Landscape Ecol (2011) 26:1373–1381
DOI 10.1007/s10980-011-9650-y

RESEARCH ARTICLE

Edge-mediated patterns of seed removal in experimentally connected and fragmented landscapes

Michael T. Craig · John L. Orrock ·
Lars A. Brudvig

Received: 10 February 2011 / Accepted: 29 August 2011 / Published online: 7 September 2011

Abstract While biological reserves remain central to biodiversity conservation, the amount of area available for terrestrial reserves may be inadequate for many taxa. Biodiversity spillover—the promotion of diversity in matrix areas surrounding reserves—might help address this shortfall in reserve area. However, the mechanistic underpinning of spillover remains uninvestigated. Two fundamental processes—seed dispersal and establishment—might generate plant biodiversity spillover. Here, we investigate the role of establishment in promoting spillover by assessing post-dispersal seed predation, a key component of establishment, in the matrix of a replicated, large-scale habitat fragmentation experiment, where spillover is elevated around patches connected by landscape corridors. Our results show that matrix seed predation may constrain the distance of this spillover effect by reducing establishment: seed removal was least at the matrix edge and increased further into the matrix. We found some support for matrix seed predation underpinning previously reported landscape-level variation in spillover. Of the three species we investigated, two showed evidence for elevated seed predation in the matrix surrounding the unconnected patches around which the lowest levels of spillover occur. However, seed predation did not explain connectivity-enhanced spillover, suggesting that seed dispersal likely drives this pattern. Management activities that increase seed deposition in the matrix may have beneficial effects via spillover. Our work also illustrates that matrix-mediated gradients in seed predation may be widespread, but likely vary depending upon matrix composition and the ecological system under consideration. In fragmented landscapes, this gradient could impact the distribution, abundance, and spread of plant species.

Keywords Matrix · Corridor · Savannah River Site · Longleaf pine plantation

Introduction

Habitat destruction poses one of the greatest threats to biodiversity (Wilcove et al. 1998). Although biological reserves remain one of the most viable strategies for reducing extinction rates (Andam et al. 2008), the area available for reserves is limited and likely inadequate

M. T. Craig (✉)
Washington University in St. Louis, One Brookings
Drive, St. Louis, MO 63130-4899, USA
e-mail: mcraig10@gmail.com

Present Address:
M. T. Craig
1722 Nineteenth Street Northwest, Apartment 707,
Washington, DC 20009-1623, USA

J. L. Orrock
Department of Zoology, University of Wisconsin,
250 North Mills Street, Madison, WI 53706, USA

L. A. Brudvig
Department of Plant Biology, Michigan State University,
East Lansing, MI 48824-1312, USA

for the conservation of many taxa (Rodrigues et al. 2004). Recent work suggests that the benefits of reserves may extend beyond reserve boundaries due to organism dispersal from reserves to adjacent non-target (“matrix”) habitats. Most research on such ‘spillover’ effects has focused on locally enhanced ecosystem services, such as fish production or crop pollination (e.g., Roberts et al. 2001; Ricketts 2004), although recent evidence suggests that biodiversity spillover effects also exist (Ricketts 2004; Brudvig et al. 2009). As future scenarios suggest that reserve creation will continue to lag behind rates of habitat destruction (Rands et al. 2010), understanding the mechanisms that promote biodiversity spillover is critical for maximizing the efficacy of conservation reserves. In spite of this practical importance, past work on spillover has focused heavily on documenting patterns, with comparatively little attention paid to underlying mechanisms.

Spillover may arise via increased dispersal of organisms from a reserve into the surrounding matrix habitat and/or increased rates of establishment of those organisms in the matrix. Empirical evidence for spillover has generally focused on understanding how densities of individuals or species within reserves might generate spillover through increased rates of dispersal (e.g. Roberts et al. 2001). In terrestrial systems, connecting fragmented habitat patches with landscape corridors elevates within-patch plant species richness (Damschen et al. 2008), which may increase spillover of plant species into the matrix surrounding connected patches (Brudvig et al. 2009). Although these examples suggest that dispersal is important for spillover, it is unknown whether increased establishment in the matrix habitat is a primary mechanism determining spillover effects. The distinction between dispersal and establishment limitation may be crucial to understanding biodiversity spillover—particularly for taxa like plants with mobile and stationary life stages—because the two lead to different conservation strategies, i.e. promoting dispersal might not generate spillover in systems where species do not readily establish after dispersing from reserve to matrix habitat.

Using large-scale, experimentally fragmented landscapes that have provided some of the most robust support for biodiversity spillover (Brudvig et al. 2009), we examined the degree to which variation in seed predation by rodents and arthropods, the dominant post-dispersal granivores in our system (Orrock et al. 2003; Orrock and Damschen 2005; Orrock et al. 2006), may reflect patterns of terrestrial plant community spillover. Our landscapes consist of three different patch types that test whether corridors improve reserve design (Fig. 1). Patches connected by corridors support elevated plant species richness in the surrounding matrix relative to unconnected patches (Brudvig et al. 2009), i.e. connectivity-enhanced spillover. The elevated species richness around connected and unconnected patches decays with increasing distance from patch edge, disappearing by 50 m. Animal-dispersed species exhibit the greatest spillover around connected patches relative to species of other dispersal modes, mirroring within-patch trends; spillover of wind-dispersed species is greatest around connected patches and patches with high amounts of edge.

Past work in these landscapes suggests that both seed dispersal and predation could affect this spillover pattern. The effects of habitat connectivity on plant species richness are predictable based on seed dispersal mode (Damschen et al. 2008). However, rates of seed predation can be high, may vary by patch shape and connectivity (Orrock et al. 2003, 2006; Orrock and Damschen 2005), and have been shown to be the primary mechanism limiting at least one plant species within these experimental landscapes (Orrock et al. 2006). Although spillover is related to seed dispersal mode in this system (Brudvig et al. 2009), dispersal mode and rates of seed predation may be related due to shared correlations

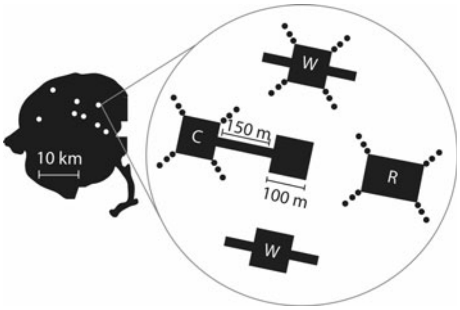

Fig. 1 One of eight replicate experimental landscapes testing corridor function (*right*) and locations of eight experimental landscapes within the Savannah River Site (*left*). Each landscape contained five ~1.4 ha patches of open habitat, which were either connected by corridors (C) or unconnected. Unconnected patches were either rectangular (R) or winged (W). *Dots* depict seed predation sampling locations in matrix pine forest, around open habitat patches

to seed size, e.g. wind-dispersed seeds tend to be small (Venable and Brown 1988), and seed size can affect seed predation rates by rodents and arthropods in this system (Orrock and Damschen 2005). As a result, it remains unclear whether seed predation, as it relates to establishment limitation, contributes to observed patterns of spillover.

Here, we test seed predation by rodents and arthropods as a mechanism for plant biodiversity spillover by quantifying seed predation in the matrix surrounding patches in our experimental landscapes. We assess levels of seed predation across a series of factors known to influence plant community spillover (e.g., distance from patch edge, seed dispersal mode, patch connectivity; Brudvig et al. 2009) to test three key predictions for how seed predation could generate biodiversity spillover in general (prediction 1) and connectivity-enhanced biodiversity spillover as documented in Brudvig et al. (2009; predictions 2 and 3). (1) Rates of seed predation will be greatest at distances further from patch edges, where there was less spillover. (2) Seeds of animal-dispersed species that provide the greatest contribution to connectivity-enhanced spillover (Brudvig et al. 2009) will experience lower rates of seed predation in the matrix surrounding connected patches relative to species dispersed by wind or gravity. (3) Rates of seed predation will be greatest around patches with low connectivity, where the least spillover occurred.

Methods

Experimental site

Experiments were conducted within eight 50 ha experimental landscapes at the Savannah River Site, an 80,000 ha National Environmental Research Park near Aiken, South Carolina. Each landscape represented a statistical block, with five open patches created by clearing mature pine plantation forest and establishing longleaf pine savanna after prescribed burns. Each block contained four peripheral patches, located 150 m from each edge of a central 100 × 100 m patch (Fig. 1). A 150 × 25 m corridor connected the central patch to one peripheral 100 × 100 m "connected" patch. The remaining three peripheral patches were either "winged" (100 × 100 m square with two 75 × 25 m wings off opposite sides) or "rectangular" (100 × 137.5 m); in each block, there was a duplicate winged or rectangular patch. Following creation of the experimental landscapes, the residual mature pine plantation formed the matrix (Orrock et al. 2003).

This design controls for patch area—winged and rectangular patches have equal area to the connected patch plus corridor—and tests for two possible mechanisms by which corridors may affect matrix seed predation: increased patch connectivity (connectivity effects) and increased patch edge-to-area ratio (patch shape effects). If corridors function via connectivity effects, matrix seed predation should be dissimilar around connected and winged patches, which differ in connectivity but are similar in shape. If corridors function via patch shape effects, matrix seed predation should be dissimilar around winged and rectangular patches, which differ in shape but not connectivity.

We used seeds of three perennial herbaceous species to quantify matrix seed predation and examine its relationship with dispersal mode, which was shown to predict the magnitude of connectivity-enhanced spillover (Brudvig et al. 2009). The three species were *Phytolacca americana* (American pokeweed; Phytolaccaceae; seed weight 4.61–7.19 mg, length 2.91–3.05 mm, and width 2.52–2.66 mm (95% CIs, n = 15); bird dispersed), *Carphephorus bellidifolius* (sandywoods chaffhead; Asteraceae; seed weight 1.15–3.17 mg, length 3.98–4.72 mm, and width 0.93–1.05 mm; wind dispersed), and *Anthaenantia villosa* (green silky scale; Poaceae; seed weight 1.32–2.38 mg, length 2.84–3.04 mm, and width 1.27–1.47 mm; unassisted). *P. americana* has previously been shown to be seed limited in this landscape (Orrock et al. 2006). The apparent viability of *A. villosa* and *C. bellidifolius* seeds was determined by gently squeezing them; those that resisted pressure were considered viable and used in experimental trials (Ball and Miller 1990). *P. americana* is consumed by vertebrate frugivores and seeds are defecated free of fruit pulp (McDonnell et al. 1984); to mimic this condition and present seeds in an ecologically realistic manner, we extracted *P. americana* seeds from berries and rinsed the seeds free of pulp. Similarly, for the other two seed species, seeds were presented with their hulls intact, as though they were naturally dispersed.

Linking seed removal to spillover

We quantified seed predation in the forested matrix surrounding one connected, winged, and rectangular patch in each block using seed removal depots (Fig. 1). The central patch and one randomly selected duplicate peripheral patch per landscape were not used in the present experiment. To facilitate comparison of our results with the spillover noted in this system (Brudvig et al. 2009), we established depots along the same transects originally used to quantify spillover by Brudvig et al. (2009), which extended 50 m into the matrix from each corner of selected patches (Fig. 1). We set three 19 × 14 × 10 cm clear plastic seed removal depots, spaced 1 m apart, at 0, 15, and 50 m from the patch edge along each transect. Depots had a 2.5 cm circular opening in two adjoining sides and a tight fitting lid, assuring no seeds were lost to wind, rain, or other non-predation events. Openings allowed both arthropods and rodents access to all depots. When placed in the field, a thin layer of sand was spread across the bottom of each depot, upon which were laid twenty seeds of a single species; one depot per species was used at each location, and depots were arranged in the same order at all locations by which seed species it contained. The number of seeds per depot is similar to that used in previous seed predation studies (e.g. Orrock and Damschen 2005). Seed removal trials were conducted at all locations over two 20 day periods in 2009, from 18 August to 7 September and 12 November to 2 December. For analysis, we pooled these two periods to gain a comprehensive picture of seed predation rates over the entire time period when seeds would be vulnerable after dispersal (e.g. in late summer) and prior to germination in early spring.

Following field trials, we quantified the number of remaining intact seeds and the number of empty (i.e., predated) seed hulls from each tray. Depots that were disturbed by wind or animals (e.g., flipped or rolled onto a side) while deployed were excluded from data analysis. Removed seeds were assumed to have been preyed upon, a common assumption in seed-removal studies (Moles et al. 2003) that was supported by our observations (see results); data from *P. americana* in this study system also suggest that removal is indicative of seed loss and subsequent plant establishment (Orrock et al. 2006).

Data analysis

Seed removal was quantified by the proportion of seeds removed, calculated by summing the number of seeds remaining across all transects in each patch for a given species and distance, then dividing by the total number of seeds initially placed in the depots. To accommodate the use of proportion data as the response variable, all of our analyses were conducted using generalized linear models that utilize a binomial response distribution. We conducted a separate analysis for each species to establish whether removal of each species varied by patch type, distance from the patch edge, or the interaction of patch type and distance, being cognizant of the split-plot nature of our design. We modeled patch type as a fixed effect; because spillover predicts a directional change in seed removal, the effect of distance was a covariate in our model. Replicate experimental units in the experimental landscapes (Fig. 1) were modeled as a random effect (Littell et al. 2006). We used a separate generalized linear model to compare overall differences in removal among species, treating replicate experimental units as a random effect and seed species as a fixed effect. Analyses were conducted using R (R Development Core Team 2009) and SAS 8.1 (Littell et al. 2006).

Results

Across all three species, 9,698 (31%) of approximately 31,000 seeds were removed from 996 of the 1,546 seed-removal depots placed in the field. Field observations suggest that seed removal is a reasonable surrogate for seed predation: 173 depots (17.4%) contained an average of 1.87 rodent fecal pellets per depot, whereas 560 depots (56.2%) contained an average of 7.33 hulls. The proportion of seeds removed was related to the number of fecal pellets ($r^2 = 0.53$, $F_{1,142} = 158.64$, $P < 0.001$) and the number of seed-coat fragments found in the trays ($r^2 = 0.54$, $F_{1,142} = 165.35$, $P < 0.001$).

There was no significant effect of patch type on seed removal of *A. villosa* ($F_{2,22.29} = 0.12$, $P = 0.889$) or *P. americana* ($F_{2,42.94} = 0.75$, $P = 0.478$; Fig. 2b). However, there was a trend of a significant patch type effect for *C. bellidifolius* ($F_{2,30.59} = 2.68$, $P = 0.085$; Fig. 2b). This was due to a strong trend of greater

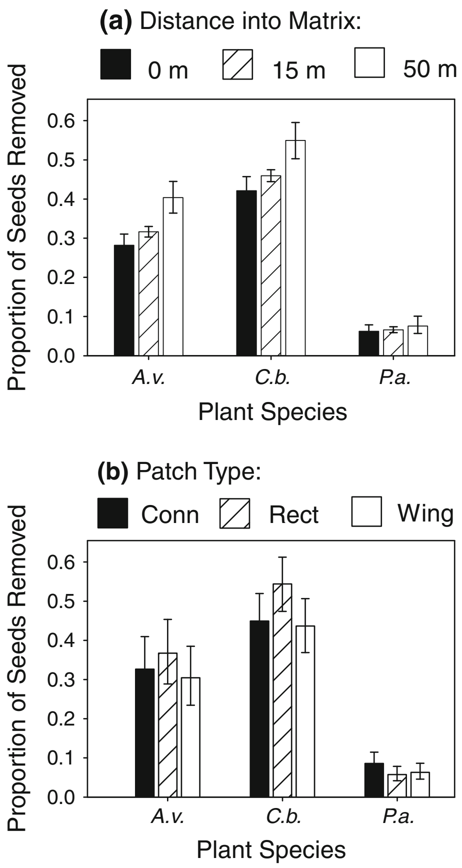

Fig. 2 Mean (±95% CIs) for proportion of seeds removed (**a**) across all patch types at 0, 15, and 50 m into matrix habitat and (**b**) across all distances around connected (conn), rectangular (rect), and winged (wing) patches. Seed removal of *A. villosa* (A.v.) and *C. bellidifolius* (C.b.) was greater with increasing distance into the matrix (**a**) and around rectangular patches (**b**). Removal of *P. americana* did not vary with patch type or connectivity (**b**)

removal in rectangular patches compared to winged patches (Fig. 2b; linear contrast, $F_{1,30.2} = 3.72$, $P = 0.063$).

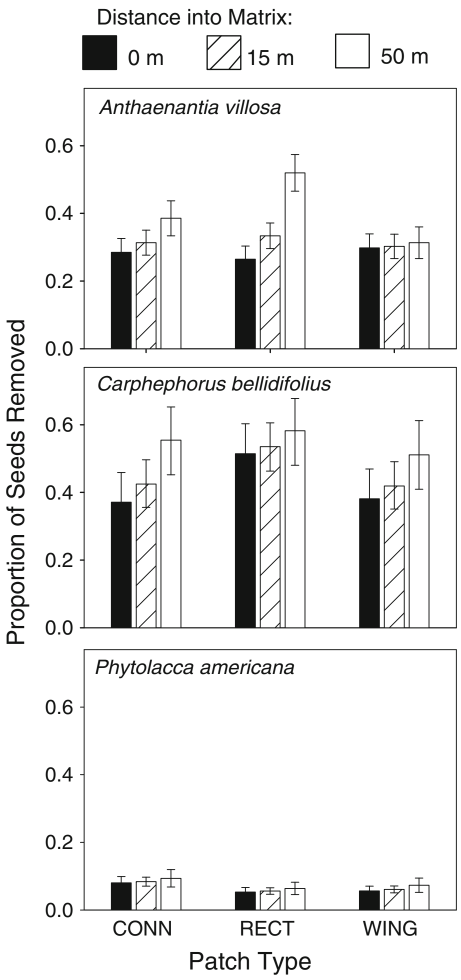

Fig. 3 Mean (±95% CIs) for proportion of seeds removed at 0, 15, and 50 m into matrix habitat surrounding connected (conn), rectangular (rect), and winged (wing) patches. The gradient over distance into the matrix for removal of *A. villosa* seeds was steeper around rectangular than winged or connected patches

Rates of seed removal increased with distance from the patch edge for *A. villosa* ($F_{1,43.53} = 14.42$, $P < 0.001$) and *C. bellidifolius* ($F_{1,43.97} = 10.49$, $P = 0.002$); however, we observed no effect of edge for *P. americana* ($F_{1,40.68} = 0.57, P = 0.456$; Fig. 2a). Removal of *A. villosa* and *C. bellidifolius* seeds increased approximately 43 and 31%, respectively, from 0 to 50 m (Fig. 2a). There was a significant interaction between patch type and distance for removal of *A. villosa* ($P = 0.019$), driven by strong patterns of increased removal with distance into the matrix that were greatest in rectangular patches (Fig. 3; 95% confidence limits (CIs) for the slope of the distance covariate = 0.017–0.025). A significant, though weaker trend of increasing seed removal was also found in the matrix adjacent to connected patches (Fig. 3; 95% CIs for the slope of the distance covariate = 0.004–0.012). There was no significant effect of distance on removal in winged patches (Fig. 3; 95% CIs for the slope of the distance covariate = −0.003 to 0.005). From the perspective of *A. villosa* seed removal, this interaction resulted in greater removal of seeds from depots at 50 m in rectangular patches compared to winged patches (Fig. 3; linear contrast, $F_{1,27.48} = 6.20.11$, $P = 0.019$). There was no interaction between patch type and distance for removal of *P. americana* or *C. bellidifolius* (both $P > 0.477$).

Rates of seed removal were 4–5 times greater for *C. bellidifolius* and *A. villosa* than *P. americana* ($F_{2,142} = 200.11$, $P < 0.001$). Removal rates were greatest for the small-seeded wind-dispersed *C. bellidifolius*, lowest for the large-seeded bird-dispersed *P. americana*, and intermediate for the small-seeded unassisted *A. villosa* (Fig. 3).

Discussion

Landscape-scale variation in biodiversity spillover could be driven by dispersal of propagules from target habitats, limitations to species establishment following dispersal into matrix habitats, or both. By investigating seed removal, one key component of establishment, within large-scale experimental landscapes, we reveal several key findings that provide some of the first insights into the mechanistic underpinnings of plant biodiversity spillover. First, seed predation may contribute to general patterns of spillover observed around all patch types: removal was least near patch edges (Fig. 2a), where spillover was greatest (Brudvig et al. 2009). Second, we found some support for seed predation contributing to reported spillover patterns in our landscapes (Brudvig et al. 2009). For two species—*A. villosa* and *C. bellidifolius*—levels of seed predation were greatest (at all or some distances) around rectangular patches—the patch type supporting the lowest levels of spillover (Brudvig et al. 2009; Fig. 3). Our results were not linked fully to connectivity-mediated spillover, however, because winged patches and connected patches had similar patterns of removal (Fig. 3). These findings suggest that predation may modify spillover effects and may contribute in part to variation in spillover around differently shaped patches; however, our findings suggest that greater spillover around connected patches (Brudvig et al. 2009) is not due to a reduction in seed predation around connected patches, but rather likely occurs because connectivity affects other components of plant establishment (e.g. seed dispersal). Our finding of edge-mediated changes in seed removal also has general implications for the establishment of plants in fragmented habitat patches.

Connectivity-enhanced spillover is likely modified by, but not created by, seed predation

Our data support the prediction that seed predation increases further into the matrix (Fig. 2a), mirroring the observed decay of biodiversity spillover (Brudvig et al. 2009). However, we find only partial support for seed predation contributing to reported patterns of spillover, and no evidence for seed predation underpinning connectivity-enhanced spillover (Brudvig et al. 2009). This suggests that seed predation may play a role in the generation of spillover as a general pattern in our system (i.e. reduced plant establishment and thus diversity with increased distance into the forest matrix, Fig. 2a). The observation that rates of removal were lowest around all patch types for a bird-dispersed species, *P. americana*, underscores this conclusion. Furthermore, we found no evidence for variation in *P. americana* seed predation around any of our patch types, in contradiction to bird-dispersed species, like *P. americana*, being the greatest contributors to connectivity-enhanced biodiversity spillover. The lack of connectivity effects on seed removal adjacent to patches is consistent with work from within the patches of our experimental landscapes, which found no difference in overall removal of *P. americana* seeds because of complementary shifts in the spatial patterns of seed predation by rodents and arthropods (Orrock et al. 2003).

Although we do not find a role for connectivity-mediated changes in seed removal, our finding that patch shape affects matrix seed removal of *A. villosa* and *C. bellidifolius* provides some evidence that patch geometry can mediate the effect of granivores (Figs. 2, 3). Given their relatively small size, arthropod seed predators are likely to be important consumers of *A. villosa* and *C. bellidifolius* seeds (confirmed by additional field observations, L. Brudvig and J. Orrock, unpublished data). One possibility is that the reduced perimeter of rectangular patches reduces the overall amount of edge/ecotone habitat between the patch and the matrix, resulting in more divergent communities of arthropods within the patch and matrix habitat and producing rich within-patch communities, such as those previously observed (Orrock et al. in press). The reduced amount of edge habitat around rectangular patches could create arthropod spillover—an avenue for future research—potentially leading to the elevated rates of seed predation we observed around rectangular patches (Figs. 2, 3). However, because the seeds consumed by granivores is likely to be a function of background seed availability (Brown and Kotler 2004), abiotic conditions (Saska et al. 2010), as well as the composition of the granivore community (Brown and Heske 1990; Howe and Brown 1999), future studies that evaluate the mechanistic basis for the strong gradients in seed removal we observed are essential.

Implications of edge-mediated changes in seed predation

Our work demonstrates a strong effect of edges in altering rates of seed predation for two of the species we studied (Fig. 2a). This represents the first documentation of edge-based patterns of seed removal within the matrix of managed longleaf and loblolly pine forests. Small-mammal consumers have been found to impose strong consumer pressure on seeds and seedlings in oldfield habitats adjacent to managed pine habitats (Orrock et al. 2003; Orrock and Damschen 2005; Orrock and Danielson 2005), in oldfields adjacent to deciduous forests (e.g. Ostfeld et al. 1997; Cadenasso and Pickett 2000; Meiners and LoGuidice 2003), along deciduous forest edges (e.g. Wolf and Batzli 2004), and in fragmented forests in the Pacific Northwest (Tallmon et al. 2003). Arthropods also likely played a role as granivores within the matrix habitats we studied, as they have been previously implicated in removal of *P. americana* (Orrock et al. 2003) and *Rubus allegheniensis* (Orrock and Damschen 2005) in adjacent patches of oldfield habitats. The abundance and richness of beetles (Haskell 2000; Ewers and Didham 2008) and ants (Haskell 2000), both of which consume seeds in our system, have been demonstrated elsewhere to increase with distance from edge into forest habitat. However, Ness (2004) found no differences in ant removal of seeds of *Sanguinaria canadensis* from edge plots (within 10 m of the forest edge) and interior plots (>30 m from the forest edge) in mesic deciduous forests. For the species in our study, we suspect that arthropods were primarily seed predators, not seed dispersers. This is supported by previous work showing a linkage between arthropod seed removal and establishment of one of our study species, *P. americana* (Orrock et al. 2003, 2006), the lack of any structures on the seeds we examined that are likely to promote ant dispersal (i.e. elaiosomes), and the frequent observation that seeds were consumed while in the trays.

Our work has multiple implications for the applied management of diversity in terrestrial plant communities. First, management practices that increase propagule deposition (i.e. seed additions) in matrix habitat, such as increasing permeability, could be successful in promoting spillover. This is especially true in regards to connectivity-enhanced spillover, which we found to be constrained, but not driven, by seed predation. Additionally, our work illustrates that management practices that affect the size of pine forest patches may influence patterns of seed consumption within those patches, with ensuing impacts on plant populations. Specifically, edge-mediated changes in seed removal may reduce the likelihood of longleaf understory species colonizing the central portion of large patches of managed pine forests. In this regard, our results run counter to many studies, which have found greatest seed predation along the edges of matrix, i.e. forest, habitat (e.g. Tallmon et al. 2003; Donoso et al. 2003). These results underscore the importance of understanding matrix-mediated effects and their context-specificity (Kupfer et al. 2006; Prugh et al. 2008; Watling et al. 2011) as well as the need for future research into the mechanistic basis of edge-mediated seed predation. Determining the specific role of consumers, including seed predators, for the spread and establishment of native longleaf pine understory populations would aid in the promotion of plant biodiversity in managed pine landscapes. This is particularly true considering the scale at which we observe significant levels of seed predation, which was less than 50 m (Fig. 2a). The distance into matrix habitat at which spillover persists may be proportional to patch or reserve area and our results may translate most directly to landscapes containing smaller patches (Kleign et al. 2011), such as Europe where 78% of natural areas are <1 km^2 (Gaston et al. 2008).

Conclusions

We provide the first evaluation of the role of seed predation in driving biodiversity spillover of plant terrestrial communities, showing that spillover may be constrained by matrix seed predation but that connectivity-mediated spillover is most likely driven by seed dispersal. Our results place an increased emphasis on processes within the matrix itself for mediating spillover and illustrate that management of focal patches may be most promising when combined with management of adjacent matrix habitats to promote permeability and establishment. Importantly, we illustrate a significant gradient in seed predation with distance into the matrix. Although some species may also exhibit patch-shape effects (e.g. *A. villosa*, *C. bellidifolius*), the general nature of this gradient is robust to patch shape and connectivity, suggesting that distance from habitat edges may be a ubiquitous factor affecting seed–consumer interactions and spread of plant populations in the heterogeneous landscapes that characterize the longleaf pine ecosystem. Our work also highlights the need for future research to determine the mechanistic basis of distance-mediated plant–granivore interactions.

Acknowledgments We thank J. Blake and the USDA Forest Service-Savannah River staff for supporting the creation and maintenance of the experimental landscapes, N. Haddad and D. Levey for their roles in designing and implementing the landscape experiment, E. Damschen, N. Haddad, D. Levey, and J. Tewksbury for their roles in maintaining the landscape experiment, and M. Burt, L. Dlugolecki, M. Habenicht, Q. Mortell, U. Nagendra, L. Peck, and S. Wagner for field assistance. We appreciate comments by N. Haddad on a previous version of the manuscript. This research was supported by an NSF Research Experiences for Undergraduates (REU) supplement to NSF DEB-0614333 and by funds provided to the Department of Agriculture, Forest Service, Savannah River, under Interagency Agreement DE-AI09-00SR22188 with the Department of Energy, Aiken, SC.

References

Andam KS, Ferrao PJ, Pfaff A, Sanchez-Azofeifa GA, Robalino JA (2008) Measuring the effectiveness of protected area networks in reducing deforestation. Proc Natl Acad Sci USA 105:16089–16094

Ball DA, Miller SD (1990) Weed seed population response to tillage and herbicide use in three irrigated cropping sequences. Weed Sci 38:511–517

Brown JH, Heske EJ (1990) Control of a desert-grassland transition by a keystone rodent guild. Science 250:1705–1707

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014

Brudvig LA, Damschen EI, Tewksbury JJ, Haddad NM, Levey DJ (2009) Landscape connectivity promotes plant biodiversity spillover into non-target habitats. Proc Natl Acad Sci USA 106:9328–9332

Cadenasso ML, Pickett STA (2000) Linking forest edge structure to edge function: mediation of herbivore damage. J Ecol 88:31–44

Damschen EI, Brudvig LA, Haddad NM, Levey DJ, Orrock JL, Tewksbury JJ (2008) The movement ecology and dynamics of plant communities in fragmented landscapes. Proc Natl Acad Sci USA 105:19078–19083

Donoso DS, Grez AA, Simonetti JA (2003) Effects of forest fragmentation on the granivory of differently sized seeds. Biol Conserv 115:63–70

Ewers RM, Didham RK (2008) Pervasive impact of large-scale edge effects on a beetle community. Proc Natl Acad Sci USA 105:5426–5429

Gaston KJ, Jackson SF, Nagy A, Cantú-Salazar L, Johnson M (2008) Protected areas in Europe. Ann NY Acad Sci 1134: 97–119

Haskell DG (2000) Effects of forest roads on macroinvertebrate soil fauna of the Southern Appalachian Mountains. Conserv Biol 14:57–63

Howe HF, Brown JS (1999) Effects of birds and rodents on synthetic tallgrass communities. Ecology 80:1776–1781

Kleign D, Rundölf M, Scheper J, Smith HG, Tscharntke T (2011) Does conservation of farmland contribute to halting biodiversity decline? Trends Ecol Evol 26:474–481

Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Glob Ecol Biogeogr 15:8–20

Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberber O (2006) SAS for mixed models. SAS Institute, Cary

McDonnell MJ, Stiles EW, Cheplick GP, Armesto JJ (1984) Bird-dispersal of *Phytolacca americana* L. and the influence of fruit removal on subsequent development. Am J Bot 71:895–901

Meiners SJ, LoGiudice K (2003) Temporal consistency in the spatial pattern of seed predation across a forest—old field edge. Plant Ecol 168:45–55

Moles AT, Warton DI, Westoby M (2003) Do small-seeded species have higher survival through seed predation than large-seeded species? Ecology 84:3148–3161

Ness JH (2004) Forest edges and fire ants alter the seed shadow of an ant-dispersed plant. Oecologia 138:448–454

Orrock JL, Damschen EI (2005) Corridors cause differential seed predation. Ecol Appl 15:793–798

Orrock JL, Danielson BJ (2005) Patch shape, connectivity, and foraging by oldfield mice (*Peromyscus polionotus*). J Mammal 86:569–575

Orrock JL, Danielson BJ, Burns MJ, Levey DJ (2003) Spatial ecology of predator–prey interactions: corridors and patch shape influence seed predation. Ecology 84:2589–2599

Orrock JL, Levey DJ, Danielson BJ, Damschen EI (2006) Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. J Ecol 94:838–845

Orrock JL, Curler GR, Danielson BJ, Coyle DR (in press) Large-scale experimental landscapes reveal distinctive effects of patch shape and connectivity on arthropod communities. Landscape Ecol

Ostfeld RS, Manson RH, Canham CD (1997) Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78:1531–1542

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci USA 105:20770–20775

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rands MRW, Adams WM, Bennun L, Butchart SHM, Clements A, Coomes D, Entwistle A, Hodge I, Kapos V, Scharlemann JPW, Sutherland WJ, Vira B (2010) Biodiversity conservation: challenges beyond 2010. Science 329:1298–1303

Ricketts TH (2004) Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conserv Biol 18: 1262–1271

Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. Science 294:1920–1923

Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004) Effectiveness of the global protected area network in representing species diversity. Nature 428:640–643

Saska P, Martinkova Z, Honek A (2010) Temperature and rate of seed consumption by ground beetles (Carabidae). Biol Control 52:91–95

Tallmon DA, Jules ES, Radke NJ, Mills LS (2003) Of mice and men and trillium: cascading effects of forest fragmentation. Ecol Appl 13:1193–1203

Venable DL, Brown JS (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. Am Nat 131: 360–384

Watling JI, Nowakowski AJ, Donnelly MA, Orrock JL (2011) Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. Glob Ecol Biogeogr 20:209–217

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615

Wolf M, Batzli G (2004) High or low quality habitat for white-footed mice (*Peromyscus leucopus*)? Ecology 85:756–769