

Importance of fragmentation-tolerant species as seed dispersers in disturbed landscapes

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Abstract Forest fragmentation can negatively affect plants if animal seed-dispersers become locally extinct in fragments. We conducted a 2-year experiment to evaluate the importance of tree squirrels (*Sciurus*) as seed dispersers for *Quercus*, *Carya*, and *Juglans*, and to assess dispersal consequences in patches where fragmentation-sensitive eastern gray squirrels (*Sciurus carolinensis*) are absent. We accounted for fates of ~15,700 seeds from five tree species in four enclosure treatments at 18 fragments during a high (2003–2004) and low seed (2004–2005) year. Two treatments excluded *Sciurus* to mimic disperser loss. We sampled nut-tree seedling density at 259 sites across eight watersheds, half of which were too fragmented to support *S. carolinensis*, but supported fragmentation-tolerant fox squirrels (*Sciurus niger*). Autumn-to-spring seed survival was low (~1%) for all species during low seed production. During high seed production, survival was higher for *Juglans nigra* (20%) and *Carya ovata* (16%) than for three *Quercus* species (~4% for *Quercus palustris* and *Quercus rubra* in two enclosure types; ~1% for *Quercus alba* in all treatments). Survival of *J. nigra*,

C. ovata, and *Q. rubra* was ≥ 2.1 –7.7 times higher for seeds in enclosures that *Sciurus* could access. Seed displacement distance was higher in the low seed than the seed-rich year, but the proportion of seeds surviving to greater distances was higher in seed-rich years for all seed types except *Q. rubra*. This affirms the importance of masting to seed survival and dispersal, but also suggests an advantage to trees of producing seed in non-mast years. Seedling densities were comparable in watersheds with and without *S. carolinensis*. These results demonstrate the importance of tree squirrels as dispersers of nut-bearing trees, but suggest that fragmentation may not disrupt dispersal of certain species if losing *S. carolinensis* from disturbed landscapes is compensated for by fragmentation-tolerant fox squirrels (*S. niger*).

Keywords *Carya* · Central hardwoods · Forest fragmentation · Masting · *Juglans*

Introduction

Many plants depend on animals to disperse to their seeds, and so conservation efforts must consider the consequences for plants whose primary seed dispersers are locally threatened or extirpated due to habitat fragmentation (Chapman and Chapman 1994; da Silva and Tabarelli 2000; Levey et al. 2002). Although many frugivores and most granivores affect trees negatively by killing seeds, a subset of consumer species provide important dispersal benefits to trees, either by failing to retrieve some scattered seed hoards, dropping seeds inadvertently or after eating the surrounding fleshy fruit, or passing viable seeds through the digestive tract

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(reviews by Howe 1986; Price and Jenkins 1986; Vander Wall 1990, 2001). These consumers can enhance seed survival and seedling establishment by: (1) removing seeds from under the parent tree where density-dependent mortality is higher (escape hypothesis; Janzen 1970; Connell 1971; Clark and Clark 1984); (2) increasing the probability that some seeds will find ephemeral suitable sites to establish (colonization hypothesis; Howe and Smallwood 1982), or (3) non-randomly placing seeds in locations favorable for seedling establishment (directed dispersal hypothesis; Howe and Smallwood 1982; Wenny 2001). Presumably then, the loss of fragmentation-sensitive animal species that provide these “services” to plants could result in a partial or total reduction in recruitment, and ultimately local extinction, for some plant species occupying the affected habitats. Understanding the potential for cascading extinctions via multi-trophic interactions has important implications for research on the effects of biodiversity on ecosystem function (Srivastava and Vellend 2005).

Whether and how the loss of animal species may affect plant recruitment should depend on the strength, specificity, type and complexity of the animal–plant interactions in question (e.g., Wright et al. 2000; Ratiarison and Forget 2005). In most cases studied, defaunation of mammal or bird communities due to habitat fragmentation reduced seed survival or seedling establishment for certain plants (Santos and Tellería 1994; Asquith et al. 1997, 1999; Cordeiro and Howe 2001, 2003). Wright et al. (2000) and Wright and Duber (2001) found that a loss of seed predators and dispersers in fragmented or poached forests increased seedling density of *Attalea* palms, but principally under the parent trees where long-term survival may have been compromised. Chapman and Chapman (2003) found lower seedling densities and richness in smaller fragments, but they also found that large-bodied frugivores such as chimpanzees and hornbills were important for dispersing seeds between forest fragments, and were probably responsible for seedlings found in fragments containing no possible parent trees. Thus, the severity of consequences for plants when a fragmentation-sensitive animal disperser is locally absent could depend on whether other, more fragmentation-tolerant species persisting in a disturbed landscape also act as seed dispersers to offset the loss of the more sensitive species.

We conducted a 2-year experiment in a highly fragmented area of the Central Hardwoods Region (CHR), USA, to evaluate the importance of tree squirrels of the genus *Sciurus* as dispersers of autumn-masting deciduous trees (oaks *Quercus*, hickories

Carya, and walnut *Juglans*), and to assess the possible consequences of forest fragmentation for tree recruitment in patches where one fragmentation-sensitive species of *Sciurus* species is absent. With about 58 species in the USA, *Quercus* is the most diverse, widespread, and arguably most important genus of North American tree (Young and Young 1992; McWilliams et al. 2002). “Upland oak” forest types constitute 43% of the entire eastern USA forest (McWilliams et al. 2002), and oak–hickory type makes up over half of all timberland in the CHR. As foundation species, oaks, and to a lesser extent hickories, influence energy and nutrient dynamics, food webs, hydrology, and biodiversity throughout the eastern deciduous forest (Johnson et al. 2002; McShea and Healy 2002; Ellison et al. 2005). Their abundance influences overwinter survival and spring breeding potential in a variety of mammals and birds (Smith and Scarlett 1987; Wolff 1996; Jones et al. 1998; Rodewald 2003), and helps to regulate both gypsy moth irruptions and Lyme disease outbreaks (Elkinton et al. 1996; Jones et al. 1998). Thus, human disturbances that cascade through systems to modify animal-mediated seed-dispersal processes for *Quercus* and *Carya* pose problems with consequences for much of North America.

Because of their feeding ecologies and broad geographic ranges (see below), eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*Sciurus niger*) are credited as the principal mammalian dispersers of *Quercus*, *Carya*, and *Juglans* in all eastern deciduous forests (reviews by Steele and Smallwood 2002; Steele et al. 2005). Other forest rodents in our study region (white-footed mice *Peromyscus leucopus*, eastern chipmunks *Tamias striatus*, southern flying squirrels *Glaucomys volans*, red squirrels *Tamiasciurus hudsonicus*) are considered mainly seed predators, but their possible roles as dispersers have not been adequately quantified. Blue jays (*Cyanocitta cristata*) are probably the only significant non-mammalian dispersers of oaks in the CHR, but jays do not utilize *Juglans* or most *Carya* species, and may not be important users of large-seeded oak species such as northern red oak (*Quercus rubra*) or bur oak (*Quercus macrocarpa*) in most years (Johnson and Webb 1989; Moore and Swihart 2006).

S. carolinensis and *S. niger* are among the most widespread mammals in the eastern USA, with *S. carolinensis* occurring throughout the entire range of eastern deciduous forest, and *S. niger* occurring in all eastern deciduous forest south and west of Pennsylvania plus the savannah–prairie habitats of the Great Plains states. These species co-occur throughout much of their ranges, including the CHR (Koprowski 1994a,

b), where they exhibit significant overlap in diet and habitat breadth (Smith and Follmer 1972; Brown and Batzli 1984; Ivan and Swihart 2000). However, *S. carolinensis* is highly sensitive to the extreme forest fragmentation characterizing much of the upper CHR, occurring only in relatively well-connected forest patches that are >4–5 ha, and only in relatively highly forested watersheds (Nupp and Swihart 2000; Moore and Swihart 2005). *S. niger*, by contrast, is tolerant of human-disturbed landscapes, moving frequently between forest fragments and occurring with equal likelihood in forest patches irrespective of patch size or isolation (Sheperd and Swihart 1995; Nupp and Swihart 2000; Moore and Swihart 2005). We recorded fates and dispersal distance of seeds placed in four types of semi-permeable exclosures across 18 different forest fragments that varied in size and rodent community composition. We also counted seedlings of *Quercus*, *Juglans*, and *Carya* in 259 forest plots to quantify relative recruitment of these tree genera at sites lacking gray squirrels. Our experiments allowed us to test the following hypotheses concerning effects of fragmentation:

1. Seeds that are removed from their source by *Sciurus* will have higher survival rates than seeds removed by other members of the rodent community.
2. Seedling recruitment in fragments lacking *S. carolinensis* will
 - a. be significantly lower than in fragments containing *S. carolinensis*, owing to the absence of this important disperser, or
 - b. not differ from fragments containing *S. carolinensis*, because the more generalist *S. niger* compensates as a seed disperser for the lack of *S. carolinensis*.

Ambient seed production varied greatly between the 2 years of our study (one bumper crop and one mast-fail year). Thus, we also were able to examine how variation in food abundance interacted with fragmentation effects, and how it affected seed fates and dispersal distances in general. Specifically, we focus on dispersal distance of seeds that survived from autumn through the following summer (ignoring distances of consumed seeds), and we focus on the total proportion of experimental seeds that survived and were dispersed to various distances from their source, rather than an average dispersal distance of surviving seeds. We will show that this latter distinction in how dispersal distance is quantified has important implications for understanding how seed-masting may affect

a seed's probability of being dispersed to greater distances (i.e., "escaping") from the parent tree.

Materials and methods

Measuring seed survival

We conducted our study in the Upper Wabash River (UWR) basin (>20,000 km²) of northern Indiana. Forest habitats, which cover only 8% of this basin, are dominated by *Quercus*, *Carya*, and *Acer* (maple), and are patchily distributed throughout a land use mosaic dominated by agriculture (corn and soybean) (Swihart and Slade 2004; Moore and Swihart 2005).

We established study plots in ten forest patches in autumn 2003, and eight patches in autumn 2004, in the Middle Wabash Little Vermillion (MWLV) watershed, one of eight major watersheds in the UWR basin. We used forest patches varying from 0.8 to 284 ha in size in an effort to sample natural variation in rodent communities, as occurrence and abundance of *Sciurus* and other rodents vary according to patch size in our region (Nupp and Swihart 2000; Moore and Swihart 2005). A study plot consisted of a 25 × 17-grid of wire-pin flags spaced at 5 m; it was thus 120 × 80 m (0.96 ha) in size. The smallest site (0.8 ha) contained a smaller grid that filled the entire forest patch. Flags were labeled by a Cartesian coordinate system (1.1, 1.2, ..., 1.17, ..., 25.17) to facilitate estimation of dispersal distances. At eight evenly spaced locations within each grid (locations 7.7, 7.11, 11.7, 11.11, 15.7, 15.11, 19.7, 19.11) we placed a semi-permeable exclosure (1 × 1-m base, wooden or rebar frame, 1.25-cm hardware cloth or chicken-wire sides) filled with seeds. The eight exclosures comprised four treatments that used different hole sizes to allow access to: (1) *P. leucopus*; (2) *P. leucopus*, *Tamias striatus*, *G. volans*, and *Tamiasciurus hudsonicus*; (3) all forest rodents, including *S. carolinensis* and *S. niger*; (4) all rodents and similar-sized consumers such as blue jays, but not larger consumers such as white-tailed deer (*Odocoileus virginianus*). Each treatment was represented by two exclosures in a grid to reduce the likelihood of having all seeds from a treatment removed by the same individuals. Exclosures were ≥20 m from each other (45 m apart for the same treatment), and 30 m from the nearest edge of a study grid. Additional details of exclosure design and construction are available elsewhere (Moore 2005; Moore et al. in review).

In late October of each year, we filled each exclosure with 50 *J. nigra* walnuts (except for treatment 1, because *P. leucopus* does not use them), 50 *C. ovata* nuts, 50 *Q. rubra* acorns, 50 *Q. palustris* acorns, and 50

Q. alba acorns (2003 only, see below). In total, we placed 31,000 seeds across all study plots, though only 29,350 were included in analysis because some exclosures were destroyed due to tree falls or flooding. We purchased most seeds for a given year's study from commercial vendors (Schumacher, Sandwich, Mass.; Sheffield's Seed, Locke, N.Y.; reported germination range 60–90%) during the previous winter and held them in cold storage until use, but we collected *Q. alba* acorns locally in autumn 2003 because white oaks are not storable. We did not use *Q. alba* in 2004 because of insufficient crop yield for collection. We used a float test to eliminate as many unsound *Q. alba* acorns as possible. We inserted a small metal tag (13–19 mm wire nail) into each seed used in the experiment. Nails were type-coded by nut species (e.g., 19-mm brad for *J. nigra*, 13-mm finishing nail for *Q. palustris*, etc.), and color-coded via spray-paint by treatment.

We placed laser-triggered cameras at roughly half of the exclosures ($n \sim 40$ exclosures) in 2003 to assess which animal species were using each treatment type. Photos ($n > 1,000$) indicated that exclosures did a good job of keeping out the intended species, and that species targeted by certain treatments actually accessed the seeds, although we never verified use of treatment 4 by blue jays.

We used metal detectors (Fisher 1225-X) to search in spring (April–June) for seeds removed from exclosures during the previous autumn. The grid of flags delineated a 24×16 -grid of quadrats; we attempted to search every other quadrat in a checkerboard fashion. Upon finding a tag, we recorded the seed type, treatment from which it came, fate (buried uneaten, unburied uneaten, eaten), and distance from source exclosure to the nearest flag from the tag. Because the number of tags found (11,439; see Results) was only a sample (39%) of those originally placed in boxes, we had to multiply the number of tags that we found by correction factors to estimate the actual number of scatter-hoarded seeds surviving to late spring, and to estimate the frequency distribution of dispersal-distances. Specifically, correction factors were necessary because: (1) not all quadrats in a grid were searched (incomplete effort over dispersal area), (2) because the search radius around a given quadrat varied from 30 to 105 m around its arc (unevenly distributed effort over dispersal area), and (3) because a pilot study, in which 13 technicians each searched a different 5×25 -m forest plot for dozens of manually placed tags (buried and unburied), revealed that the probability of detecting a metal tag in a searched quadrat varied from 0.3 to 0.92 depending on tag type and whether the tag was buried or on the surface (imperfect data). The correction factor was:

$$CF_{fibr} = 1/(q_f/4) \times 1/d_{t,b} \times l_r,$$

where q_f is the number of quadrats searched around a particular flag f (varies from 1 to 4), $d_{t,b}$ is the estimate of detectability for a given tag type t that was buried ($b = 1$) or unburied ($b = 0$), and $l_r = 1.5$ for seeds found 30–50 m from their sources, 3 for seeds found >50 m from their sources or 1 otherwise. Details and further justification for this correction factor are in Moore (2005) and Moore et al. (in review).

We used hierarchical generalized linear models (HGLMs; Raudenbush and Bryk 2002) to estimate the probability of a seed being found buried and uneaten (pBU) in spring as a function of possible predictor variables. We used the HGLM framework because we expected the fates of individual seeds to be correlated within study grids, which we treated as random effects. We specified a binomial error distribution for the response, with the number of “trials” equaling the number of seeds of given type in a given treatment at a study grid (usually 100) and the number of “events” equaling the estimated number of buried uneaten seeds on a grid from a set of trials. Seeds found uneaten but not buried [e.g., in surface larders ($n = 498$) or still in exclosures ($n = 1,954$)] were not considered events because these presumably had a much lower chance of successfully germinating and establishing seedlings (e.g., Sork 1983; Fuchs et al. 2000; García et al. 2002; Haas and Heske 2005). The total number of scatter-hoarded seeds we found intact (i.e., number of events, before applying corrections) was 1,635. We fit three model types to the data, ordered here to reflect our prior beliefs about which effects would be decreasingly important:

1. $\text{Logit}(pBU) \sim \text{year} \times \text{seed type}$.
2. $\text{Logit}(pBU) \sim \text{year} \times (\text{seed type} + \text{treatment})$.
3. $\text{Logit}(pBU) \sim \text{year} \times (\text{seed type} + \text{treatment} + \text{rodent})$.

Model 1 estimates main and interacting effects of year and seed type on pBU (buried uneaten). We expected year to be important because ambient nut production is known to affect seed survival (Sork 1993; Kelly and Sork 2002; Forget et al. 2002; Jansen et al. 2004). Model 2 additionally included an effect of treatment type that was also allowed to interact with year; we expected pBU would be lower for seeds from treatments 1 and 2 (inaccessible to *Sciurus*) than from 3 and 4 (accessible to *Sciurus*). Finally, model 3 included an effect of natural variation in rodent abundance; we were interested in whether seeds at sites with higher abundance of *S. carolinensis* (or *S. carolinensis* + *S. niger*) and lower *P. leucopus* abundance would have higher survival probabilities. Ideally we also would

have tested for effects of *Sciurus* occurrence versus absence, because just a few individual tree squirrels could potentially affect seed survival as much as many squirrels, but at least one *Sciurus* species was detected at all experimental sites except one, and *S. carolinensis* occurred at all but two sites. We coded year, seed type, and treatment as dummy variables. We indexed squirrel and mouse abundance as the number of captures per trap night, following 5 days of summer live-trapping using a 5 × 5-grid of Sherman traps spaced at 15 m and 3 × 3-grid of Tomahawk traps spaced at 30 m (see Moore and Swihart 2005). After accounting for traps disturbed (principally by raccoons *Procyon lotor*) each site received an average of 42 Tomahawk trap-days (for squirrels), 111 Sherman trap-days (for chipmunks), and 56 Sherman trap-nights (for mice).

Model selection is difficult for random effects models because parameters are estimated using methods that generate “pseudo-likelihoods”, which are not comparable across models. Therefore, we first evaluated relative support of the first two models with only fixed effects included (i.e., no random intercept across sites). For these, we used Aikake’s information criteria (AIC), corrected for overdispersion (i.e., QAIC; Burnham and Anderson 2002). There was clear support for a model containing all effects listed in model 2, but additional post-hoc model fitting was required to determine which treatments differed from each other. After selecting an appropriate fixed effects model, we used this as a starting point for a random effects model that included rodent abundance or site-characteristic indices and a random intercept (along with a scale parameter for overdispersion; McCullagh and Nelder 1999). Two rodent-effect models were evaluated; both contained an index of *P. leucopus* abundance, but one contained an index of *Sciurus* (gray + fox squirrel) abundance, whereas the other contained an index of *S. carolinensis* abundance only. The importance of rodent effects was evaluated by simple inspection of *t*-values and confidence intervals for coefficient estimates.

Seed dispersal distance

We used a two-factor multivariate ANOVA (MANOVA) to analyze the effects of year and seed type (white oak not included), and their interaction, on the proportion of experimental seeds at each site that both survived from fall to spring and were dispersed to each of five distance classes: (1) seeds left uneaten in exclosures, and seeds dispersed between (2) 0–10 m, (3) 10–20 m, (4) 20–30 m, and (5) >30 m. Width of bin-distance cutpoints was somewhat arbitrary, but we pooled all distances >30 m so that all classes contained

at least 5% of total observations. We did not test for an effect of exclosure type because this factor was not found to be important in a previous analysis of seed-removal distances (Moore 2005; Moore et al. in review). This is presumably because many tags we found were probably those that were ultimately scatterhoarded by tree squirrels, regardless of who initially removed them from exclosures. We performed a square-root arcsin transformation on proportions to make data more normal before analysis. MANOVA results were highly significant for both main effects and their interaction ($P < 0.0001$), so we then performed univariate ANOVAs to determine in which distance classes the treatments affected the response.

Seedling abundance

From summer 2001 to 2003, we inventoried both small mammals and woody plants at two hundred and fifty-nine 10 × 30-m study plots distributed across thirty-five 23-km² study “landscapes”, representing all eight major watersheds in the UWR basin (12 to sites 81 per watershed; Moore and Swihart 2005). Importantly, *S. carolinensis* did not occur in half of the sampled watersheds, and were rare (occurrence rate ≤5%) in all but the MWLV watershed (occurrence rate = 42%). At each plot, we measured diameter at breast high (DBH) of all woody stems taller than 1 m and with DBH > 5 cm. We simply counted, by species, the number of woody stems taller than 1 m and with DBH < 5 cm. For *Quercus*, *Carya*, and *Juglans*, stems of this size correspond to seedlings roughly 5–10 years in age (D. Jacobs, personal communication).

We constructed generalized linear models in SAS (proc Glimmix) to estimate the effects of gray squirrel occurrence (GRSQ = 1 if trapped at the site, zero if not detected) and total basal area of possible parent trees in a 10 × 30 m plot (mastBA; normalized) on the number of *Quercus*, *Carya*, and *Juglans* seedlings in the plot. We assumed a Poisson error distribution for stem counts, with variances scaled by χ^2/df to correct for overdispersion (McCullagh and Nelder 1999).

Results

Seed survival

In spring 2004 and 2005, we found and recorded fates for 11,439 (39%) of ~29,350 tags that we searched for. After applying correction factors, we estimate to have accounted for 15,731 tags (54%). Remaining tags were presumably larder-hoarded in trees and deep burrows,

and a small number may have been dispersed off the study grids (Sork 1984; Steele et al. 2001; J. E. M. and R. K. S., unpublished data). As expected, there was a strong annual effect on seed survival (Fig. 1, Table 1). Across all seed types and treatments, we estimated the average seed survival (proportion of total found buried and uneaten) from autumn 2003 to spring 2004 (following high autumn seed production) to be 0.08, compared with only 0.01 in the next year (following almost no seed production in autumn 2004).

Survival from autumn 2003 to spring 2004 was strongly dependent on species and treatment type (Fig. 1; Table 1). By contrast, survival from autumn 2004 to spring 2005 was uniformly low, less than 0.01 for most seed types in most treatments, although *Q. rubra* acorn survival was about 0.025 in this year overall, similar to its overall survival in the previous year. From autumn 2003 to spring 2004, seeds of

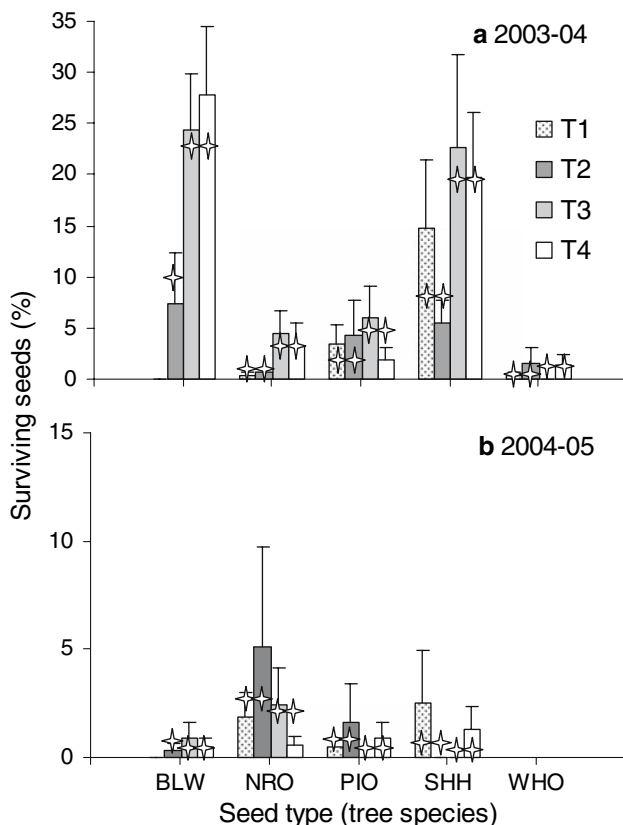


Fig. 1 Seed survival (mean percentage +1 SE) of five seed types (tree species) in four treatment exclosures (T1–T4) during **a** 2003–2004 and **b** 2004–2005. Eastern grey squirrels (*Sciurus carolinensis*) were unable to access T1 and T2 but could access T3 and T4. Stars show predicted values from hierarchical generalized linear models. Observed estimates adjusted by correction factors. See text for treatment explanations. BLW Black walnut, NRO northern red oak, PIO pin oak, SHH shagbark hickory, WHO white oak (not used in 2004–2005)

Table 1 Coefficient estimates from the best-fitting hierarchical generalized linear model of seed survival^a in 18 forest fragments of north-central Indiana, USA. BLW Black walnut, NRO northern red oak, PIO pin oak, SHH shagbark hickory, WHO white oak

| Covariate ^b | Estimate (β) | SE | <i>T</i> | <i>df</i> ^d | <i>P</i> |
|------------------------|----------------------|------|----------|------------------------|----------|
| Intercept ^c | -5.61 | 0.70 | -7.97 | 17 | <0.001 |
| Y04 | -0.66 | 0.94 | -0.71 | 299 | >0.477 |
| TSci | 0.99 | 0.24 | 4.19 | 299 | <0.001 |
| BLW | 3.36 | 0.66 | 5.09 | 299 | <0.001 |
| NRO | 1.00 | 0.75 | 1.33 | 299 | 0.19 |
| PIO | 1.61 | 0.70 | 2.29 | 299 | 0.02 |
| SHH | 3.23 | 0.66 | 4.90 | 299 | <0.001 |
| Y04 × TSci | -1.54 | 0.69 | -2.23 | 299 | 0.027 |
| Y04 × BLW | -2.00 | 1.31 | -1.53 | 299 | 0.13 |
| Y04 × NRO | 1.85 | 0.99 | 1.87 | 299 | 0.06 |
| Y04 × SHH | -1.80 | 1.16 | -1.56 | 299 | 0.12 |

^a Survival, the probability of a seed being buried and remaining uneaten from late October to May or June, is $\exp(x_i\beta)/[1 + \exp(x_i\beta)]$

^b Dummy variable coding: Y04 = 1 if 2004; TSci = 1 if treatment 3 (T3) or T4; BLW = 1 if black walnut; NRO = 1 if northern red oak, PIO = 1 if pin oak, SHH = 1 if shagbark hickory

^c Intercept is the log-odds of survival for white oak acorns from autumn 2003 to spring 2004

^d *df* for random intercept is number of sites - 1, and for fixed effects is the number of site × treatment × seed-type combinations minus the number of fixed effects in model - 1

J. nigra and *C. ovata* displayed much higher overall survival (0.20 and 0.16, respectively), than did seeds from any of the oak species. *Q. palustris* acorns, and *Q. rubra* acorns from treatments 3 and 4 (accessible by *Sciurus*), had higher survival rates (~0.04) than *Q. rubra* acorns in treatments 1 and 2 or *Q. alba* acorns (<0.01). For *Juglans*, *C. ovata*, and *Q. rubra*, survival of seeds removed from exclosures of treatments 3 and 4 was 3.6, 2.1, and 7.7 times higher, respectively, than for seeds in treatments 1 or 2 (estimated odds ratio across all five species = 2.7). Model evaluation by QAIC weights suggested that treatments 3 and 4 were effectively the same with respect to their effect on seed survival (Table 2). The lowest-QAIC model also suggested that treatments 1 and 2 were effectively the same as each other, but there was almost equal support ($\Delta\text{QAIC} = 0.3$) for a model suggesting that treatment 1 was more like treatments 3 and 4 than like 2. We view the former as the more plausible biologically, not only because of its QAIC model rank, but also because of its more sensible biological interpretation. In addition, visual inspection of the data suggests that support for the latter model was driven principally by higher survival for *C. ovata* seeds from treatment 1 in the first study year (Fig. 1).

Table 2 Model selection results for fixed-effects models of seed survival. *QAIC* Aikake’s information criteria corrected for overdispersion

| Model ^a | No. parameters | $\Delta QAIC$ | Model weight ^b |
|--|----------------|---------------|---------------------------|
| Year \times (seed type + TSci) ^c | 11 | 0.0 | 0.427 |
| Year \times (seed type + T2) ^d | 11 | 0.3 | 0.364 |
| Year \times (seed type + T1 + T2) ^e | 13 | 1.7 | 0.182 |
| Year \times (seed type + T1 + T2 + T3 + T4) ^f | 15 | 5.6 | 0.026 |
| Year \times seed type | 9 | 11.2 | 0.002 |

^a The top four models specify different forms of an enclosure-treatment effect

^b Model weights indicate the relative likelihood that a model is the “best” model (Burnham and Anderson 2002)

^c *Sciurus* effect; T1, T2 (inaccessible to *Sciurus*) differ from T3, T4 (a priori model)

^d T2 differs from T1, T3, T4 (post hoc model)

^e T1 differs from T2, both differ from T3, T4 (post hoc model)

^f All treatments differ (a prior model)

We did not find support for an effect of rodent abundance at a site on survival of experimental seeds. Consistent with our predictions, coefficient estimates indicated a positive relationship between *Sciurus* abundance and seed survival. However, the sign of coefficient for *P. leucopus* abundance was reversed for the 2 years of study, indicating an inverse (hypothesized) relationship between mouse abundance and seed survival in the first year, but a positive relationship in the second year. None of the main effects or interaction coefficients for either rodent group was statistically different from zero ($P = 0.15\text{--}0.76$).

Seed dispersal distance

Interannual differences were evident in the proportion of all experimental seeds placed in enclosures that we found subsequently as intact nuts at various distance classes from their source (Fig. 2). The distribution was less strongly skewed for the seed-poor year (2004–2005), indicating that average dispersal distance of surviving seeds was greater in this year than in 2003–2004. However, proportional survival differed by an order of magnitude between these 2 years. ANOVA analyses (following the statistically significant MANOVA) demonstrated that the proportion of total experimental seeds surviving into each distance class, with the exception of *Q. rubra* acorns, was greater for all distances in the seed-rich year (2003–2004) than in the seed-poor year (Table 3). For all five distance classes, we found significant year effects, and we found significant seed-type effects for the shortest three

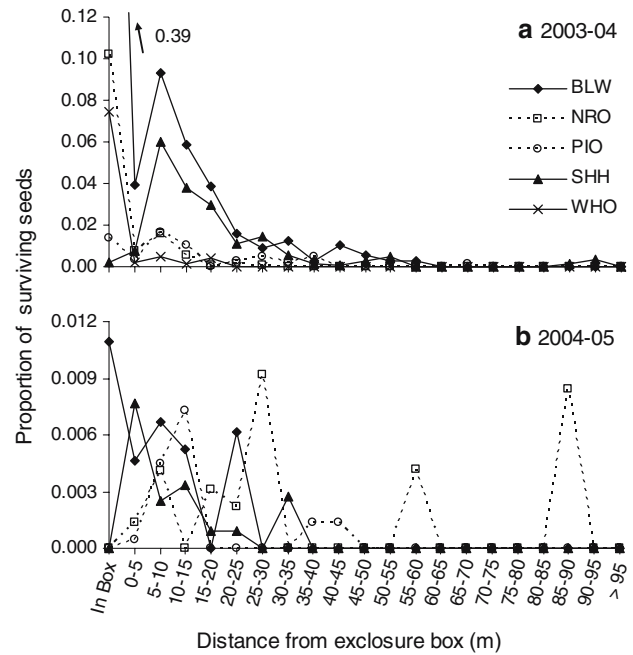


Fig. 2 Estimated proportion of seeds (across all sites) of five tree species that survived from autumn to spring and were found at various distances from source enclosure boxes in **a** 2003–2004 (high-mast year) and **b** 2004–2005 (low-mast year). WHO were not used in 2004–2005. For abbreviations see Fig. 1

distance classes. Significant interaction terms for all distance classes (marginally so for the 20–30 m class) indicated that the effect of year differed by seed type. For *Q. rubra* acorns in the 20–30 m and >30 m classes, the proportion of surviving seeds was actually greater in the seed-poor year (~1% survival in 2004–2005 vs ~0% survival in 2003–2004). For the other three seed types in this analysis, and for *Q. rubra* acorns at shorter distance classes, the proportion of seeds surviving to each distance class was greater in the seed-rich year. For all distances except the zero class (seeds not removed from enclosures), there were higher proportions of dispersed *J. nigra* and *C. ovata* nuts than *Q. palustris* or *Q. rubra* acorns. *J. nigra* and *Q. rubra* had the greatest proportion of seeds remaining in the enclosures in the seed-rich year (0.39 and 0.10, respectively).

Seedling abundance

We did not find evidence that seedling abundance at a forest site depended on gray squirrel occurrence there. In the log-linear model (Poisson GLM), coefficient estimates for *S. carolinensis* occurrence and basal area of nut-trees at sites throughout the UWR basin were not statistically different from zero ($\beta_{GRSQ} = -0.12$, $SE = 0.19$, $P = 0.50$; $\beta_{mastBA} = 0.04$, $SE = 0.06$, $P = 0.53$). A lack of relationship between basal area of

Table 3 Summary of univariate ANOVA tests, following multiple ANOVA, for proportion of experimental seeds surviving and being dispersed to one of five distance categories. Mean

proportions are for 2003–2004, and 2004–2005, respectively, within each distance class

| Distance classes | | In box ^a | 0–10 m | 10–20 m | 20–30 m | >30 m |
|------------------|-----------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|
| Source term | <i>df</i> | <i>F</i> -ratio (<i>P</i>) | <i>F</i> -ratio (<i>P</i>) | <i>F</i> -ratio (<i>P</i>) | <i>F</i> -ratio (<i>P</i>) | <i>F</i> -ratio (<i>P</i>) |
| Year | 1 | 30.4 (<0.001) | 56.20 (<0.001) | 19.52 (<0.001) | 5.25 (0.025) | 4.30 (0.042) |
| Seed type | 3 | 18.23 (<0.001) | 10.37 (<0.001) | 8.35 (<0.001) | 1.57 (0.206) | 0.70 (0.553) |
| Year × seed type | 3 | 10.77 (<0.001) | 5.48 (0.002) | 5.98 (0.001) | 2.51 (0.066) | 3.46 (0.021) |
| Error, total | 64, 71 | | | | | |
| | | Mean proportions | | | | |
| Black walnut | | 0.391, 0.011 | 0.152, 0.011 | 0.080, 0.010 | 0.025, 0.004 | 0.033, ~0.00 |
| Red oak | | 0.103, ~0.00 | 0.030, 0.005 | 0.001, 0.003 | 0.001, 0.010 | ~0.00, 0.010 |
| Pin oak | | 0.014, ~0.00 | 0.023, 0.005 | 0.008, 0.006 | 0.008, ~0.00 | 0.008, 0.005 |
| Shagbark hickory | | ~0.00, ~0.00 | 0.076, 0.018 | 0.060, 0.002 | 0.026, ~0.00 | 0.021, 0.002 |

^a In box class is for seeds that were uneaten and never left their enclosure

mature trees and seedling abundance may indicate that most tree recruitment is not occurring under parent trees, but rather is due to dispersal of seeds away from under parent crowns. Additionally, the average number of seedlings per 10 × 30-m plot was not noticeably different—certainly not greater—in watersheds containing *S. carolinensis* than in those where this species was absent (Fig. 3).

Discussion

Fragmentation and seed survival

We used semi-permeable enclosures to effectively alter the rodent community available to consume and

potentially disperse seeds, thereby mimicking possible scenarios induced by habitat fragmentation. Our primary interest with this manipulation was to contrast the relative survival rates of seeds subject to an entire suite of forest rodents versus seeds that had little chance of being scatter-hoarded by *Sciurus* (i.e., if this genus was absent from a forest remnant). Consistent with our predictions, we found that seed survival was lower when *Sciurus* was functionally absent as a seed dispersal agent. Most previous evidence that loss of certain seed consumers can have negative impacts on tree recruitment comes from the tropics (e.g., Levey et al. 2002). Our study extends this phenomenon to temperate systems and provides an additional example of how human disturbances can cascade through ecological systems to have important indirect consequences for ecosystem functioning. The differential effects we observed of rodents on seeds highlights the importance of considering individual species' "roles" in a system in management decisions (Sinclair and Byrom 2006).

Across all seed types, HGLM estimates of survival rates in treatments 1 and 2 (inaccessible to *Sciurus*) were only 0.37 that of seeds in treatments 3 and 4 (accessible to *Sciurus*) during the bumper seed year. However, we did not model an interaction between treatment and seed type, and examination of species-specific survival estimates (Fig. 1) suggests that the importance of *Sciurus* varied for different seed types. In the first year of our study (high food abundance), overall survival of *J. nigra* nuts and *Q. rubra* acorns not accessed by *Sciurus* was only 0.28 and 0.13 that of seeds that were accessible to these tree squirrels, respectively. *Q. alba* acorns, in contrast, did not benefit from *Sciurus*; survival from all treatments was uniformly low. Other studies have shown *S. carolinensis* to preferentially consume rather than cache *Q. alba* acorns,

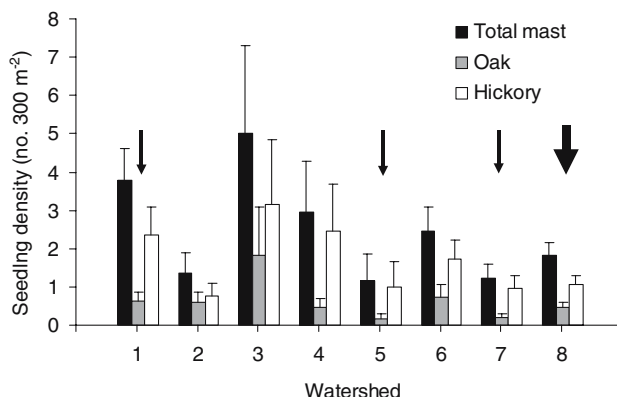


Fig. 3 Total mast (black bars), oak (gray bars) and hickory (white bars) seedling density in study plots (2001–2003) in forest patches of the eight major watersheds that constitute the Upper Wabash River basin, Indiana. Arrows indicate watersheds known to support gray squirrels [occurrence rate <5% (small arrows) or ~42% (large arrow)]. Seedlings were <5 cm diameter at breast height but >1 m tall. 1 Upper Wabash, 2 Salamonie, 3 Mississinewa, 4 Eel, 5 Middle Wabash–Deer, 6 Tippecanoe, 7 Wildcat, 8 Middle Wabash–Little Vermillion

and to excise embryos from the relatively few white oak acorns that are cached (Hadj-chikh et al. 1996; Steele et al. 2001). Thus, *Sciurus* may be important dispersers of *Juglans*, *Carya*, and *Quercus* species of the “red oak group” (subgenus *Erythrobalanus*), but less important as dispersers for *Quercus* species of the “white oak group” (subgenus *Leucobalanus*), at least in years when both food types are available in abundance.

Odds ratios in the previous paragraph probably underestimate the importance of *Sciurus*, because a certain proportion of seeds in treatments three and four probably were removed by other seed predators (e.g., mice, chipmunks, red squirrels). Thus, overall seed survival under these treatments was probably lower than for the subset of seeds in these exclosures that actually were moved by *Sciurus*. Similarly, many of the seeds we found scatter-hoarded from treatments 1 and 2 may have initially been removed from exclosures by smaller larder-hoarding rodents, and then were pilfered and re-cached by *Sciurus*. In this case, survival of seeds from treatments 1 and 2 was probably higher than if *Sciurus* was completely absent from study sites, highlighting the importance in this system of secondary dispersal processes (Chambers and MacMahon 1994; Roth and Vander Wall 2005; Vander Wall et al. 2005). *S. carolinensis* and *S. niger* are unlikely to have pilfered larders that were actively defended by red squirrels or placed in deep burrows by chipmunks, but they may have pilfered scatter-hoards or surface-larders of *P. leucopus*, or larders of *Tamiasciurus hudsonicus* that for some reason were not defended. Differential susceptibility to pilferage could explain why survival of hickory nuts from 2003 to 2004 was higher for seeds initially moved by *P. leucopus* (treatment 1) than for seeds accessible to other larder-hoarders (treatment 2) (Fig. 1; Table 2).

Although we found strong direct evidence for the importance of dispersal by *Sciurus* to seed survival, we found no important indirect effect of current fragmentation levels (via negative effect on *S. carolinensis*) on seedling recruitment in our study region. First, relative abundances of *Sciurus* and *P. leucopus* were not important predictors of seed survival at our experimental sites. Clearly, the relative abundance (or occurrence) of different rodent species should affect seed survival, so we do not interpret our model result as a lack of importance of these species. Rather, rodent abundances sampled in the spring presumably are less appropriate predictors of autumn-to-spring seed survival than rodent abundances in autumn, or sample size (number of sites) and data precision (e.g., estimation of rodent abundance) were insufficient to detect patterns

within a high degree of site-level variation in seed survival. Moreover, all of our study grids except two contained *S. carolinensis*, and all but one contained *S. carolinensis* or *S. niger*. Since relatively few individuals could be responsible for the survival rates we estimated, our experimental design may therefore not have allowed us to adequately test site-level effects of rodent abundance. Nevertheless, it seems safe to conclude that relative abundances in white-footed mice and tree squirrels at our sites were not a driving factor of observed seed survival rates at our experimental sites.

Second, seedling abundance sampled throughout the UWR basin did not differ between watersheds that contained *S. carolinensis* and those that did not. Again, this certainly does not imply that *S. carolinensis* do not play a role in seed dispersal, and we did not control for a number of factors that could have affected seedling densities in our plots, such as relative abundance of other seed or seedling consumers. Thus, detection of pattern attributed to *S. carolinensis* effects may have been difficult. However, we can conclusively state that *S. carolinensis* occurrence was not imperative for seedling recruitment; otherwise seedling densities in many watersheds would have been close to zero.

We believe, based on the results of our study, that in highly fragmented regions of eastern deciduous forests where *S. carolinensis* cannot persist, *S. niger* may be critical as dispersers of hardwood tree species, especially for those with large seeds and hard shells (e.g., *J. nigra* and *Carya*) that cannot be dispersed by blue jays. Ehrlich and Mooney (1983) distinguished the importance of individual species versus species guilds as “controllers” of ecosystems, noting that the loss of one member of a controlling guild (e.g., American chestnut *Castanea dentata* from deciduous forests of eastern USA) may be relatively inconsequential for ecosystem function. Similarly, Schwartz et al. (2000) found that within a trophic level, ecosystem function was maximized at relatively low levels of species richness. This could occur if relatively few, common species provide a vast majority of ecosystem functioning, or if multiple species provide similar functional roles (Walker et al. 1999; Schwartz et al. 2000; Srivastava and Vellend 2005). Our case study provides an example of how fragmentation-tolerant or habitat-generalist species may help stabilize important ecological functioning in highly disturbed regions where more sensitive species are declining or already have disappeared. Other studies also have pointed to the importance of “landscape generalists” that include multiple habitat patches within a home range and can thus disperse seeds to degraded areas (e.g., Kaplin and

Lambert 2002) or between patches where other disperser species no longer occur.

Of course, a loss of one species cannot always be ecologically compensated for by another. The geographic range of *S. carolinensis* extends farther north-east than does that of *S. niger*, and the two species are more ecologically distinct in other parts of their range than in the Midwestern USA (Edwards et al. 1998; Weigl et al. 1998). Thus, in the extreme northeastern limit of *S. carolinensis*' range, or in regions where *S. niger* seem to occupy more distinct niches from *S. carolinensis*, decline or local extirpation of *S. carolinensis* due to forest fragmentation or other causes could have more serious consequences for tree recruitment. Moreover, the occurrence of multiple functionally similar species may add functional resilience to a community in the face of a changing environment (Walker et al. 1999; Lyons et al. 2005). The likely importance of *S. niger* in areas where *S. carolinensis* has been lost may exemplify this very point, but simultaneously stresses the importance of managing to maintain both species where possible, along with other forest rodents that also may contribute seed-dispersal services.

Food abundance and seed dispersal

Positive relationships between annual seed abundance and per capita seed survival have been documented repeatedly (e.g., review by Kelly and Sork 2002) and provide common-sense support for predator-satiation hypotheses. A less intuitive outcome (from a dispersal-strategy perspective) is that seeds may be moved shorter distances on average in food-rich conditions (Vander Wall and Joyner 1998; Jansen et al. 2004; Roth and Vander Wall 2005; Moore et al. in review). Moreover, a higher percentage of the seed crop may not be dispersed at all in a seed-rich year; 39% of our experimental walnuts were not removed from exclosures in the mast year. These results seem at odds with the escape hypothesis of dispersal, which states that seeds benefit from dispersing farther from the parent tree. Kelly and Sork (2002) suggested that dispersal is "typically unaffected or worsened in high seed years", and that benefits of masting are entirely due to increased escape from predation. Jansen et al. (2004) stated that shorter average dispersal distance in food-rich years is "more than counterbalanced by disproportionately greater survival" in the same years. These statements are somewhat ambiguous, implying perhaps that a dearth of surviving seeds at long distances in food-rich years are simply overcompensated for by an abundance of surviving seeds near the parent tree. In

this case, a trade-off could exist between dispersal strategies (few far vs. many near), which could have implications for evolution of masting behavior. For most tree species we studied, we found that in spite of lower average cache distances in seed-rich years, the net effect of masting was not just that proportionately more seeds survive in seed-rich years, but that proportionately more seeds survive at greater distances in high-seed years. Thus, both the total per capita number of surviving seeds and the per capita number of seeds dispersed at longer distances may have been maximized by the strategy of masting. However, for *Q. rubra*, we recovered more intact seeds at greater distances (>20 m) in the seed-poor year than the seed-rich year. This suggests that a possible trade-off in dispersal strategies may exist, whereby longer-distance dispersal is more likely to be achieved in a year of low seed production and higher seed mortality, due to the effect of seed production on cache management strategies of rodents. This could help explain why trees still produce some amount of seed even in non-mast years.

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