Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition

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Abstract: In forests characterized by a dense woody and herbaceous understory layer, seedling recruitment is often directly suppressed via interspecific competition. Alternatively, these dense layers may indirectly lower tree recruitment by providing a haven for seed and seedling predators that prey on neighboring plant species. To simultaneously test for resource competition and indirect, habitat-mediated effects, we factorially manipulated understory plant cover (removed versus intact) and predation (exclosures versus controls) at three forested sites. We found that vegetation cover created privileged foraging areas that increased seed removal and seedling predation rates. Predator preference was directly related to seed size with larger seeded species including *Prunus serotina* Ehrh. and *Fagus grandifolia* Ehrh. removed more readily than smaller seeded species such as *Fraxinus americana* L. We found strong species-specific evidence for habitat-mediated indirect effects; establishment of *P. serotina* and *Acer saccharum* Marsh.was significantly lower under an intact hay-scented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore) canopy when small mammals were present. Competition also played a strong role; both *P. serotina* and *Acer rubrum* L. survival as well as *A. rubrum* emergence were reduced under a fern canopy with or without seed predators. The impact of habitat-mediated indirect effects and resource competition appear to vary predictably based upon predator preferences and differences in the timing of woody seed dispersal and germination relative to vegetation cover phenology. Overall, our results suggest that habitat-mediated indirect effects may be common and occur wherever vegetation provides the potential for creating privileged foraging areas.

Résumé : Dans les forêts caractérisées par un sous-étage dense composé d'espèces ligneuses et herbacées, la compétition interspécifique empêche souvent de façon directe le recrutement de semis. De façon indirecte, ces strates denses peuvent aussi diminuer le recrutement de semis en fournissant un refuge aux prédateurs de graines et de semis qui s'attaquent aux espèces environnantes. Dans le but de tester simultanément les effets directs de la compétition pour les ressources et les effets indirects par l'intermédiaire de l'habitat, nous avons établi un dispositif factoriel en manipulant la couverture végétale en sous-étage (enlevée et intacte) et la prédation (exclos et témoins) dans trois stations forestières. Nous avons observé que le couvert végétal créait des aires d'alimentation privilégiées dans lesquelles les taux de prélèvement de graines et de prédation des semis étaient plus élevés. La préférence des prédateurs était directement reliée à la taille des graines puisque les graines des espèces qui produisent de grosses semences, comme *Prunus serotina* Ehrh. et *Fagus grandifolia* Ehrh., étaient prélevées plus rapidement que celles des espèces qui produisent de petites semences, comme *Fraxinus americana* L. Nous avons trouvé de sérieux indices spécifiques que l'habitat a des effets indirects : l'établissement de *P. serotina* et d'*Acer saccharum* Marsh. était significativement réduit sous un couvert intact de *Dennstaedtia punctilobula* (Michx.) T. Moore lorsque de petits mammifères étaient présents. La compétition a aussi joué un rôle important : la survie de *P. serotina* et d'*A. rubrum* L. ainsi que l'émergence d'*A. rubrum* étaient réduites sous un couvert de fougère que des prédateurs soient présents ou non. L'impact de la compétition indirecte par l'intermédiaire de l'habitat et de la compétition directe pour les ressources semble varier de façon prévisible en fonction des préférences des prédateurs et des différences dans la période de dispersion et de germination des graines des espèces ligneuses par rapport à la phénologie du couvert végétal. Dans l'ensemble, nos résultats indiquent que les effets indirects par l'intermédiaire de l'habitat peuvent être fréquents et peuvent survenir partout où la végétation offre la possibilité de créer des aires d'alimentation privilégiées.

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Introduction

In many forested areas worldwide, understory herbs and shrubs often form dense clonal patches that dramatically shift patterns and rates of tree species recruitment during critical juvenile stages (Mallik 2003; Royo and Carson 2006). Available evidence suggests that these understory layers delay and alter forest regeneration by pre-empting light and soil resources from newly established seedlings (Beckage et al. 2000; Nilsen et al. 2001). These studies rarely consider the alternative that a dense understory layer

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can indirectly suppress seedling establishment by increasing seed and seedling predation rates beneath their canopies (Gill and Marks 1991). In this alternative, dense vegetation cover provides a preferred microhabitat for herbivores that subsequently feed on seeds and seedlings of target species (Reader 1993; Bonser and Reader 1998). In both cases, it appears that interspecific resource competition causes the reductions in the target species when, in fact, the reductions are indirectly mediated by predation (granivory, herbivory, or both).

Several lines of evidence are required to demonstrate that habitat-mediated indirect effects are important in structuring understory plant communities. First, variation in the microhabitat must influence predator behavior; specifically, the presence of a dense understory canopy should increase small mammal activity. Second, increased use of a particular patch by small mammals must translate to increased foraging risk to seeds and seedlings beneath this patch type. Finally, this increased herbivory risk should negatively impact woody plant recruitment. Such conditions may be present in a broad array of plant communities. Experimental evidence demonstrates that small mammals are able to assess risk from aerial predators and thereby shift their foraging behavior to safer patches that lie beneath dense vegetation (Manson and Stiles 1998; Kotler et al. 2004). Second, postdispersal seed predation studies repeatedly demonstrate that seed and seedling predation rates increase beneath a protective vegetation layer, often disproportionately for larger or poorly defended species (e.g., Ivan and Swihart 2000; Schreiner et al. 2000). Finally, these differences in predation risk across microhabitats and species are known to alter seedling abundance and species composition (Ostfeld and Canham 1993; Bonser and Reader 1998).

The potential for indirect interactions creating what appear to be competitive outcomes may be a pervasive yet generally overlooked phenomenon (Reader 1992). To date, explicit tests of indirect effects in plant communities remain scarce, and those that do exist usually are observational, conducted in artificial systems, and short term (reviewed by Chaneton and Bonsall (2000)). Furthermore, few empirical studies employ the full-factorial design necessary to rigorously test the relative importance of each factor independently as well as any interaction among the factors (Reader 1992; Royo and Carson 2006). Decoupling the two processes is critical because community dynamics may not be a function of competitive outcomes but rather a product of differential predation risk.

In this study, we present an integrated set of experiments to test the importance of direct resource competition and habitat-mediated indirect effects in Allegheny hardwood forest understories dominated by hay-scented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore) and to determine whether these impacts vary depending on the target woody species. By experimentally manipulating the presence of fern cover and small mammal access in a factorial design, we directly evaluated (*i*) whether fern cover influences small mammal activity, (*ii*) whether woody seed removal rates vary among microhabitats and species, (*iii*) whether fern cover exerts a direct competitive effect on seedling establishment, (*iv*) whether fern cover exerts an indirect effect on tree seedling establishment by mediating increased seed or seedling predation, and (*v*) the generality of these effects by replicating our experiment at three widely dispersed field sites.

Methods

Research sites

We conducted our study at three Allegheny hardwood forest sites (separated by at least 2 km) in northwestern Pennsylvania (Marienville, 41°32′N, 79°09.77′W; Clermont, 41°42′N, 78°27.65′W; and Long Run, 41°37′N, 78°42.68′W). The Allegheny hardwood forests cover about 12 × 10^6 acres (1 acre = 0.405 ha) in western Pennsylvania and adjacent areas of New York, West Virginia, Maryland, and Ohio. This forest type is a variant of the northern hardwood forests that is characterized by a canopy highly dominated by black cherry (*Prunus serotina* Ehrh.) and red maple (*Acer rubrum* L.) (Marquis 1973). These two species together accounted for 65% of the canopy trees (>20 cm diameter at breast height (DBH)) in Clermont and ~98% of the canopy trees in both Long Run and Marienville (A.A. Royo, unpublished data). For details of the local climate and forest composition, see Whitney (1990).

Understory layer

Hay-scented fern is a native rhizomatous perennial that is unpalatable to white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) and forms a dense layer covering as much as 60% (121 000 ha) of the forests in the Allegheny Plateau region (Royo and Carson 2006). It can spread aggressively in forest understories, particularly when overstory disturbance increases understory light levels and browsing reduces the abundance of competing understory vegetation (de la Cretaz and Kelty 2002). Once established, this dense vegetation layer severely inhibits tree establishment, growth, and survival (Horsley 1993; George and Bazzaz 1999).

Experimental design

At each of the three sites, we conducted a 2 × 2 factorial experiment where we removed fern cover with an herbicide and excluded small mammals in 2 m × 2 m × 1 m plots. Within each site, we established five experimental blocks, with each block containing one plot each of the following four treatments: (*i*) control, (*ii*) no fern cover, (*iii*) exclosure, and (*iv*) no fern cover and exclosure. Herbicide application consisted of a 1.5% solution of Roundup Pro™ (active ingredient: glyphosate) applied to the 4 m^2 area of the treatment plot using a compression tank sprayer. Exclosures were cages constructed using 1 cm^2 hardware cloth, and unfenced plots were surrounded by 75 mm hexagonal wire netting to allow access by small mammals while controlling for potential fence effects. All treatment plots within a block were located in close (<2 m apart) proximity to decrease the potential variability across plots in seed rain and other biotic and abiotic factors.

We assessed small mammal activity using live traps (Sherman Traps, Tallahassee, Florida) baited with a peanut butter and oatmeal mixture. We placed one trap within each plot (20 traps/site) for a 24 h period on five dates in fall 2002, beginning after exclosure construction and on 12 dates

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(at 2–3 week intervals from May to August) in both 2003 and 2004. In total, each site was trapped 13–15 times, for a total of 810 trap-nights. The mean capture rate (captures/100 trap-nights) per treatment was used as a measure of small mammal activity (Wilson et al. 1996). Captured animals were identified by morphological characteristics and released in the immediate vicinity of their area of capture. Any animals caught inside a fence were released outside the fence. Exclosures were inspected and repairs were made (e.g., filling burrows and patching fencing) as needed. Five plots were destroyed by a major windstorm in July 2003 and excluded from further monitoring.

We conducted small mammal feeding trials at four dates (July–September 2003) to determine if seed predation varied among microhabitats and among species. We used seeds of five tree species that span a wide range of both shade tolerance (*Fagus grandifolia* Ehrh. (American beech) > *Acer saccharum* Marsh. (sugar maple) > *A. rubrum* > *P. serotina* > *Fraxinus americana* L. (white ash); Burns and Honkala 1990) and seed mass (*Fagus grandifolia* > *P. serotina* > *A. saccharum* > *F. americana* > *A. rubrum*; USDA Forest Service 1989). Although adult trees (>20 cm DBH) of *A. saccharum*, *F. americana*, and *Fagus grandifolia* were rare or absent at some sites, all are commonly associated with the Allegheny hardwood forest type (Burns and Honkala 1990). In each plot, we placed five seeds of each species in 100 cm^2 aluminum screen trays (25 seeds/tray) and monitored seed removal rates over a 24 h period (0, 4, 16, and 24 h after introduction) after which most seeds were gone. Although seed removal does not necessarily equate with predation as some seeds are secondarily dispersed and cached, the vast majority of these seeds are subsequently relocated and consumed or cached in microsites that are unsuitable for successful establishment (reviewed by Vander Wall 1993 and Hulme 1998).

We monitored seedling emergence and mortality by species in the center 1 m^2 of each 4 m^2 plot in June 2003 and 2004. Seedlings within a cohort were tagged to identify year of establishment. Because the plots were heavily dominated by *P. serotina* and *A. rubrum*, we sowed 10 *Fagus grandifolia* seeds into marked locations and transplanted five *A. saccharum* seedlings (mean height = 7.0 cm) into each plot to allow an evaluation of treatment effects on additional species. *Fagus grandifolia* seeds were obtained from local seed stock from a commercial distributor (Sheffield Seed Supply, Locke, New York) and sown in November 2002. *Acer saccharum* seedlings were collected from naturally germinating individuals in a stand located central to all three field sites and transplanted directly into the field without fertilization in late May 2003. We observed no *Fagus grandifolia* germination from our marked seeds in 2003 and, thus, recovered all remaining seeds from each plot to obtain an estimate of overwinter in situ seed removal (seeds recovered/seeds sown).

Statistical analysis

We tested the effect of site, block, fern cover, and exclosure as well as their interactions on each response variable (small mammal capture rate, seed removal, seedling emergence, and seedling mortality). Incorporating the random site and block variables into the model allowed us to statistically account for the potential variability in biotic and abiotic factors (e.g., light, seed fall, and moisture) across blocks and sites.

Following Reader (1993) and Bonser and Reader (1998), we further explored differences among treatments via three a priori contrasts. We tested whether means differed between (*i*) exclosures versus no exclosures in plots devoid of fern cover, (*ii*) fern cover versus no fern cover within exclosures, and (*iii*) fern cover versus no fern cover outside exclosures. The first comparison isolates the effect of predation, and the second isolates the effect of resource competition. Finally, if fern manipulations within exclosures have no effect (the second comparison) but manipulations outside exclosures do (the third comparison), this provides evidence for a habitat-mediated indirect effect (see Bonser and Reader 1998). Although such a difference may yield a significant fern × exclosure term in the overall model, these comparisons allow a direct evaluation of whether fern cover exerts a relatively greater impact on seedling recruitment parameters in the presence of small mammals than in their absence.

We utilized two seed removal metrics following Hulme (1994): (*i*) seed encounter rate (the rate at which at least one seed was removed from a tray) and (*ii*) seed removal rate (the rate at which seeds were removed once the tray was encountered). Seed encounter and removal rates were estimated using a Kaplan–Meier survival function (PROC LIFETEST; SAS Institute Inc. 2005). The advantage of this procedure is that it allows for the inclusion of right-censored cases (i.e., not all seeds removed by the end of the 24 h monitoring period). In such cases, complete removal times exceeded our monitoring period and influenced overall survival rates, making their inclusion necessary for appropriate estimation (Jansen et al. 2004). The time when a removal event occurred was set halfway between the last census time when all seeds were still present and the time at which at least one seed was removed (encounter) or all seeds were removed (removal). We used the log-rank test to statistically compare overall seed encounter rates among microhabitats. We used median survival times for each species as a measure of seed removal rate and then calculated differences among species and treatments using mixed linear models (Jansen et al. 2004).

For all analyses, we assessed whether the response variable distributions fit the assumptions of normality using residual plots. We did not transform any data as transformations often critically alter the outcome and interpretation of statistical models (Billick and Case 1994). Rather, when data exhibited large deviations from normality we modeled the most precise distribution structures using generalized linear mixed models (PROC GLIMMIX; SAS Institute Inc. 2005). Appropriate distributions were selected using Akaike's information criterion adjusted for small sample sizes (AIC_c), where the best model is the one with the lowest AIC_c value (Johnson and Omland 2004). Small mammal capture rate and all emergence data exhibited an overdispersed Poisson distribution and were best modeled using a negative binomial function. Beech seed removal data were U-shaped and were most appropriately modeled using a beta distribution. All other data were modeled utilizing a normal (Gaussian) error distribution.

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Results

Small mammal activity

Exclosures significantly reduced the presence of small mammals, primarily deer mice (*Peromyscus* Gloger, 1841 spp.), chipmunks (*Tamias striatus* (L., 1758)), and red-backed voles (*Clethrionomys gapperi* (Vigors, 1830)) (Fig. 1A and Table 1). Outside exclosures, the mean capture rate was an order of magnitude greater than within exclosures. In unfenced plots, the mean capture rate was significantly greater in plots with fern cover versus unfenced, fern-free plots (Fig. 1A and Table 1).

Seed removal in different microhabitats and among species

Seed encounter rates differed significantly among microhabitats with the highest seed encounter in unfenced plots with fern cover and virtually no encounter in fenced plots (log-rank test: χ^2 = 228.32, df = 3, and P < 0.0001; Fig. 2A). Averaged across all four feeding trial dates, seed removal rates significantly differed among species (F = 33.05 and P < 0.0001) and microhabitats (species × fence × fern: F = 5.59 and P < 0.0001). Because foraging was negligible within exclosures, we focused our preference analyses on the unfenced plots (Fig. 2B). In unfenced plots, small mammals removed species in the following order: *Fagus grandifolia* > *P. serotina* > *Acer* spp. > *F. americana*. This hierarchy was most pronounced in the fern-free plots. The removal of marked *Fagus grandifolia* left in situ to overwinter exhibited a similar pattern with greatest removal rates occurring in the unfenced, fern-covered plots (Table 1 and Fig. 1B).

Tree seedling recruitment and establishment

There were species-specific differences in the mechanisms controlling natural seedling establishment with predation and habitat-mediated predation risk structuring *P. serotina* establishment and competition structuring *A. rubrum* establishment. For *P. serotina*, excluding small mammals increased emergence in both 2003 and 2004 (Table 2 and Figs. 3A and 3B). Although fern cover appeared to lower *P. serotina* emergence in 2004 and increase seedling mortality, the contrasts suggest this negative impact of fern cover is a consequence of habitat-mediated predation risk rather than competition, because this increased risk is only significant in unfenced plots (Table 2 and Figs. 3B and 3C).

Acer rubrum density increased 600% from 2003 versus 2004 because of a mast event (Figs. 4A and 4B). Fern cover significantly lowered *A. rubrum* emergence in 2004 and increased seedling mortality, regardless of whether the plots were fenced or unfenced, suggesting that this impact was driven by competition (Table 2 and Fig. 4C). In fact, excluding mammals did not alter either emergence or mortality of *A. rubrum* in the overall model nor in the contrast isolating predation (Table 2).

Excluding small mammals significantly increased *A. saccharum* seedling mortality in the overall model; however, closer inspection of the contrasts revealed that this mortality is likely driven by habitat-mediated effects rather than competition, because fern cover significantly increased mortality only in the unfenced plots (Table 1 and Fig. 1C).

Finally, we recorded sporadic emergence of *A. saccharum*, *Rubus* L. (blackberry) spp., cucumber-tree (*Magnolia acuminata* (L.) L.), and pin cherry (*Prunus pensylvanica* L.f.) For *A. saccharum* and *M. acuminata*, we recorded a total of nine individuals, thus precluding any rigorous analysis. The other two species (*Rubus* spp. and *P. pensylvanica*) emerge primarily from a long-lived seedbank (Marquis 1975; Peterson and Carson 1996) and, thus, are not likely to be impacted by the present granivory regime.

Discussion

Disentangling the direct and indirect effects of fern cover

Our experimental design allowed us to rigorously parse out the direct effects of small mammal predation and competition as well as the habitat-mediated predation risk under dense vegetation. We found that an understory fern layer suppresses seedling establishment through both direct competitive and indirect, habitat-mediated impacts. Furthermore, our results suggest that the relative importance of these processes is species specific.

We found that small mammal activity was greatest underneath fern cover. Although small mammal abundances are known to vary across years in response to food availability (e.g., Schnurr et al. 2002), our capture rates outside fences were fairly typical for this region and in eastern forests in general (e.g., Yahner 1992; Elias et al. 2004). Furthermore, increased small mammal activity underneath fern-covered patches enhanced the impact of fern as a barrier to seedling establishment by facilitating greater seed encounter and removal rates, by lowering *P. serotina* emergence, and by increasing *A. saccharum* and *P. serotina* seedling mortality. Prior work documenting decreased seedling densities in fern-covered areas relative to fern-free areas attributed much of these differences solely to interspecific competition with fern (e.g., Horsley 1993). This study provides the first evidence that habitat-mediated predation is a key interference mechanism of *D. punctilobula*.

In contrast, small mammals exerted neither a direct nor indirect impact on *A. rubrum* establishment, even though small mammals readily consume seeds and seedlings of this species (e.g., Schnurr et al. 2002). This may have occurred because *A. rubrum* is less preferred than *P. serotina* (Fig. 2B) and thus potentially less limited by seed predation, or because the mast crop in 2004 overwhelmed the available predator population and allowed seedling recruitment (Silvertown 1980; Sork 1993). Additionally, the absence of predation on *A. rubrum* may occur because of life-history-based differences in the timing of seed fall. *Acer rubrum* seeds disperse throughout the spring and early summer (Burns and Honkala 1990) before *D. punctilobula* cover becomes dense (Horsley 1993; Hill and Silander 2001). Thus, *D. punctilobula* is less likely to provide a preferred foraging patch for small mammals and thereby indirectly increase the risk of seed predation. In contrast, peak *P. serotina* seed fall is from August to September (Burns and Honkala 1990) when the fern canopy is dense and provides well-protected foraging areas.

Phenological differences may also explain the strong direct competitive effect of *D. punctilobula* on *A. rubrum* emergence, but not *P. serotina*. *Prunus serotina* germinates

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Fig. 1. Small mammal predation and fern cover effects on small mammal capture rate (A), overwinter seed removal of American beech (*Fagus grandifolia*) seeds (B), and mortality of transplanted sugar maple (*Acer saccharum*) seedlings from 2003 to 2004 (C) averaged across three study sites in northwestern Pennsylvania. Bars are means and error bars are SEs. Asterisks denote a significant difference between fern versus no fern within an exclosure treatment.

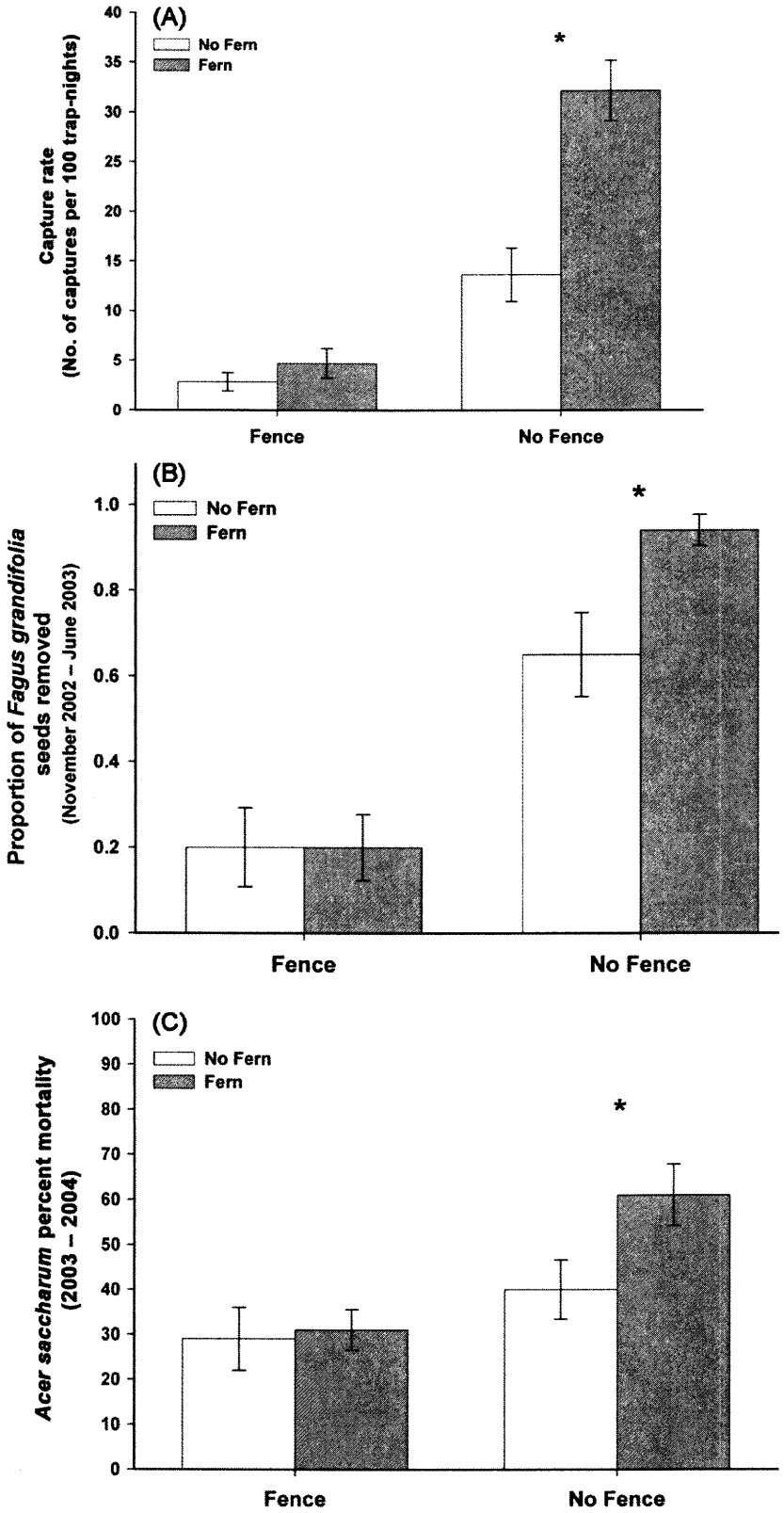

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Table 1. Results from a 2 × 2 factorial manipulation of fern cover and small mammal exclosures on small mammal capture rate (fall 2002–summer 2004), overwinter American beech (*Fagus grandifolia*) seed removal (November 2002–June 2003), and sugar maple (*Acer saccharum*) mortality (May–June 2003) in northwestern Pennsylvania.

	Small mammal capture rate		American beech seed removal		Sugar maple mortality	
	F	*P*	*F*	*P*	*F*	*P*
Factors						
Exclosure	**64.36**	**0.0001**	**7.8**	**0.02**	**8.97**	**0.004**
Fern	**9.94**	**0.003**	**3.31**	**0.09**	1.54	0.219
Fern × exclosure	1.54	0.22	2.16	0.167	1.76	0.19
Contrasts						
Predation versus no predation	**21.65**	**0.0001**	0.7	0.424	1.24	0.27
Fern +/– (within exclosures)	1.55	0.219	0.09	0.76	0	0.96
Fern +/– (outside exclosures)	**11.79**	**0.002**	**8.09**	**0.01**	**5.74**	**0.02**

Note: The orthogonal contrasts test: (*i*) predation (exclosures +/– without any fern cover), (*ii*) fern cover +/– (within exclosures), and (*iii*) fern cover +/– (outside exclosures). Significant *P* values (<0.05) are given in boldface.

in early to middle April (Horsley 1993) before the *D. punctilobula* canopy casts deep shade (Hill and Silander 2001). In contrast, *A. rubrum* emergence extends into summer (Burns and Honkala 1990) making *A. rubrum* seedlings more susceptible to fern canopy closure (George and Bazzaz 1999). These findings suggest that there may be a strongly predictable temporal component to the intensity of direct and indirect effects that is shaped by the phenology of *D. punctilobula* relative to the timing of seed fall and patterns of emergence of tree species.

Finally, *P. serotina* and *A. saccharum* seedlings suffered increased mortality under fern cover only in unfenced plots. Examination of tagged seedlings revealed that this mortality often resulted from herbivores clipping, but not consuming, the entire seedling. This behavior may occur because clipping the seedling might facilitate consumption of only the relatively large, epigeal cotyledons of these species. This nonconsumptive behavior kills seedlings under vegetation in both old fields and forests (Gill and Marks 1991; Horsley 1993) and can cause mortality levels as high as 42% (Gill and Marks 1991). We argue that this pattern of increased mortality under fern cover only in the presence of small mammals also supports the existence of strong habitat-mediated indirect effects.

Statistical tests and indirect effects

Factorial experimentation and analyses remain the most frequently employed method of detecting indirect effects as significant interaction terms demonstrate nonadditive relationships between main effects (Underwood 1997). However, this approach has been criticized for lacking power to detect indirect effects, particularly in experiments that manipulate densities to a higher or lower level (e.g., exclosures, competitor removals; Stehman and Meredith 1995). Hambäck and Beckerman (2003) argued that this lack of power in manipulative experiments of cover and mammalian herbivores results, in part, from biases introduced by the scale of experimental manipulations. They argue that small-scale understory canopy manipulations of only a few square metres may be too small to alter small mammal foraging behavior. This bias did not occur in our study, because our trapping data clearly indicated that small mammals reliably perceive and respond to small openings in the fern canopy (see also Gill and Marks 1991; Vandenberghe et al. 2006).

Lack of statistical power to detect significant interaction terms in ANOVAs may also result from high heterogeneity among replicates. For example, natural seedling emergence exhibited high variability among plots and, thus, was not closely connected to our observed pattern of mammalian activity or seed removal. We could have assessed the emergence of seedlings from a known number of hand-sown seeds, which may reduce plot to plot variation. However, experience in the region has shown us that germination is extremely low (<<10%), particularly from prepared, hand-sown seeds (Wendel 1972; Marquis 1975). Had we relied on this approach alone, the likely widespread germination failure would have precluded any analyses!

Our results for *A. saccharum* or *P. serotina* mortality, capture rate, and seed removal demonstrate how high variability (coefficient of variation: 54%–148%) dilutes the power to detect a significant interaction term despite clear graphical and statistical evidence (i.e., contrasts) that fern cover results in greater risk only in unfenced plots. Thus, we agree with Stehman and Meredith (1995) and Foster (2001), who suggested that the high variability often found in field-based studies makes it difficult to detect anything but the strongest interactions using ANOVA. They argued that testing specific a priori contrasts pertinent to the hypotheses is a powerful alternative (Stehman and Meredith 1995; Foster 2001).

Is habitat-mediated predation risk ubiquitous in forest understories?

Habitat-mediated predation is likely a common and important plant–animal interaction in forests because dense understory layers are common in forested systems worldwide (Royo and Carson 2006) and small mammal predators are nearly ubiquitous (Hulme 1998). Several studies of post-dispersal seed predation in habitats with dense understories have demonstrated that a dense vegetation layer intensifies predation risk (e.g., Manson and Stiles 1998; Schreiner et

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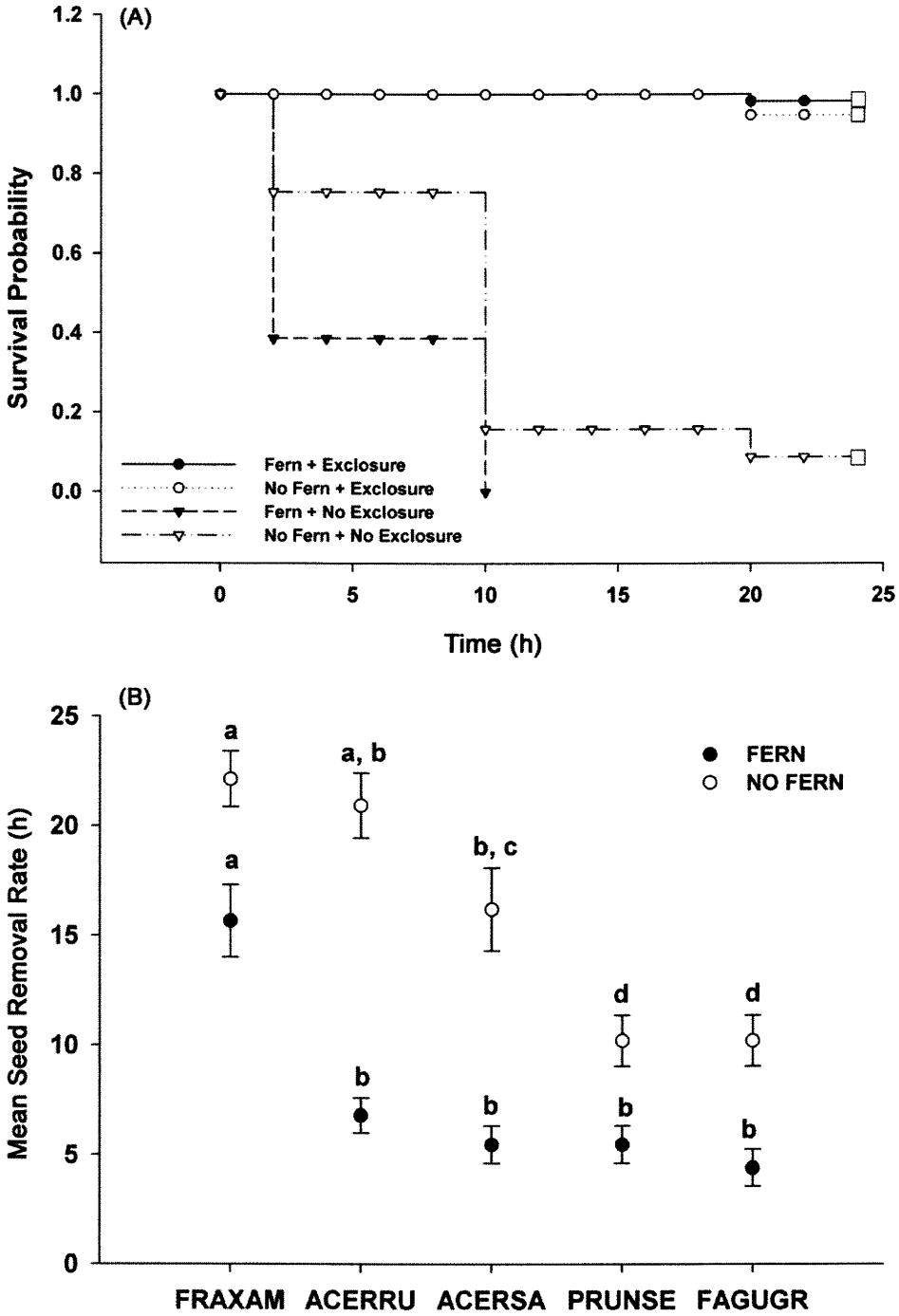
Fig. 2. Seed encounter and removal rates based on the seed tray experiments conducted from July to September 2003 at three sites in northwestern Pennsylvania. (A) Survival probability to first encounter (at least one seed removed from tray) across all four microhabitats in the seed removal trials. Open boxes show right-censored probabilities. Risk of first encounter differs among microhabitats (log-rank test: $\chi^2 = 228.32$, df = 3, and $P < 0.0001$) with unfenced fern-covered plots experiencing lowest survival and fenced plots experiencing highest survival. (B) Seed removal rate based on mean seed "half-life" (Kaplan–Meier median survival) by species in fern-covered plots (●) and fern-free plots (○). Error bars are SEs. Values with different letters are significantly different among species within a fern-removal treatment (Bonferroni adjustment; $P < 0.05$). FRAXAM, *Fraxinus americanus*; ACERRU, *Acer rubrum*; ACERSA, *Acer saccharum*; PRUNSE, *Prunus serotina*; and FAGUGR, *Fagus grandifolia*.



al. 2000); however, these studies could not distinguish between habitat-mediated indirect effects and resource competition. Nevertheless, Gill and Marks (1991) argued the potential for such an indirect effect was an important and "novel mechanism" of interference.

We know of only two tests that experimentally assessed the importance of resource competition relative to predation in forest communities using factorial manipulations of understory cover and herbivory (Cornett et al. 1998; Beckage and Clark 2005). Cornett et al. (1998) used an incom-

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Table 2. Results from a 2 × 2 factorial manipulation of fern cover and small mammal exclosures on natural emergence (June 2003 and 2004) and mortality (2003–2004) of black cherry (*Prunus serotina*) and red maple (*Acer rubrum*) seedlings in northwestern Pennsylvania.

	Black cherry						Red maple					
	Emergence 2003		Emergence 2004		Mortality		Emergence 2003		Emergence 2004		Mortality	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Factors												
Exclosure	**21.7**	**0.0001**	**29.25**	**0.0001**	0.01	0.92	0.14	0.71	0.91	0.35	0.4	0.53
Fern	2.3	0.14	**9.32**	**0.004**	**7.21**	**0.01**	**5.58**	**0.023**	**15.8**	**0.0003**	**37.72**	**0.0001**
Fern × exclosure	0.76	0.39	1.06	0.31	1.25	0.27	3.08	0.09	0.32	0.58	0.05	0.82
Contrasts												
Predation versus no predation	**7.61**	**0.009**	**11.72**	**0.002**	0.51	0.48	0.84	0.36	1.19	0.28	0.23	0.64
Fern +/– (within exclosures)	0.25	0.62	2.82	0.1	1.29	0.26	**8.51**	**0.006**	**5.61**	**0.02**	**18.1**	**0.0002**
Fern +/– (outside exclosures)	2.47	0.12	**6.54**	**0.01**	**6.84**	**0.01**	0.18	0.67	**10.72**	**0.002**	**19.89**	**0.0001**

Note: The orthogonal contrasts test: (*i*) predation (exclosures +/– without any fern cover), (*ii*) fern cover +/– (within exclosures), and (*iii*) fern cover +/– (outside exclosures). Significant *P* values (<0.05) are given in boldface.

plete factorial study with control, fenced-unweeded plots, and unfenced-weeded plots and found compelling evidence that emergence and survival of both balsam fir (*Abies balsamea* (L.) Mill.) and eastern white pine (*Pinus strobus* L.) was caused by habitat-mediated indirect effect. More recently, Beckage and Clark (2005) assessed the importance of great laurel (*Rhododendron maximum* L.) cover and small mammal predation on tree seedling emergence in forests using a full-factorial design. They found *Quercus rubra* L. (northern red oak) and *A. rubrum* emergence under *Rhododendron* was significantly increased within small mammal exclosures providing more support for habitat-mediated predation risk. Additionally, they found that the strength of the indirect effect was greater for the larger seeded *Q. rubra* than the smaller seeded *A. rubrum*.

Overall, evidence suggests that habitat-mediated indirect effects may frequently suppress seedling recruitment regardless of community type and that the strength of this indirect effect on seedling establishment will increase as relative seed and seedling preference increases. Seed preference is influenced by a variety of factors including seed size, nutritional content, and toxicity (Kerley and Erasmus 1991; Ivan and Swihart 2000). Our seed removal results (Fig. 2B) generally parallel the seed mass rankings (*Fagus grandifolia* > *P. serotina* > *A. saccharum* > *F. americana* > *A. rubrum*; USDA Forest Service 1989). Taken as a whole, our results suggest that tree species with larger seeds and cotyledonary reserves (e.g., *Fagus grandifolia*, *P. serotina*, and *A. saccharum*) are at greater risk of habitat-mediated predation than relatively smaller seeded species (i.e., *A. rubrum*). Although seed tray experiments may introduce biases in preference trials (e.g., artificially high reward densities, associational risk, and novelty items), they remain useful for providing preliminary estimates of seed removal among taxa (Perez et al. 2006). As measures of granivory intensity among microhabitats, our results provide robust support that risk to seeds, both in terms of encounter and removal rate, are greatest under fern cover.

Although we caution that interpretation of our results is limited to the few species in our study, our data indicating a disproportionate risk for larger seeded species underneath vegetation cover is consistent with other work (e.g., Manson and Stiles 1998; Kollmann and Buschor 2003). Additionally, because small mammal abundances and foraging are linked to spatial and temporal variation in seed availability, we predict the strength of habitat-mediated predation risk will shift as palatable species become relatively more abundant. Thus, although seed-bearing adults of *Fagus grandifolia* were rare at our study sites, our results make the specific prediction that the strength of the indirect effect should shift towards the larger and highly preferred *Fagus grandifolia* seeds. Further experiments are needed to elucidate the relative strength of direct and indirect effects exerted by dense interfering layers and how these may vary across a range of forest systems.

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Fig. 3. Effect of small mammal predation and fern cover on black cherry (*Prunus serotina*) emergence in 2003 (A) and 2004 (B) as well as mortality of the 2003 seedling cohort (C) averaged across three study sites in northwestern Pennsylvania. Asterisks show a significant differences between fern versus no fern within an exclosure treatment ($P < 0.05$). Bars are means, and error bars are SEs.

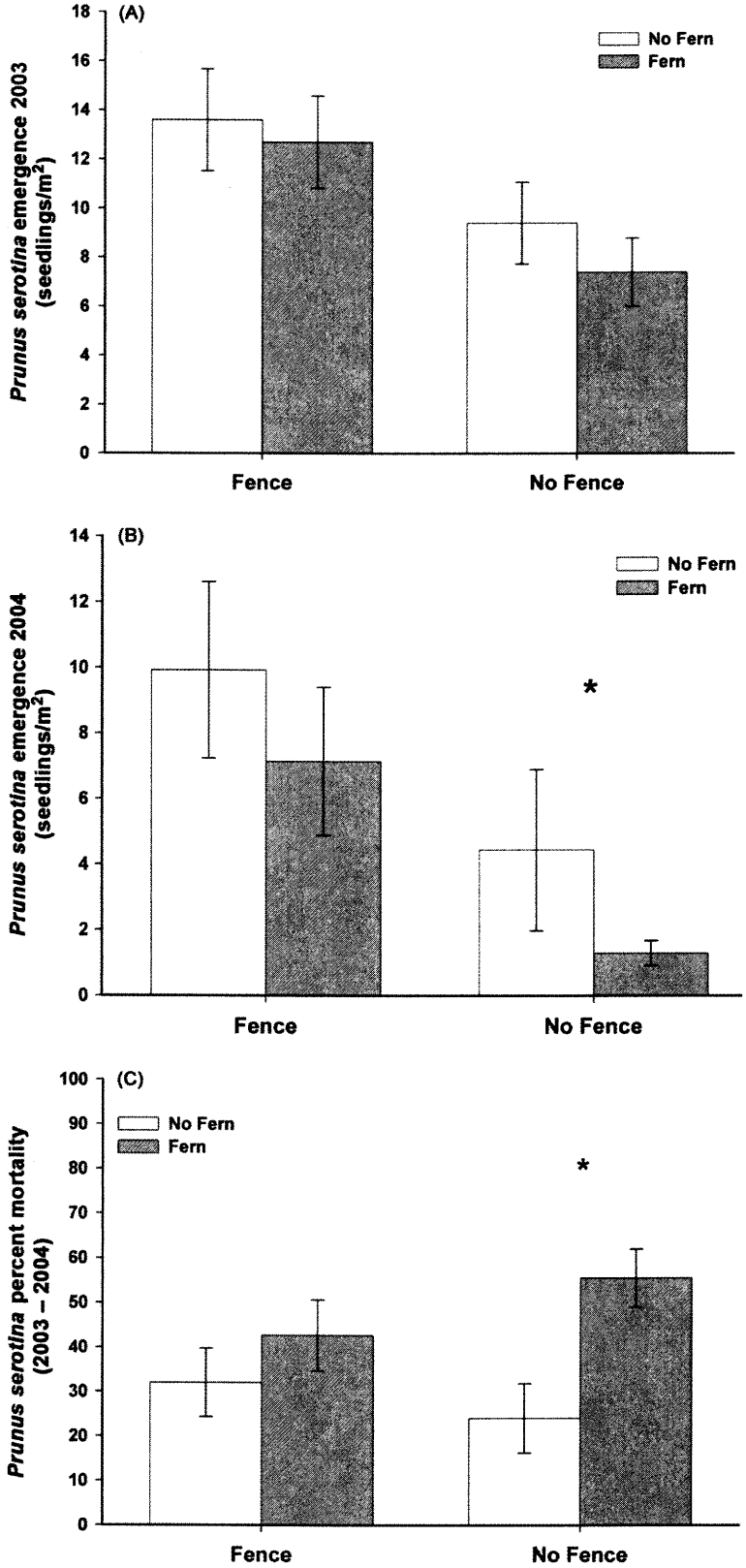

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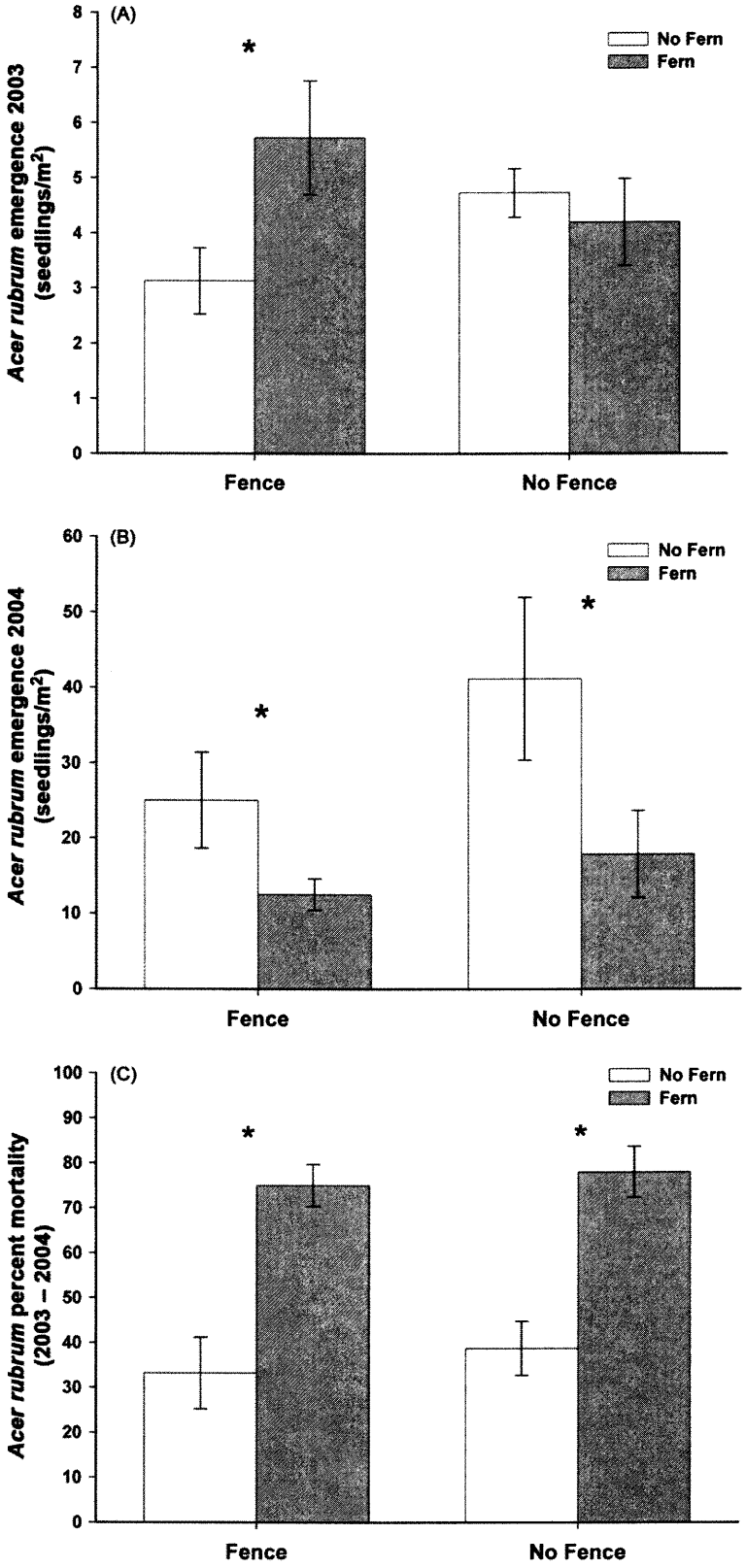
Fig. 4. Effect of small mammal predation and fern cover on red maple (*Acer rubrum*) emergence in 2003 (A) and 2004 (B) as well as mortality of the 2003 seedling cohort (C) averaged across three study sites in northwestern Pennsylvania. Asterisks show a significant difference between fern versus no fern within an exclosure treatment ($P < 0.05$). Bars are means, and error bars are SEs.



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