Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant

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Summary

1 Plants may not occur in a given area if there are no suitable sites for seeds to establish (microsite limitation), if seeds fail to arrive in suitable microsites (dispersal limitation) or if seeds in suitable microsites are destroyed by predators (predator limitation).

2 We conducted a large-scale study to determine the importance of dispersal limitation and predator limitation in affecting the distribution of pokeweed, *Phytolacca americana*, in 401-ha experimental patches arrayed in eight groups of five patches distributed across a 300-km^2 region.

3 Microsite limitation was minimized by clearcutting and burning existing vegetation, creating the type of disturbed habitat in which *P. americana* readily germinates and establishes. The role of dispersal limitation was examined by adding approximately 7000 seeds to each of eight patches in March 2000. The role of seed predation was examined in all 40 patches using experimental exclosures from June 2000 to July 2001.

4 The number of *P. americana* plants in September 2000 was unchanged by seed addition. However, fewer *P. americana* plants were found in patches where seed predators removed more *P. americana* seeds from experimental exclosures. These data suggest that *P. americana* is not limited by seed dispersal. Rather, in habitats where microsites are readily available, the abundance of *P. americana* among patches appears to be limited by the activities of seed predators.

5 When dispersal and microsites are not limiting, the role of local seed predators can be important for generating emergent, large-scale patterns of plant abundance across landscapes. Moreover, because predators may generate large-scale patterns that resemble other forms of limitation and predators may target specific species, predator impacts should be more frequently incorporated into experiments on the role of seed limitation and plant community composition.

Key-words: microsite limitation, predator limitation, seed addition, seed dispersal, seed limitation

Introduction

The distribution and abundance of plants may hinge upon the fate of their seeds (Nathan & Muller-Landau 2000). Seeds may fail to become seedlings if all suitable sites for establishment are already occupied (i.e. microsite limitation affects recruitment), or if seeds are not produced or dispersed in sufficient numbers to locate and occupy available microsites. Such seed limitation may be especially important in early-successional communities (Turnbull *et al.* 2000) and in communities where seedbanks have low persistence (Seabloom *et al.* 2003); understanding its role is important because it can change the composition of plant communities

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(Primack & Miao 1992; Foster & Tilman 2003) and may contribute to the dominance of invasive plant species (Seabloom *et al*. 2003). However, large-scale experimental examination of seed limitation has often been hampered because of the enormous spatial and temporal variation inherent in seed dispersal and establishment (Willson & Whelan 1990; Whelan *et al*. 1991; Hulme 1998; Nathan & Muller-Landau 2000).

Seed limitation can occur via two mechanisms: either seeds never arrive at a suitable microsite (dispersal limitation; Turnbull *et al*. 2000), as might occur if seed production is low or seed dispersal distances are short (Nathan & Muller-Landau 2000), or seeds that arrive at a suitable microsite are destroyed by predators or pathogens before they can establish (predator limitation; Crawley 2000). Empirical studies suggest that both dispersal limitation (Eriksson & Ehrlén 1992; Turnbull *et al*. 2000; Pywell *et al*. 2002; Foster & Tilman 2003; Seabloom *et al*. 2003) and predator limitation (Brown & Heske 1990; Hulme 1998; Crawley 2000; Howe & Brown 2000, 2001) can affect the distribution and abundance of plants. Both may also play an important role in the landscape-dependent patterns of plant establishment that have been repeatedly noted (e.g. Quintana-Ascencio & Menges 1996; Ehrlén & Eriksson 2000; Dupré & Ehrlén 2002). These patterns might be generated by landscape characteristics affecting either biotic and abiotic dispersal (Nathan & Muller-Landau 2000; Tewksbury *et al*. 2002; Haddad *et al*. 2003) or seed predators (Tallmon *et al*. 2003; Orrock & Damschen 2005), or both (Santos & Telleria 1994). Despite the importance of dispersal and predator limitation, untangling their influence has rarely been accomplished because it requires simultaneously quantifying the impacts of seed addition and of seed predators in a system where microsite availability is high (Edwards & Crawley 1999; Crawley 2000).

We combined experimental seed additions and predator exclosures to examine the importance of dispersal limitation and predator limitation in affecting the landscape-level distribution of pokeweed, *Phytolacca americana* (L.). *Phytolacca americana* is a perennial herb indigenous to the eastern United States that produces purple berries containing seeds 2.5–3 mm in diameter and 1 mm wide (Radford *et al*. 1968; Mitich 1994). Its fruits are consumed and disseminated by a variety of vertebrates (Martin *et al*. 1951; McDonnell *et al*. 1984), and it establishes quickly in disturbed habitats or areas where there is little understorey (Mitich 1994; Hyatt 1999). We controlled for microsite limitation by conducting our study in a recently cleared and burned pine forest, where 94% of the soil surface was suitable for germination (see below). Our experiments were conducted at a scale and level of replication that is very rare for ecological field experiments (Debinski & Holt 2000), utilizing forty 1-ha experimental patches distributed over approximately 300 km² (Fig. 1). This large-scale experimental approach allows us to integrate the spatial heterogeneity in seed dispersal and seed predation revealed by
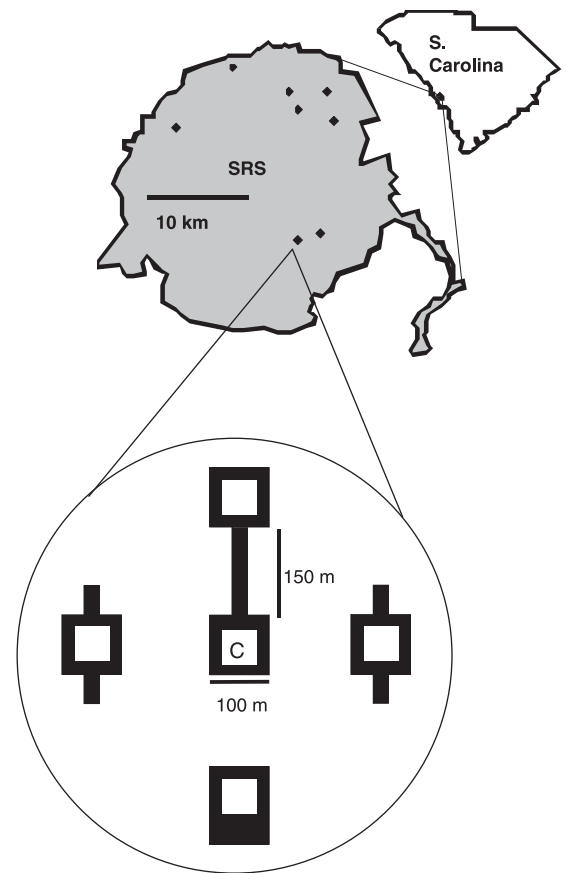
Fig. 1 The experimental landscape used to examine whether *Phytolacca americana* recruitment was limited by seed dispersal or seed predators. Patches were clearcut and burned in winter 1999 and were surrounded by a matrix of mature pine forest. Seeds of *P. americana* were added to the central patch, indicated by 'C', in March 2000. Seed predation trials were conducted in all patches by placing two exclosures along a central 8-m square in each patch. Within each patch, *P. americana* plants were counted in September 2000 within the square portion of each patch 12.5 m from the edge (highlighted in white). To maintain a consistent sampling area among all patches, portions shown in black were not sampled (these portions were designed as part of a larger experiment on connectivity and patch shape that are not considered here).

previous studies (Willson & Whelan 1990; Whelan *et al*. 1991; Hulme 1998; Nathan & Muller-Landau 2000) to dissect the importance of dispersal and predator limitation in affecting the landscape-level abundance of *P. americana*.

Methods

STUDY AREA

Our research was conducted in eight replicated experimental blocks created at the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina, USA. Each block consisted of five patches created by clear-cutting mature pine forests in winter 1999, followed by prescribed burning. In the centre of each block was a 1-ha patch ('central' patch).

Table 1 Summary of ancillary experiments to characterize the germination behaviour of unstratified *Phytolacca americana* seeds. All seeds were field-collected from *P. americana* in the study area and washed free of pulp prior to experiments. Depth trials were conducted using a blend of sand and potting medium that was mixed at 1 : 1 by volume. Seeds used in substrate trials were all placed on the soil surface. When studies were conducted in growth chambers, superscripts indicate references where growth chamber conditions can be found

Characteristic	Location	Replication	Proportion germination (± 95% CI)
Depth			
0 cm	Growth chamber[a]	10 Replicates of 20 seeds each	0.39 ± 0.05
1 cm	Growth chamber[a]	10 Replicates of 20 seeds each	0.03 ± 0.05
3 cm	Growth chamber[a]	10 Replicates of 20 seeds each	0.03 ± 0.05
Substrate			
Sand	Growth chamber[b]	40 Replicates of 40 seeds each	0.16 ± 0.03
Potting mix	Glasshouse	50 Replicates of 5 seeds each	0.29 ± 0.07
Sand/potting mix (1 : 1)	Growth chamber[a]	10 Replicates of 20 seeds each	0.39 ± 0.05

[a]Settings described in Orrock *et al*. (2003).
[b]Settings described in Orrock & Damschen (2005b).

Surrounding the central patch were three types of peripheral patches (Fig. 1), created to examine the role of corridors on dispersal of organisms from the central patch (see Tewksbury *et al*. 2002; Orrock *et al*. 2003; Levey *et al*. 2005). 'Connected' patches were joined to the central patch by a corridor of 25×150 m of the same habitat type as the patches. 'Winged' patches had two blind-ended corridors projecting from opposite sides. 'Rectangular' patches were rectangular due to the addition of 0.38 ha on the side of the patch furthest from the central patch, to control for the 0.38 ha represented by corridors in connected and winged patches. We restricted our work on *P. americana* to the central 1-ha portion of each patch (i.e. we did not work within the corridor, the wings or the rear 0.38 ha of rectangular patches). Although our experiment was conducted within this experimental landscape, we did not focus on the role of patch shape and connectivity. Rather, we took advantage of the large-scale nature of the study landscape (Fig. 1) to examine the roles of dispersal and predator limitation. This was possible because previous work has shown that, although patch shape and connectivity affect the relative roles of arthropod and vertebrate seed predators, patch shape and connectivity do not affect overall *P. americana* seed predation (i.e. total seed removal; Orrock *et al*. 2003; additional analyses below).

SEED ADDITION EXPERIMENT

In March 2000, we added 7185 ± 125 (SE) *P. americana* seeds to the 75×75 m middle area of each central patch in each block by walking through the patch and casting seeds by hand, yielding a total of eight patches where seeds were added and 32 peripheral patches where seeds were not added (Fig. 1). No attempt was made to bury seeds when adding them, as *P. americana* seeds are generally deposited on the soil surface by vertebrate frugivores (Martin *et al*. 1951; McDonnell *et al*. 1984), seeds have no morphological structures to promote burial (Radford *et al*. 1968) and germination of unstrati-

fied *P. americana* seeds is negligible unless seeds are near the soil surface (Table 1). Because we observed no *P. americana* in the forest surrounding our study sites during the course of the study, and sites were cleared and burned prior to our study, we expected all recruitment to be from added seeds or seeds present in the seedbank rather than from existing root stocks. We found no germinable *P. americana* seeds in 32 seedbank samples (each of 1250 cm^2 to 3 cm depth, totalling 40 000 cm^2) from eight different mature pine forest sites in the study area, suggesting that density of *P. americana* in the seedbank was less than 2500 seeds per hectare, i.e. less than five times the number sown. Similarly, Cohen *et al*. (2004) found that *P. americana* is rare in the seedbank of mature loblolly pine forests, averaging 1.04 *P. americana* seeds m^{-2} (assuming that the germinable seedbank is within the top 3 cm of soil; Table 1).

Microsite limitation was virtually eliminated because clearing and burning the plots removed essentially all standing vegetation and created the type of disturbed and exposed soil on which *P. americana* readily establishes. In July 2000, we assessed microsite availability using six 1-m^2 quadrats uniformly distributed within the same central portion of each patch where surveys of *P. americana* were conducted. Microsite availability was estimated as the proportion of area within each quadrat covered by bare soil, fine woody debris (portions of bark or twigs < 5 cm in diameter) or remnants of leaf litter (usually charred remains of pine needles). Our classification of suitable microsites was based upon glasshouse and growth chamber observations that *P. americana* seeds readily germinate atop substrates of sand, potting mix made of pine bark or a mix of both substrates (Table 1). Areas of the quadrat containing coarse woody debris (woody debris > 5 cm diameter) were considered unsuitable microsites.

Phytolacca americana plants were censused in nine 25×25 m plots in all 40 patches in September 2000. The nine plots were in a 3×3 array that was centred in each patch, leaving a buffer strip of 12.5 m along patch

edges that was not censused (37.5 m along one side of each rectangular patch; Fig. 1). Within each plot, the same observer walked four equally spaced, 6-m-wide transects and recorded all *P. americana* plants that were visible and easily identified without squatting; stems that appeared joined at the base were counted as single plants. In essence, this technique provided an estimate of established plants because we were rarely able to detect small seedlings. We conducted this census in 2000 because unstratified *P. americana* seeds were expected to germinate rapidly (Farmer & Hall 1970), making impacts of seed addition most noticeable in the first season following addition.

SEED PREDATION EXPERIMENT

We quantified seed predation using two types of experimental exclosures. Each exclosure was a short, cylindrical cage approximately 16 cm high and 32 cm in diameter. One exclosure type (ALL exclosures) excluded all seed predators (birds, rodents and invertebrates) and had walls constructed of 1.5 cm^2 of hardware cloth covered with fibreglass window screening (< 1-mm^2 mesh). The second exclosure type allowed all seed predators access (NONE exclosures), and had walls constructed of wire fencing with 30-cm^2 openings. Because each exclosure had a top constructed of fibreglass window screen, exclosures excluded most seed rain, including seeds of *P. americana*.

We randomly placed one of each exclosure type within a central 8-m square in each of the 40 patches, yielding 80 total exclosures (two exclosures per patch in 40 patches). At each exclosure site, leaf litter, debris and resident plants were removed and the top 7 cm of soil was disturbed to standardize conditions among exclosures. Field-collected *P. americana* seeds [mean 1.98 ± 0.01 g (SE), equivalent to 312 ± 3.7 seeds] were placed on the soil surface, and the exclosure was placed over the seeds. This amount of seeds is similar to the amount that might collect under a suitable perch in the field (our unpublished data). A 4-cm steel cylinder was projected into the soil around the edge of each exclosure so that 1 cm was above the soil surface. The cylinder did not prevent access to the exclosure by seed predators, but reduced the likelihood of seeds washing in or out of the exclosures during occasional heavy rains. The base of the exclosure and the retaining cylinder were anchored to the soil using 15-cm steel turf stakes. For additional details regarding exclosure establishment, see Orrock *et al*. (2003).

Once established in June 2000, exclosures were visited at least twice per month during the growing season (April–September). Germinants of *P. americana* were counted, and all germinants were removed, regardless of species. In July 2001, seeds were exhumed from exclosures to a depth of 7 cm; the same person exhumed all samples to minimize bias in collection techniques. *Phytolacca americana* seeds were sieved from the soil and counted. Total seed removal was calculated as the difference between seeds (and germinants) collected from ALL exclosures and seeds (and germinants) collected from NONE exclosures. Using this difference as an estimate of seed predation accommodates potential differences in seed recovery rates among patches. We assumed that seed removal was equivalent to seed predation.

STATISTICAL ANALYSES

To determine if seed addition and seed predation affected the abundance of *P. americana* plants, we used an analysis of covariance (ANCOVA). The dependent variable was the number of *P. americana* plants in each patch in September 2000. Our ANCOVA model specified experimental block as a random effect and the addition of *P. americana* seeds as a fixed effect. To examine the importance of seed predation, the number of *P. americana* seeds removed from experimental exclosures from June 2000 to July 2001 was included as a covariate in the model. To reduce the influence of our unbalanced treatment assignment (i.e. eight patches with seed addition and 32 patches without addition; Fig. 1), we treated seed addition as the main plot of a split-plot design (Quinn & Keough 2002). As such, each experimental block provided two observations for the main plot analysis. We treated the effect of seed removal as the small plot of our split-plot design, because independent observations (the number of seeds remaining in exclosures) were obtained for each patch. The potential interaction between seed addition and seed removal was also examined. In our analyses, we do not consider patch type (connected, rectangular, or winged; Fig. 1) because patch type was not significant when included in the ANCOVA model ($F_{2,28}$ = 0.34, P = 0.71), and because patch type does not affect overall levels of *P. americana* seed predation (Orrock *et al*. 2003).

All analyses were conducted using SAS v.8.1 (SAS Institute 2000). Histograms suggested that data for the abundance of *P. americana* plants were skewed. As such, these observations were log-transformed [$\log10(x + 0.1)$] to stabilize variance prior to analysis (Quinn & Keough 2002). Subsequent histograms suggested that transformed *P. americana* abundance and non-transformed seed predation data were normal, and examination of residuals suggested that variance was homogeneous (Quinn & Keough 2002).

Results

Seed addition did not result in greater abundance of *Phytolacca americana* plants (Table 2, Fig. 2a), even though 94 ± 0.9% (SE) of the area in each patch represented a suitable microsite. In patches with seed addition, the average number of *P. americana* plants was 184.37 ± 84.76 (SE). In patches without seed addition, an average of 208.21 ± 102.04 (SE) *P. americana* plants were found. There was a strong negative relationship between the number of seeds removed by predators from

Table 2 Split-plot analysis of covariance (ANCOVA) to determine the effect of seed addition and seed removal on the abundance of *Phytolacca americana* plants

Source	d.f.	MS	F	P
Seed addition	1	0.022	0.19	0.68
Block	7	0.786	6.42	0.01
Main-plot error (block × seed addition)	7	0.120		
Seed removal	1	2.366	7.53	0.01
Split-plot error (residual)	23	0.314		
Total	39			
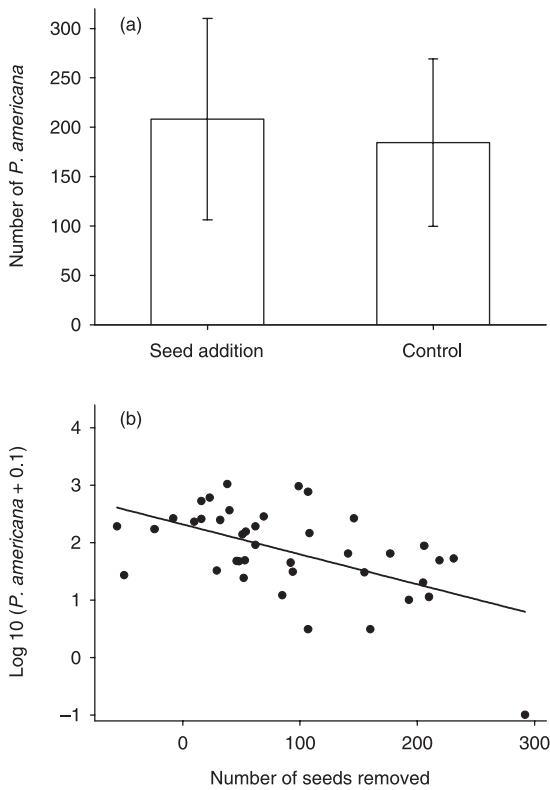
Fig. 2 (a) The addition of seeds of *Phytolacca americana* did not change the number of *P. americana* plants observed in central patches (seed addition, $n = 8$) relative to control patches ($n = 32$). Non-transformed data are presented ± 95% CI; analyses were conducted using log-transformed data. (b) The log-transformed abundance of mature *P. americana* in 40 clearcut patches in September decreased with increasing levels of seed removal from experimental exclosures from June 2000 to July 2001. Line fitted with least-squares regression ($R^2 = 0.30$, $F_{1,38} = 15.98$, $P < 0.01$). The relationship is still significant ($R^2 = 0.18$, $F_{1,37} = 8.24$, $P < 0.01$) after the potentially influential data point where seed removal is very high is not included in the analysis. Number of seeds removed could be less than zero because of differences in seed recovery among exclosures.

experimental exclosures over the study period and the number of naturally recruiting plants (Table 2, Fig. 2b), suggesting that seed predators play an important role in affecting the abundance of *P. americana*. There was no interaction between seed addition and seed removal ($F_{1,23} = 0.86$, $P = 0.36$); the interaction term was not

retained in the final model. The lack of an interaction between seed addition and seed removal suggests that seed predators did not increase in abundance or alter foraging patterns in patches where seeds were added, and that additions did not swamp seed predators by providing more seeds than predators were capable of consuming. This was also supported by unchanging patterns of seed removal in patches where seeds were and were not added ($F_{1,7} = 0.77$, $P = 0.41$). Taken together, these results suggest that seed predators were capable of reducing *P. americana* seeds and abundance in 2000, regardless of seed addition.

To investigate whether our design was capable of detecting significant changes in the abundance of *P. americana* due to seed addition, we performed retrospective power analysis (Thomas 1997). We used the method and formulae of Stroup (2002), the observed variance from our mixed-model analysis (Thomas 1997), and a two-tailed type I error rate (alpha) of 0.05 for calculating power. Based upon our sample sizes, we had ample power (80%; Thomas 1997) to detect an increase of 1150 additional *P. americana* plants in each patch where seeds were added. As such, our design was capable of detecting significant effects of seed addition as long as 16.0% of the seeds we added were capable of becoming mature plants (i.e. if adding 7185 seeds created 1150 plants per patch). Germination of field-collected *P. americana* seeds on the soil surface is generally well above 16.0% (Table 1). Given the lack of microsite limitation ensured by clearing patches and the lack of *P. americana* seedling mortality observed in our system (Orrock *et al.* 2003), our design had sufficient power to detect an effect of seed addition if a difference truly existed.

Discussion

Seed limitation may occur via dispersal or predation and may be an important determinant of plant communities (Turnbull *et al.* 2000), yet it remains unclear whether predator limitation or dispersal limitation is more important for generating large-scale patterns of plant distribution. By combining a seed addition experiment with a seed predation experiment and quantifying subsequent *P. americana* recruitment, we demonstrated that dispersal limitation was negligible across a large-scale landscape (Fig. 2a), that seed limitation was probably generated by seed predation (Fig. 2b) and that the impact of granivore-mediated seed limitation may influence *P. americana* abundance (Fig. 2b). The large-scale nature of our study (Fig. 1) reveals that the activities of local seed predators can be important determinants of landscape-level plant abundance, explaining variation in the abundance of adult plants at sites many kilometres apart (Figs 1 & 2).

Lack of large-scale dispersal limitation may be due to the effectiveness of vertebrate seed dispersers and the longevity of *P. americana* in the seedbank. *Phytolacca americana* fruits are consumed and disseminated by a variety of birds (Martin *et al.* 1951; McDonnell

et al. 1984), and seeds can remain viable for at least 39 years (Toole & Brown 1946). Thus, although seed predators may consume seeds before incorporation into the seedbank, spatial variation in seed predation (e.g. Willson & Whelan 1990) coupled with seed longevity may allow seeds to accumulate until *P. americana* potentially becomes a dominant component of the seedbank (Hyatt 1999; Hyatt & Casper 2000). However, the seedbank may poorly represent the ultimate number of *P. americana* that establish (Hyatt & Casper 2000). This disconnection between seed availability and recruitment may be because any disturbance that brings *P. americana* seeds closer to the soil surface and eliminates existing vegetation is also likely to make *P. americana* seeds more available to seed predators (Reichman 1979; Hulme 1998; Crawley 2000; removal of *P. americana* seeds on the soil surface is nearly six times greater than seeds buried 1 or 3 cm, our unpublished data), which include arthropods, birds and rodents (Hyatt 1998; Orrock *et al*. 2003). This general model may explain why *P. americana* recruitment from the seedbank may be highly variable and relatively unrelated to the amount of seed input (Hyatt & Casper 2000; Fig. 2a): when present within suitable microsites (i.e. open patches of soil close to the soil surface), *P. americana* seeds are also susceptible to predators. Because many species are capable of maintaining a persistent seedbank (Baskin & Baskin 1998), many species are consumed by seed predators (Crawley 2000) and many species only germinate near the soil surface (Baskin & Baskin 1998), predators may play an important role in shaping the distribution of plants other than *P. americana*.

Could other mechanisms have produced the patterns we observed, whereby seed addition did not generate increased recruitment? Seed additions may have failed to yield significant changes in *P. americana* density for several reasons: adding insufficient seeds to generate an effect large enough to be detected (i.e. a lack of statistical power), undetected microsite limitation, or reduction in recruitment due to biotic interactions (e.g. competition, allelopathy, seedling predation). Based on estimates of the seedbank in adjacent mature pine forests (we found fewer than 1406 seeds of *P. americana* per 5625 m^2), we added over five times the number of seeds present (7185 seeds per 5625 m^2). Power analysis suggests that, if at least 16.0% of the seeds we added contributed to recruitment, we had 80% power to detect a significant effect of seed addition. Rates of germination observed in this (Table 1) and other studies (Farmer & Hall 1970; Armesto *et al*. 1983; Edwards *et al*. 1988; Hyatt 1998, 1999) are 1.0–6.2 times greater than this amount (i.e. germination rates of 16–99%). The role of microsite limitation was largely eliminated by conducting the experiment in an area devoid of existing vegetation, leaving over 94% of the study area suitable for *P. americana* germination. Because there were no *P. americana* plants present at the start of the study, adult *P. americana* could not have affected recruitment by reducing germination of *P. americana* seeds through

allelopathy (Edwards *et al*. 1988). Although seedling competition could also have impacted plant recruitment (Edwards & Crawley 1999), our seed additions produced densities that were unlikely to result in seedlings that were in close proximity (i.e. we added approximately 1.3 seeds m^{-1}). Density-dependent seedling predation could have weakened the link between seed abundance and plant establishment, but clipped or otherwise damaged seedlings were never observed during visits to exclosures and only occasionally observed when quantifying *P. americana* plants.

Ultimately, none of these alternative mechanisms, including latent seedbank effects, is consistent with the significant relationship between seed removal from experimental exclosures between 2000 and 2001 and the number of *P. americana* plants in the plots in autumn 2000 (Fig. 2). That is, although we added sufficient seeds to generate a readily detectable effect size, the effect was never realized because seed predators probably removed seeds before they could germinate and contribute to recruitment. Moreover, the small effect size we observed suggests, even if our large-scale design had more patches and thus more statistical power, the biological relevance of the effect size we observed is likely to be small (i.e. an average difference of 24 *P. americana* plants; Fig. 2a). Data from ancillary *P. americana* surveys conducted a year later as part of a long-term monitoring effort suggest that the impact of seed predators continued to shape the abundance of *P. americana* a year later: the number of *P. americana* in 2001 was not related to seed addition ($F_{1,7} = 1.29$, $P = 0.30$), but fewer *P. americana* were found in patches where seed removal was higher ($F_{1,23} = 4.93$, $P < 0.04$).

Seed dispersal could override predator limitation if seed densities become great enough to satiate or swamp local seed predators (Crawley 2000). However, evidence suggests that predator-swamping densities may rarely occur in the field, at least for *P. americana*: such seed densities did not appear to occur in the 40 sites used in this study, despite considerable variation in the number of *P. americana* found in censuses (and thus presumably different densities of *P. americana* in the seedbank; Fig. 2). Moreover, below perches where seed input is highest, recruitment from seed is quite low, with 0.13% of arriving *P. americana* seeds becoming plants (McClanahan & Wolfe 1993). Rather than predator swamping, *P. americana* distribution seems to hinge upon locating predator-free space: in our experimental landscape, there were significant differences in the abundance of *P. americana* (Table 2), rodent granivores (Brinkerhoff *et al*. 2005) and invertebrates (our unpublished data) among experimental blocks (Fig. 1). Animal-mediated dispersal (Martin *et al*. 1951; McDonnell *et al*. 1984) and seedbank longevity (Toole & Brown 1946) may thus facilitate *P. americana* persistence by making it possible for *P. americana* seeds to disperse widely through the 'landscape of risk' represented by this heterogeneity in predation pressure, such that some

seeds are always able to locate habitats where predation is low and survival is high.

IMPLICATIONS OF PREDATOR-MEDIATED SEED LIMITATION

Seed limitation may be a common factor structuring plant communities in early successional systems (Turnbull *et al.* 2000). Our study suggests that seed predators may cause local seed limitation, and that these effects may shape the landscape-level abundance of *P. americana*, explaining variation in the abundance of adult plants at sites many kilometres apart (Figs 1 & 2). As such, our results suggest that the reduced occupancy and persistence of plant species in small, isolated patches (Quintana-Ascencio & Menges 1996; Ehrlén & Eriksson 2000; Dupré & Ehrlén 2002) may be generated by seed limitation due more to seed predation than to limited dispersal. Because studies that couple large-scale seed additions with measures of seed predation are rare, it is unknown how frequently seed limitation attributed to dispersal is actually seed limitation due to predation. Distinguishing between the two mechanisms of seed limitation is important because dispersal and predation provide different insights into which seeds are likely to be present in a community. For example, if predators frequently generate large-scale patterns of seed limitation, seeds with large amounts of defensive tissues for predator deterrence are less likely to experience limitation. Conversely, if seeds are primarily dispersal-limited, seeds without effective dispersal syndromes or poor seedbank persistence are more likely to experience limitation. An important point is that predators often exhibit preferences for particular species, and the activities of predators can lead to changes in plant communities (Brown & Heske 1990; Howe & Brown 2000, 2001). Thus, it seems likely that the landscape-level abundance of species other than *P. americana* may be limited by seed predators, especially if predators prefer to consume those species. Determining the degree to which the structure of early successional communities is limited by dispersal and predation will require more studies that couple seed additions with measurements of predator impact across the landscape.

Understanding whether seed limitation is driven primarily by predator limitation or by dispersal limitation also has applied implications. By revealing that seed predation, not dispersal, can limit the landscape-level abundance of an early-successional species, our work also suggests that success of conservation and restoration strategies that reduce dispersal limitation via direct seed addition (e.g. Primack & Miao 1992; Pywell *et al.* 2002; Seabloom *et al.* 2003) or via habitat 'corridors' that increase deposition of bird-dispersed seeds (Tewksbury *et al.* 2002; Haddad *et al.* 2003; Levey *et al.* 2005) may depend upon the activities of local seed predators. The success of these efforts may be further impacted by changes in local food webs that affect the abundance and activities of seed predators; for example, the pres-

ence of invasive species that alter native predator communities, such as the invasive fire ant (*Solenopsis invicta*; Porter & Savignano 1990), may change predator-limited plant recruitment.

Our work demonstrates that understanding the dynamics of early-successional species and the communities they comprise may ultimately require understanding the dynamics of local seed predators that can shape the abundance of plants across the landscape (Fig. 2b). Seed predation often differs among plant species in the same community (Willson & Whelan 1990; Whelan *et al.* 1991; Howe & Brown 2000), and seed predation can lead to differences in plant community composition (Brown & Heske 1990; Howe & Brown 2000, 2001). Coupled with our findings, these two observations suggest that predators may play an important, and yet largely unknown, role in determining the landscape-level abundance and distribution of plants. As such, future landscape-level studies that separate dispersal and predator limitation for multiple plant species are needed to elucidate the ultimate impacts of local predators on large-scale patterns in plant communities.

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