	0.284	1.56	0.72
Plot 4	0.77	0.401	0.016	2.89	0.46
Plot 5	0.93	0.398	0.007	3.58	0.40
Plot 6	0.44	0.397	0.158	1.82	0.65
Plot 7	-0.37	0.309	0.242	0.60	1.45
Plot 8	-0.17	0.306	0.568	0.79	1.18
Plot 9	-0.54	0.306	0.134	0.48	1.71
Plot 10	-1.67	0.429	< 0.001	0.10	5.32
Plot 11	-1.36	0.430	0.002	0.15	3.89
Plot 12	0.38	0.401	0.303	1.68	0.69
Random effect variance	0.89	0.50			

The odds ratio compares the odds of mortality of a seedling with a particular treatment versus without it or for a 1-unit increase in a continuous covariate. The accelerated time interpretations reflect the amount by which time is increased by a factor variable or 1-unit increase in a covariate; accelerated time is associated with increased mortality.

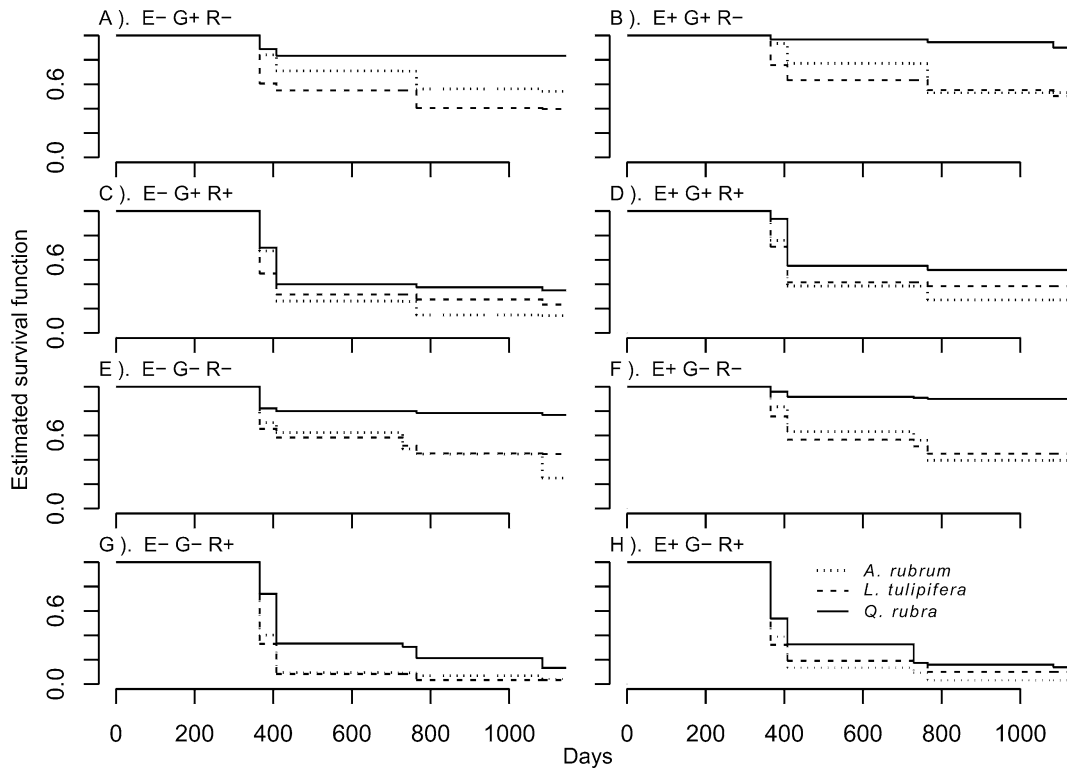
The Protection factor estimates the effect of exclosures, the Overstory factor estimates the effect of closed canopy, and the Understory factor estimates the effect of *R. maximum*.

be increased by caching. *Q. rubra* seedlings also had higher survival than *A. rubrum* and *L. tulipifera* across treatments (Fig. 3), while *L. tulipifera* had higher RGRs (Fig. 4). Predation decreased seedling emergence and survival but did not affect seedling growth, implying that predators kill seedlings rather than simply graze them. This is an important distinction as predation promotes species diversity by creating empty space that is available for subsequent colonization while herbivory alters competitive hierarchies among species (Hulme 1996). For predation to contribute to the diversity of tree recruitment, predators must show a preference toward the superior competitor (e.g., large-seeded species) or predator preferences must vary with microsite conditions. Our study failed to find evidence for either of these mechanisms, suggesting that differential predation of seeds or seedlings does not contribute to seedling bank diversity in our study system. Rey et al. (2002) also found little variation in predator seed preferences across habitats in sites that coincided with lowered plant diversity. In addition, they found that rodents displayed no preference for larger-seeded species, while ants actually preferred smaller-seeded species. In an extensive survey of seed predation with respect to size, Moles et al. (2003) also found no apparent relationship between seed size and predation rate. Fine et al. (2004), however, found that differential herbivory of tree seedlings in adjacent habitats contributed to different species guilds across sites (beta diversity) but they did not claim that her-

bivory contributed to species diversity patterns within habitats (alpha diversity).

We did find evidence of large annual variation in recruitment processes that may contribute to the maintenance of species diversity. Species rankings of seedling emergence were constant across microsites within a single year, but changed dramatically across years. Other studies of tree recruitment have also found evidence of large annual variability in seedling survival compared to spatial variability (Schupp 1990; Beckage 2000), implying that temporal variability may be more important to species coexistence than spatial variability. Observed annual variability in recruitment processes is likely driven both by environmental conditions as well as fluctuations in seed production and predation intensity (Schupp 1990). Annual seed production can vary greatly across years within a tree species and these fluctuations are unlikely to be strongly correlated across species (Clark et al. 1998; Abrahamson and Layne 2003). Populations of small mammals, which were the likely seed and seedling predators in our study, also show large annual fluctuations in density that affect tree recruitment (Ostfeld and Canham 1993). Temporal variability in recruitment processes together with the timing of gap formation may determine which species will capture gaps, rather than static, competitive relationship between species (e.g., Runkle 1989). The large annual variability in recruitment processes that is uncorrelated across species, together with the long life of tree species can provide a temporal buffer or storage effect that





**Fig. 3** Survival of *A. rubrum*, *L. tulipifera*, and *Q. rubra* seedlings across all eight treatments in the seedling predation experiment. *Q. rubra* seedlings had higher survivorship than either *A. rubrum* or *L. tulipifera* across all treatments. *Q. rubra* is significantly different (log rank tests,  $P \leq 0.05$ ) from *A. rubrum* and *L. tulipifera* in A, B,

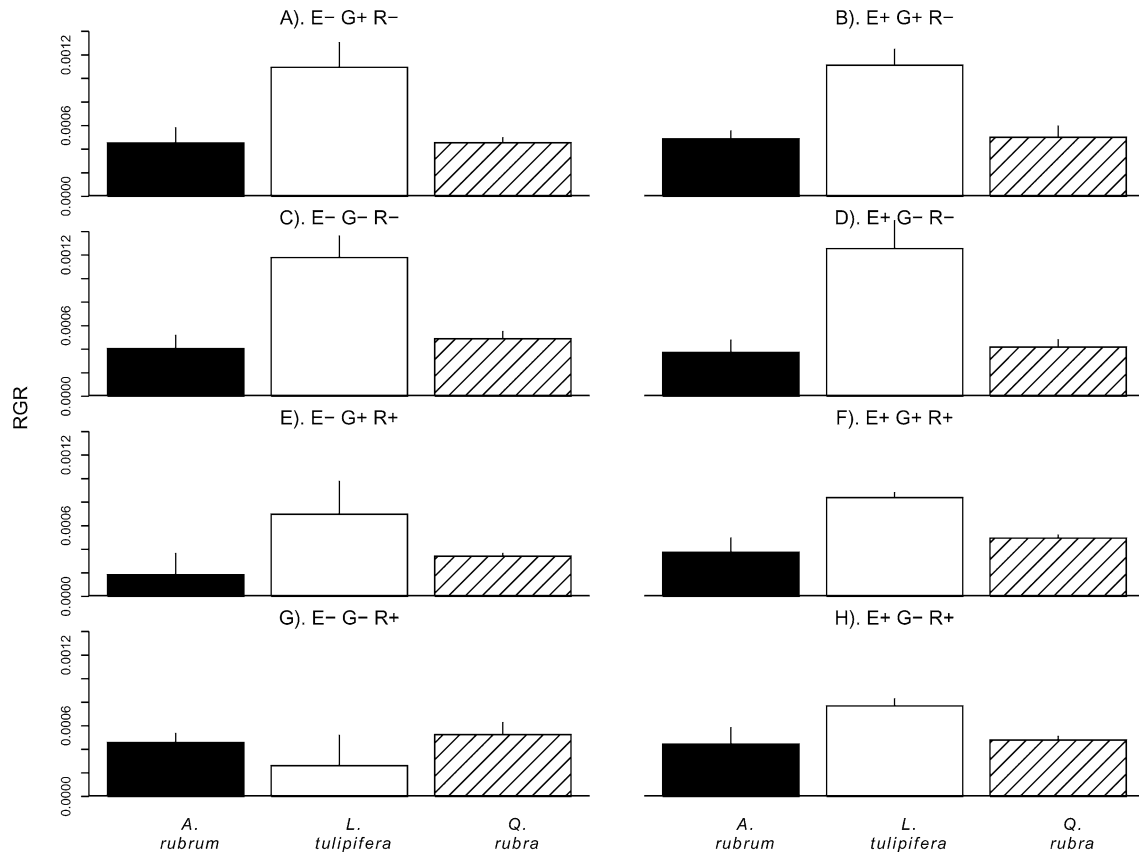
D, E, F, and G. *Q. rubra* is significantly different from *A. rubrum* in C and H but not from *L. tulipifera*. The survival functions are nonparametric Kaplan-Meier estimates. Treatment codes are defined in Fig. 2

promotes species diversity. A given tree species can persist through periods of low recruitment, when years of high fecundity or survivorship do not coincide with gap formation, until these events occur simultaneously to maintain a non-negative long-term population growth rate (Chesson and Warner 1981; Warner and Chesson 1985; Kelly and Bowler 2002).

We found evidence that life-history tradeoffs may also contribute to the diversity of tree regeneration. Our estimate of expected seedling bank composition showed that a tradeoff between tree fecundity and seedling emergence and survival resulted in a more equitable relative abundance of species. When we did not account for differential fecundity, the result was a seedling bank dominated by *Q. rubra* with *L. tulipifera* seedlings expected to be absent in 1% of years. This was because *Q. rubra* had consistently high emergence and survival across microsites, which may stem from a competitive advantage due to its large seed size relative to the other study species (364 compared to 40 mg and 33 mg for *L. tulipifera* and *A. rubrum*, respectively). A larger seed size, however, comes at the cost of lowered fecundity, resulting in fewer seeds to compete for regeneration sites (Guo et al. 2000). The incorporation of the tradeoff between seed size and fecundity into our estimates of seedling bank composition, i.e., by considering differential species fecundity, resulted in more diverse seedling

regeneration with all three species capturing a sizable portion of regeneration sites. We also note that *L. tulipifera* had the lowest survivorship but also the maximal growth rate in favorable microsites, consistent with a tradeoff between seedling survivorship and maximal growth, widely observed in empirical studies, and proposed as a principle axis of niche differentiation for forest trees (Pacala et al. 1996; Hubbell 2001). This tradeoff could also contribute to tree coexistence as surviving seedlings of *L. tulipifera* would be more likely to capture canopy gaps and a position in the forest overstory. More generally, tradeoffs between survival in low light and growth in high light, and between species fecundity and seedling performance may provide the basis for fitness invariance of species and neutral dynamics (Hubbell 2001). Finally, we point out that annual fluctuations in fecundity that are uncorrelated across tree species, or the directed dispersal of tree seeds to particular microsites by animal vectors might also promote seedling bank diversity. We would not expect preferential dispersal to particular microsites for *A. rubrum* or *L. tulipifera*, however, since they are primarily wind-dispersed, but active caching of *Q. rubra* acorns by small mammals could potentially result in directed dispersal.

Canopy gaps are thought to play a central role in promoting tree regeneration and diversity by providing



**Fig. 4** Relative growth rates (*RGR*) of *A. rubrum*, *L. tulipifera*, and *Q. rubra* seedlings across all eight treatments in the seedling predation experiment (mean + SE). *L. tulipifera* had higher *RGR*s than either *A. rubrum* or *Q. rubra* in all treatments except that of

*G. L. tulipifera* is significantly different ( $P \leq 0.05$ ) from *A. rubrum* and *Q. rubra* in the treatments that either lacked the understory shrub *R. maximum* or had canopy gaps (i.e., *A–F*). Treatment codes are defined in Fig. 2

transient increases in light that many species require to reach the canopy (Pickett and White 1985; Platt and Strong 1989). Previous studies of seed predation in gaps have produced mixed results with predation both reduced (Boman and Casper 1995) and increased in canopy gaps (Webb and Willson 1985). In our study, canopy gaps increased seedling survivorship, but had little effect on predation intensity, seedling emergence, or growth. The failure of seedlings to respond more broadly to gap formation may be related to the characteristics of our canopy gaps. Our gaps were intermediate in size and contained standing dead trees (Beckage et al. 2000), which may have limited increases in the understory light environment. Light levels in our canopy gaps increased by 4.7% compared to a 7.3% increase in natural windthrow gaps (Beckage and Clark 2003). This limited increase in light levels is consistent with observed increases in seedling survival, rather than growth, as seedling survival is a more sensitive indicator of light environment (Kobe et al. 1995; Chen 1997). However, gaps of this size and nature predominate in this region of the southern Appalachians (Clinton et al. 1993; Beckage et al. 2000) and have been postulated to maintain the high tree diversity of the region (Barden 1979, 1980; Runkle 1981). Neither our current study nor our previous studies support the efficacy of the ‘small gap’ para-

digm (Beckage et al. 2000; Beckage and Clark 2003). Larger canopy gaps, however, may contribute to the maintenance of tree diversity.

We found evidence of interactive and often contradictory microsite effects on seedling regeneration. The understory shrub *R. maximum*, for example, had a larger impact on seedling dynamics than did canopy gaps, but the effects were contradictory across seedling life-history stages (Schupp 1995). *R. maximum* increased seedling emergence of *L. tulipifera*, perhaps because of increased moisture beneath its deep shade (see De Steven 1991), but strongly decreased seedling survival and growth, likely due to reduced light levels beneath *R. maximum* (Lei et al. 2002). Seedling emergence of *A. rubrum* and *Q. rubra* increased beneath *R. maximum* but only in predator exclosures, suggesting that *R. maximum* is associated with increased predation risk for these two species, which is also consistent with observations of others (Lei et al. 2002). The herbaceous layer beneath *R. maximum* is virtually nonexistent and may increase the findability of seeds by predators, so that the shade that increases seedling emergence also increases predation and lowers seedling survival and growth. Leaf litter also had contrasting effects on seedling emergence. *A. rubrum*'s emergence was enhanced by mineral soil but litter removal also

resulted in increased losses to predators, consistent with studies finding that leaf litter lowers predation risk (Myster and Pickett 1993; Cintra 1997). *Q. rubra*'s emergence was increased by litter even with predators excluded—suggesting that litter had a positive effect other than decreasing seed findability by predators, perhaps by maintaining higher moisture levels (Molofsky and Augspurger 1992). Garcia et al. (2002) found that treatments that maintained moisture levels of *Q. rubra* resulted in increased germination rates, possibly leading to the increased emergence we observed beneath both litter and *R. maximum*. These results demonstrate the difficulty in deriving a mechanistic understanding of regeneration processes without considering the multiple processes that affect recruitment success (Houle 1995; Schupp 1995; Schupp and Fuentes 1995).

## Conclusions

We found little evidence that seed or seedling predation contributed to seedling diversity or to the coexistence of *A. rubrum*, *L. tulipifera*, and *Q. rubra*. Differential exposure to predators affected seedling emergence, survival, and growth, but species rankings were constant across heterogeneous microsites. Species rankings of seedling emergence changed markedly across years, however, suggesting that annual variability in recruitment processes is an important contributor to species coexistence. Estimated seedling bank composition that only incorporated differential seedling emergence and survival probabilities across microsites resulted in a seedling bank dominated by a single species. The inclusion of species-specific fecundities, however, resulted in more equitable interspecific competition for regeneration sites and a more diverse seedling bank, illustrating the potential importance of a tradeoff between fecundity and seedling performance.

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## References

- Abbott HG (1974) Some characteristics of fruitfulness and seed germination in red maple. *Tree Plant Notes* 25:25–27
- Abe M, Miguchi H, Nakashizuka T (2001) An interactive effect of simultaneous death of dwarf bamboo, canopy gap, and predatory rodents on beech regeneration. *Oecologia* 127:281–286
- Abrahamson WG, JN Layne (2003) Long-term patterns of acorn production for five oak species in Xeric Florida Uplands. *Ecology* 84:2476–2492
- Baker TT, Van Lear DH (1998) Relations between density of rhododendron thickets and diversity of riparian forests. *Forest Ecol Manag* 109:21–32
- Barden LS (1979) Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the Southern Appalachians, Tennessee. *Oecologia* 44:141–142
- Barden LS (1980) Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* 35:16–19
- Beckage B (2000) A long-term study of Red Maple (*Acer rubrum* L.) in Southern Appalachian forests: the effects of canopy gaps and shrub understories. Masters thesis, Duke University
- Beckage B, Clark JS (2003) Seedling survival and growth of three southern Appalachian forest tree species: the role of spatial heterogeneity. *Ecology* 84:1849–1861
- Beckage B, Clark JS, Clinton BD, Haines BL (2000) A long-term study of tree seedling recruitment in Southern Appalachian forests: the effects of canopy gaps and shrub understories. *Can J Forest Res* 30:1617–1631
- Boman JS, Casper BB (1995) Differential postdispersal seed predation in disturbed and intact temperate forest. *Am Midland Nat* 134:107–116
- Bonfil C (1998) The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). *Am J Bot* 85:79–87
- Bonito GM, Coleman DC, Haines BL, Cabrera ML (2003) Can nitrogen budgets explain differences in soil nitrogen mineralization rates of forest stands along an elevation gradient? *Forest Ecol Manag* 176:563–574
- Buckner CA, Shure DJ (1985) The response of *Peromyscus* to forest opening size in the southern Appalachian mountains. *J Mammal* 66:299–307
- Burns RM, Honkala BH (1990) *Silvics of North America*, vol 2. Hardwoods, USDA, Washington
- Caswell H (1978) Predator-mediated coexistence: a non equilibrium model. *Am Nat* 112:127–154
- Chen HYH (1997) Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. *Can J Forest Res* 27:1383–1393
- Chesson PL, Warner RR (1981) Environmental variability promotes coexistence in lottery competitive systems. *Am Nat* 117:923–943
- Cintra R (1997) Leaf litter effects on seed and seedling predation of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in Amazonian forest. *J Trop Ecol* 13:709–725
- Clark JS, Macklin E, Wood L (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecol Monogr* 68:213–235
- Clinton BD, Boring LR, Swank WT (1993) Canopy gap characteristics and drought influences of the Coweeta basin. *Ecology* 74:1551–1558
- Condit R, Hubbell SP, Foster RB (1992) Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *Am Nat* 140:261–286
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) *Dynamics of populations*. Centre for Agricultural Publication and Documentation, Wageningen, pp 298–312
- De Steven D (1991) Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. *Ecology* 72:1066–1075
- Farmer RE, Cunningham M (1981) Seed dormancy of red maple in east Tennessee. *Forest Sci* 27:446–448
- Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in Amazonia forests. *Science* 305:663–665
- Foster SA, Janson CH (1985) The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66:773–780
- Garcia D, Banuelos MJ, Houle G (2002) Differential effects of acorn burial and litter cover on *Quercus rubra* recruitment at the limit of its range in eastern North America. *Can J Bot* 80:1115–1120

- Gelman A, Carlin JB, Stern HS, Rubin DB (1995) Bayesian data analysis. Chapman and Hall, New York, p 526
- Gilks WR, Richardson S, Spiegelhalter DJ (1996) Markov chain Monte Carlo in practice. Chapman and Hall, New York, p 486
- Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52:107–145
- Guo Q, Brown JH, Valone TJ, Kachman SD (2000) Constraints of seed size on plant distribution and abundance. *Ecology* 81:2149–2155
- Hansen R (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81:1120–1132
- Houle G (1995) Seed dispersal and seedling recruitment: the missing link(s). *Ecoscience* 2:238–244
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton
- Hulme PE (1996) Herbivory, plant regeneration, and species co-existences. *J Ecol* 84:609–615
- Huston M (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Great Britain
- Janzen DH (1971) Seed predation by animals. *Annu Rev Ecol Syst* 2:465–492
- Jordano P, Herrera CM (1995) Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* 2:230–237
- Kelly CK, Bowler MG (2002) Coexistence and relative abundance in forest trees. *Nature* 417:437–440
- Klein JP, Moeschberger ML (1999) Survival Analysis, Techniques for Censored and Truncated Data. Springer, Berlin Heidelberg New York
- Kobe RK, Pacala SW, Silander JA Jr, Canham CD (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecol Appl* 5:517–532
- Lei TT, Semones SW, Walker JF, Clinton BD, Nilsen ET (2002) Effects of *Rhododendron maximum* thickets on tree seed dispersal, seedling morphology, and survivorship. *Int J Plant Sci* 163(6):991–1000
- Manson RH, Stiles EW (1998) Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos* 82:37–50
- Moles A, Warton DI, Westoby M (2003) Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology* 84:3148–3161
- Molofsky J, Augspurger CK (1992) The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73:68–77
- Myster RW, Pickett STA (1993) Effects of litter, distance, density, and vegetation patch type on postdispersal tree seed predation in old fields. *Oikos* 66:381–388
- Ostfeld RS, Canham CD (1993) Effects of meadow vole population density on tree seedling survival in old fields. *Ecology* 74:1792–1801
- Ostfeld RS, Manson RH, Canham CD (1997) Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78:1531–1542
- Pacala SW, Crawley MJ (1992) Herbivores and plant diversity. *Am Nat* 140:243–260
- Pacala SW, Canham CD, Saponara J, Silander JA Jr, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis, and dynamics. *Ecol Monogr* 66:1–43
- Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic, Orlando
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and Splus. Springer, Berlin Heidelberg New York, p 528
- Platt WJ, Strong DR (1989) Gaps in forest ecology. *Ecology* 70:535
- Plucinski KE, Hunter ML (2001) Spatial and temporal patterns of seed predation on three tree species in an oak-pine forest. *Ecography* 24:309–317
- Rey PJ, Garrido JL, Alcantara JM, Ramirez JM, Aguilera A, Garcia L, Manzaneda AJ, Fernandez R (2002) Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. *Funct Ecol* 16:773–781
- Rich PM (1989) A manual for analysis of hemispherical canopy photography. Los Alamos National Laboratory Report, LA-11733-M
- Runkle JR (1981) Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041–1051
- Runkle JR (1989) Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70:546–547
- Schupp EW (1990) Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. *Ecology* 71:504–515
- Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am J Bot* 82:399–409
- Schupp EW, Fuentes M (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2:267–275
- Schupp EW, Howe HF, Augspurger CK, Levey DJ (1989) Arrival and survival in tropical treefall gaps. *Ecology* 70:562–564
- Steel RGD, Torrie JH, Dickey DA (1997) Principles and procedures of statistics, a biometrical approach, 3rd edn. McGraw-Hill, New York
- Steele M, Smallwood P (1994) What are squirrels hiding? *Nat Hist* 10:40–45
- Swank WT, Crossley DA (1988) Introduction and Site Description. In: Swank WT, Crossley DA (eds) Forest hydrology and ecology at Coweeta. Springer, Berlin Heidelberg New York, pp 3–16
- Tanaka H (1995) Seed demography of three co-occurring Acer species in a Japanese temperate deciduous forest. *J Veget Sci* 6:887–896
- Warner RR, Chesson PL (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am Nat* 125:769–787
- Webb SL, Willson MF (1985) Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia* 67:150–153
- Weisberg S (1985) Applied linear regression. Wiley, New York
- Whitmore TC, Brown ND (1996) Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Philos Trans R Soc Lond B Biol Sci* 351:1195–1203
- Whittaker RH (1956) Vegetation of the Great Smoky Mountains. *Ecol Monogr* 26:1–80