SPATIAL ECOLOGY OF PREDATOR–PREY INTERACTIONS: CORRIDORS AND PATCH SHAPE INFLUENCE SEED PREDATION

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Abstract. Corridors that connect patches of disjunct habitat may be promising tools for mediating the negative impacts of habitat fragmentation, but little is known about how corridors affect ecological interactions. In eight 12-ha experimental landscapes, we examined how corridors affect the impact of invertebrate, rodent, and avian seed predators on pokeweed, *Phytolacca americana*. Over 13 months in 2000 and 2001, we quantified the effects of patch shape, connectivity, and predator type on the number of seeds germinating in the field (germinants), seed removal, and the viability of remaining seeds.

Corridors did not affect the number of *P. americana* germinants in experimental exclosures or the viability of seeds remaining in exclosures. However, corridors affected the removal of seeds in a predator-specific manner: invertebrates removed more seeds in unconnected patches, whereas rodents removed more seeds in connected patches. Seed removal by birds was similar in connected and unconnected patches. Total seed removal by all seed predators was not affected by corridors, because invertebrates removed more seeds where rodents removed fewer seeds, and vice versa. Overall, seed predation significantly reduced the number and viability of remaining seeds, and reduced the number of germinants in 2000 but not in 2001. The abundance of naturally occurring *P. americana* plants in our experimental patches in 2000 decreased with increasing seed removal from exclosures but was not related to viability or germinants in 2000, suggesting that seed removal may shape the distribution and abundance of this species.

Complementary patterns of seed removal by rodents and invertebrates suggest that corridors alter the effects of these predator taxa by changing the relative amounts of edge and core (nonedge) habitats in a patch. Because invertebrates and rodents do not completely overlap in the seeds they consume, corridors may change predation pressure on seeds that are primarily consumed by one predator type, with potential consequences for the composition of plant and seed predator communities.

Key words: corridors; patch shape; Phytolacca americana; *predator–prey interactions; Savannah River Site, South Carolina (USA); seed predation.*

INTRODUCTION

Habitat fragmentation and species loss are occurring on a global scale, yet few experimental studies have examined the effects of fragmentation on ecological communities (Gonzalez et al. 1998, Collinge 2000, Debinski and Holt 2000, Davies et al. 2001). Corridors connect habitat fragments and are thought to promote population persistence by promoting gene flow, population rescue, and increasing abundance (Rosenberg et al. 1997). However, corridors have been criticized because mechanisms underlying purported corridor effects are unknown (Simberloff et al. 1992). Perhaps more worrisome, the population-level focus of most corridor studies neglects the rest of the ecological milieu, with largely unknown consequences. For example, imagine the impact of constructing corridors to pre-serve a target species only to discover that an important predator uses corridors more effectively than the species of concern.

By facilitating predator movement, corridors may impact prey that rely upon "predator-free" space (e.g., Holt and Lawton 1993). Moreover, corridors could alter the spatial or temporal asynchrony that promotes the persistence of some predator–prey interactions (e.g., Earn et al. 2000). Empirical work in microcosms reveals that corridors can affect persistence of predator–prey systems (Holyoak and Lawler 1996), but also warns that connecting patches can sometimes lead to counterintuitive outcomes (Burkey 1997, Holyoak 2000). We use an experimental landscape to evaluate how corridors affect the ecology of predator–prey interactions.

Study system: corridors, seeds and seed predators

Seeds can be considered sedentary prey consumed by vertebrate and invertebrate predators (Janzen 1971, Hulme 1998). Seed predation can lead to dramatic re-

ductions in the standing crop of seeds and may be the primary determinant of plant distribution in some systems (e.g., Louda 1989, Brown and Heske 1990, Hulme 1998, Howe and Brown 1999, 2000, 2001). By increasing the deposition of bird-dispersed seeds (Tewksbury et al. 2002, Haddad et al. 2003), corridors could have positive impacts on bird-dispersed plants. However, the ultimate effect of corridors on bird-dispersed plants could be negative if corridor-mediated changes in seed predation offset or outweigh corridor-mediated increases in seed deposition.

Corridors may affect seed predation by altering the movement of seed predators between connected patches of suitable habitat (''corridor effects'') or by making it more likely that an individual moving through an uninhabitable matrix will encounter a suitable patch (''drift-fence effects'' [Rosenberg et al. 1997]). Corridors also add area to a patch, and may affect seed predation by providing more habitat for seed predators (''area effects'' [Haddad and Baum 1999]). Moreover, because corridors tend to be relatively long, linear elements, they can induce area effects by changing the amount of edge habitat relative to the amount of core habitat in a patch. Mammals (Bennett 1990, La Polla and Barrett 1993, Bennett et al. 1994, Bowne et al. 1999, Coffman et al. 2001, Haddad et al. 2003), invertebrates (Haddad 1999, 2000, Haddad and Baum 1999, Collinge 2000), and frugivorous birds respond to corridors (Tewksbury et al. 2002). By affecting the movement and abundance of a particular type of seed predator, corridors could change seed predation by that predator type.

Pokeweed, *Phytolacca americana*, is a perennial plant indigenous to eastern North America that is typically found in early successional habitats (Mitich 1994). *Phytolacca americana* produces berries consumed by many bird species (Mitich 1994), which subsequently disperse *P. americana* seeds (McDonnell et al. 1984, Mitich 1994). Pokeweed seeds are 2.5–3 mm in size (Radford et al. 1968) and can remain viable in the seed bank for at least 40 years (Toole and Brown 1946). Predispersal seed predation is probably minimal, as rodents reject pokeweed fruits, but readily consume *P. americana* seeds (McDonnell et al. 1984, Hyatt 1998), and damage to *P. americana* fruits by rodents or invertebrates was never observed during field collection of several thousand fruits (J. L. Orrock et al. personal observation). Thus, if corridors affect seed predators, there may be direct consequences for *P. americana* population dynamics.

We used an experimental landscape composed of clearcut patches separated by a pine forest matrix to evaluate the effect of corridors on seed predators and *Phytolacca* seeds. For 13 months, we measured three different metrics to determine the impact of seed predators on *P. americana*: the number of seedlings emerging (hereafter called germinants), the number of seeds removed, and the viability of remaining seeds. The du-
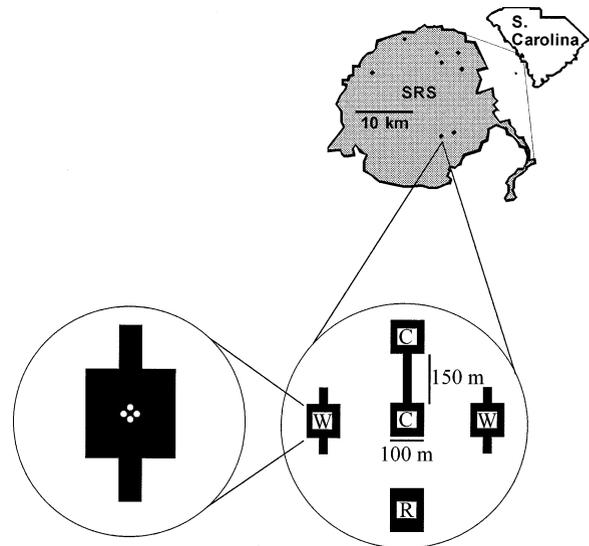

FIG. 1. Layout of the experimental landscape at the Savannah River Site, South Carolina. Eight experimental units were created by clearing mature pine forest. Each experimental unit consisted of connected (C) and unconnected patches that were either rectangular (R) or winged (W). All patches were clearcut habitats separated by 150 m of mature pine forest. Within each patch, one of each exclosure type was installed around the center of the patch (final inset).

ration of our study allowed us to integrate temporal variation in seed predation (Whelan et al. 1991) not incorporated in many seed predation studies. (Most studies last <4 wk, e.g., Hyatt 1998.) Moreover, the duration of our experiment allowed us to evaluate the importance of corridors, patch shape, and seed predation during a critical period of establishment for *P. americana* in our study system.

Our objectives are framed as three questions: (1) Do corridors affect seed predation by invertebrates, rodents, and birds? (2) Are rates of overall seed predation affected by corridors? (3) Is the abundance of naturally occurring *P. americana* plants in our study system related to rates of seed predation, i.e., is there evidence that seed predators affect the distribution of *P. americana*?

METHODS

Experimental design

Experimental landscape.—The experiment was conducted in eight replicated experimental units created at the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina. Each experimental unit consisted of five patches created during the fall and winter of 1999 by clear-cutting mature pine forest (the matrix) followed by prescribed burning (Fig. 1). In each experimental unit, there were three different patch types: connected, rectangular, and winged (Fig. 1). Connected patches were joined by a 25 m wide corridor that was 150 m in length. Rect-

TABLE 1. Three effects may lead to the increased predation of seeds in corridors, because corridors change patch shape as well as patch connectivity. Each effect leads to testable predictions for the intensity of seed predation in connected patches (Conn), rectangular patches (Rect), or winged patches (Wing).

Effect	Description	Predicted predation intensity
Area effects	Corridors increase total amount of habitat and also increase edge relative to core habitat in patch. Effects differ depending upon predator's response to edge:	
	Edge-selecting predators	Conn > Rect; Conn ≈ Wing
	Edge-neutral predators	Conn ≈ Rect ≈ Wing
	Edge-avoiding predators	Rect > Conn; Conn ≈ Wing
Corridor effects	Predator abundance is increased because movement between connected patches dampens effects of stochastic events on predator populations. Predators may also harvest more seeds by moving between connected patches.	Conn > Wing; Wing ≈ Rect
Drift-fence effects	Predators moving through the matrix encounter the corridor and follow it into the patch.	Wing ≈ Conn; Wing > Rect

angular patches consisted of a 1-ha square patch with 0.375 ha of additional area, representing the area added by the corridor (Fig. 1). Winged patches consisted of a 1-ha square patch with two extending ''drift-fence'' sections, each 75 m long and 25 m wide (Fig. 1). Two connected patches were in each experimental unit. Four of the experimental units had two rectangular patches and one winged patch, whereas the other four experimental units had two winged patches and one rectangular patch, yielding a total of 12 winged patches, 12 rectangular patches, and 16 connected patches.

Dissecting the role of corridor, drift-fence, and area effects.—Our design allowed us to determine the relative importance of corridor, drift-fence, and area effects on seed predation because each type of effect makes a specific prediction (Table 1). It is important to note that, although patches were of similar area, each patch type differed in the relative amounts of edge and area habitat because of changing patch shape. This is simply illustrated by the area/perimeter ratio for each patch type: 22.62 for connected patches, 19.64 for winged patches, and 28.95 for rectangular patches. If seed predation is affected by edge, then edge-neutral, edge-selecting, and edge-avoiding seed predators should display different patterns (Table 1) in response to the changing perimeter (because area is relatively constant) among patch types.

Winged and rectangular patches had the same area (1.375 ha), whereas connected patches had slightly less area than unconnected patches because they shared a corridor (central patch area plus half of the corridor = 1.1875 ha). The small difference in total area between connected and unconnected patches does not change the qualitative order of our predictions (Table 1). Rather, it provides a more stringent test of the importance of movement through corridors as a means for predators to exploit seeds. If seed predation is greatest in connected patches, despite the slightly reduced overall area and drift fence in connected patches, we have a stronger case for movement-mediated changes in seed predation.

Seed predation.—We used exclosures to determine the effect of different types of seed predators on *P. americana* seeds. All exclosures were cylindrical wire cages ~32 cm in diameter and 16 cm high. The four treatment types were: (1) access by no seed predators (hereafter referred to as NONE); (2) access by invertebrates (I); (3) access by invertebrates and rodents (IR); (4) access by invertebrates, rodents, and birds (ALL). To exclude all seed predators, NONE treatments used exclosures with walls of 1.5-cm^2 mesh hardware cloth covered with fiberglass window screen (<1-mm^2 mesh); although smaller ants could enter these exclosures, they could not remove seeds. Exclosures with sides constructed of hardware cloth with 1.5-cm^2 openings were used to exclude birds and rodents for invertebrate-access treatments (I). IR treatments used exclosures with walls constructed of hexagonal poultry wire with 4-cm^2 openings. ALL treatments used exclosures with sides constructed of wire fencing with 20-cm^2 openings. Each exclosure had a top constructed of fiberglass window screen that excluded most seed rain, including seeds of *P. americana*.

We randomly placed one of each exclosure type along a central 8-m square within each of the 40 patches (Fig. 1), yielding 160 total exclosures (4 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 mixed to standardize conditions among exclosures. A weighed portion of field-collected *P. americana* seeds (mean ± 1 SE = 1.98 ± 0.01 g; equivalent to 312 ± 3.7 seeds) was placed on the soil surface, and the exclosure was placed over the seeds. This amount of seeds approximates the number of seeds that collects under isolated perches at our site (D. J. Levey, *unpublished data*). A 4-cm galvanized steel ring was pushed into the soil around the edge of each exclosure so that 1 cm was above the soil surface. This did not prevent access to the exclosure by seed predators (ants readily traversed the ring), but reduced the likelihood of seeds washing or blowing into or out of the exclo-

sures. The base of the exclosure and the retaining ring were anchored into the soil with 15-cm steel turf stakes.

Once established in June 2000, exclosures were visited twice per month during the growing season (March–September). Germinants of *P. americana* were counted and removed during each visit. Germinants of all other species were removed. During the course of the experiment, small anthills were observed within two NONE exclosures. Ant-repellent granules (Spectrum Brands, St. Louis, Missouri, USA) sprinkled around the outside of the exclosures eliminated this problem. At the conclusion of the seed predation trials in July 2001, all seeds were exhumed from exclosures to a depth of 7 cm by one person to minimize any bias in soil collection techniques. Pokeweed seeds were sieved from the soil and counted.

Because local habitat characteristics can affect seed predation (Reader and Beisner 1991, Hulme 1997, Manson and Stiles 1998), substrate and vegetation characteristics were measured in a 1 m radius extending from the center of all exclosures open to predators (i.e., I, IR, and ALL treatments) in late July 2000. For consistency, only two investigators quantified habitat characteristics, visually estimating the percent cover of downed woody debris, woody plant material, vegetative plant material, bare soil, and leaf litter.

Seed viability.—We used germination trials to test the viability of exhumed seeds. This estimate of viability may be conservative because dormancy and sensitivity to environmental factors varies seasonally and annually in *P. americana* (Baskin and Baskin 2001). As such, seeds removed from the field in July may be less likely to germinate than seeds collected during optimal germination times earlier in the year (Baskin and Baskin 2001).

For each exclosure, we filled a 5 × 5 × 6-cm compartment of a standard plastic seedling flat with heat-sterilized sand and placed recovered *P. americana* seeds on the surface of the sand. Seedling flats were placed in a growth chamber with a 14:10 light:dark photoperiod and a 31°:27°C temperature regime (Farmer and Hall 1970). Seeds were watered daily from 1 September to 31 October 2001, with the exception of one day due to logistic difficulties. Germinants were counted and removed weekly. The remaining seeds were sieved from the sand and counted.

Surveys of naturally recruiting P. americana.—Pokeweed plants were censused in nine 25 × 25-m plots in all patches in September of 2000. The nine plots were in a 3 × 3 array that was centered in each patch, leaving a buffer strip of 12.5 m along patch edges that was not censused. Within each plot, we walked four equally spaced transects, ~6 m wide, and recorded all *P. americana* plants that were visible and easily identified without squatting. In essence, this technique provided an estimate of established plants because we were rarely able to detect small seedlings. Stems that appeared joined at the base were counted as single plants. Since

P. americana is rarely found in the understory of mature pine forest, plants counted in our census almost certainly established from seed after our plots were cleared seven months earlier.

Statistical analyses

Corridors and seed predation by invertebrates, rodents, and birds.—We used multivariate analysis of covariance (MANCOVA, Scheiner 2001) to accommodate the inherent dependencies among exclosure treatments: rodents and invertebrates could forage from more than one exclosure type, interactions among predators could alter foraging among exclosures, and the recovery rate of seeds may have differed among patches. A separate MANCOVA was used for each metric of seed predation: number of germinants, seed removal, and seed viability. Each MANCOVA had four dependent variables corresponding to the values obtained from the four different exclosure treatments (NONE, I, IR, and ALL). Because preliminary analyses indicated significant differences in field germination between 2000 and 2001 (paired t test, $t = 3.60$, df $= 39$, $P < 0.001$), we performed two MANCOVA analyses for field germination, one for each year of germination data.

Our models specified experimental unit and the type of patch (connected, rectangular, or winged) as fixed effects (random effects cannot be modeled with MANCOVA, Scheiner 2001). Substrate and vegetation data were examined as possible covariates. Comparing the number of remaining seeds (our second metric of seed predation) assumes that the number of germinants was constant among treatments. Although the qualitative outcome of our analyses would be the same if this assumption were not met, comparison of germinants over the entire sampling period supports this assumption (paired t tests, df $= 39$, $t < 0.77$, $P > 0.44$; see also Table 2).

If significant patch type effects were found in MANCOVAs, we used planned pairwise multivariate contrasts of patch type effects (Scheiner 2001) to test the predictions that distinguish corridor, drift-fence, and area effects (Table 1). We follow the multivariate contrasts with univariate ANCOVAs that use the difference between exclosure types as the dependent variable (Scheiner 2001) to determine if the relationship between exclosure treatments changed with patch type. For example, if rodents removed more seeds than invertebrates in one patch type, but not in another, the univariate ANCOVA would detect a significant effect of patch type on the difference between I and IR exclosures. This approach also allows us to assess the contribution of each predator type to overall seed predation in each patch type. These analyses were all planned, i.e., we did not perform tests in an exploratory fashion. As such, we did not adjust α for multiple tests (Day and Quinn 1989), although such an adjustment

TABLE 2. Effect of patch type (connected, rectangular, winged) and experimental unit (EU) on three different metrics of seed predation.

Metric of predation	Factor	Pillai's trace	F	df	P
Field germination 2000	patch type	0.49	1.14	8, 28	0.37
	EU	1.29	1.10	28, 64	0.37
	patch type × EU	1.91	1.04	56, 64	0.43
Field germination 2001	patch type	0.27	0.54	8, 28	0.82
	EU	0.99	0.76	28, 64	0.79
	patch type × EU	1.55	0.72	56, 64	0.89
Number of seeds remaining	patch type	0.94	2.88	8, 26	0.02
	EU	1.48	1.53	28, 60	0.21
	patch type × EU	2.30	1.45	56, 60	0.09
	woody debris	0.78	10.46	4, 12	<0.01
Multivariate contrasts	Conn vs. Wing	0.20	0.74	4, 12	0.58
	Conn vs. Rect	0.72	7.58	4, 12	<0.01
	Rect vs. Wing	0.71	7.26	4, 12	<0.01
Viability of remaining seeds	patch type	0.62	1.45	8, 26	0.23
	EU	1.55	1.35	28, 60	0.16
	patch type × EU	2.19	1.29	56, 60	0.16
	leaf litter	0.69	6.39	4, 12	<0.01

Notes: Each metric of predation is composed of four dependent variables representing data from NONE, I, IR, and ALL exclosures in connected (Conn), rectangular (Rect), and winged (Wing) patches. If significant, covariates describing microhabitat in a 1-m radius around exclosures were included (e.g., woody debris). If significant patch type effects were found, we conducted multivariate contrasts to compare patch types.

would not change the significance of our comparisons at $\alpha = 0.05$.

Corridors and overall seed predation.—We use MANCOVA to examine the net effect of all seed predators on the number of germinants in 2000 and 2001, seed removal, and viability. For these analyses, the dependent variables were the values from NONE and ALL treatments (analogous to Hotelling's T^2 test [Scheiner 2001]). Our model was otherwise the same as used for examining predator-specific effects, including covariates. If significant effects were found due to patch type, we conducted planned pairwise contrasts to examine the predictions that distinguish the effects of corridors (Table 1), as with our predator-specific models. If significant differences were not found due to patch type, we used paired t tests for each measure of seed predation to determine if overall predator effects were significant.

Seed predation and the distribution of P. americana.—We used multiple regression to examine the relationship between the abundance of naturally recruiting *P. americana* in our study system and our experimental measures of seed predation (changes in germinants, seeds remaining, and viability). As with the ANCOVAs, we used the difference between exclosure treatments to partition the effects of each predator type. For example, the reduction in seed number due to rodents was obtained by subtracting the number of seeds recovered from I treatments from the number of seeds recovered from IR treatments. In this way, we generated nine variables, representing the change in germinants in 2000, seed removal, and viability due to invertebrates, rodents, and birds. Because the calculations for rodent and bird effects include more than one predator type, the rodent and bird estimates assume

that any effect of each predator is additive (generally supported for IR and ALL treatments, see *Results*). We used backward selection to identify which variables were most related to the abundance of naturally recruiting *P. americana* plants.

Analyses were performed with SAS version 8.1 (SAS Institute 2000). Germinant counts were square-root transformed and counts of *P. americana* plants were log-transformed (Zar 1999).

RESULTS

Corridors and seed predation by invertebrates, rodents, and birds.—Corridors did not affect the number of germinants in each exclosure type in 2000 or 2001 (Table 2). Corridors and patch type affected the number of seeds removed by each predator type, and downed woody debris was a significant covariate (Table 2, Fig. 2). Examination of standardized canonical coefficients suggests that more seeds were removed from treatment I (coefficient = 1.29) and fewer seeds were removed from treatments IR and ALL as woody debris increased (coefficients = −0.92 and −0.79, respectively). The magnitude of the coefficients indicates that treatments I and IR were most responsible for the significance of woody debris as a covariate (Scheiner 2001). The viability of remaining seeds in each treatment did not differ among patch types (Table 2), although leaf litter was a significant covariate in the analysis. The significance of leaf litter was mostly attributable to a positive relationship between leaf litter and viability in treatments I and ALL (coefficients = 1.06 and 1.37, respectively) rather than a weaker negative relationship between viability and leaf litter in treatment IR (coefficient = −0.83).
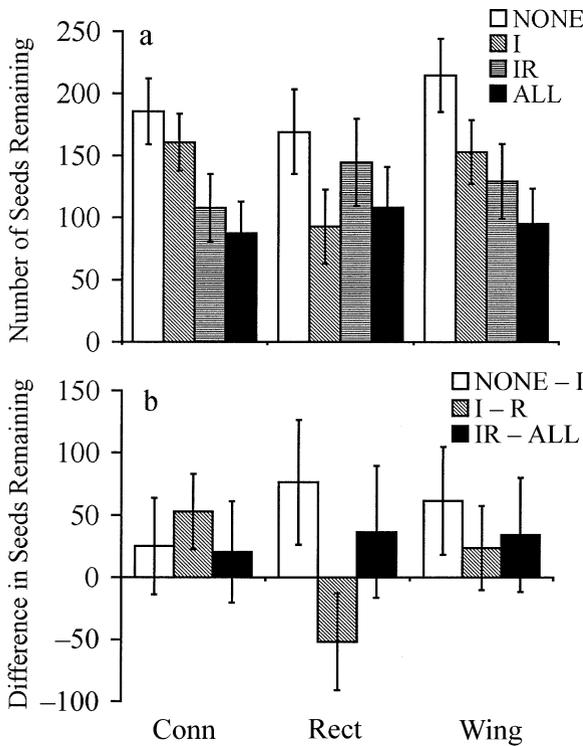
FIG. 2. Seed removal from exclosure treatments located in connected (Conn), rectangular (Rect), and winged (Wing) patches. (a) Mean number of *P. americana* seeds remaining (and 95% confidence intervals) in treatments exposed to no seed predators (NONE), invertebrates only (I), invertebrates and rodents (IR), and invertebrates, rodents, and birds (ALL). (b) The effect of adding a particular predator type, as reflected by the mean difference between exclosure treatments that differ by only one predator type.

There were significant multivariate differences in seed removal between connected and rectangular patches, between winged and rectangular patches, but not between winged and connected patches (Table 2, Fig. 2). Univariate ANCOVA on the difference between treatments NONE and I found no significant differences due to patch type ($F_{2,15} = 1.52$, $P = 0.25$; Fig. 2b). The difference between NONE and I treatments was significantly different from zero in winged ($t = 3.04$, df = 15, $P < 0.01$) and rectangular ($t = 3.25$, df = 15, $P < 0.01$) patches (Fig. 2a). In winged and rectangular patches, invertebrates removed 29% and 45% more seeds relative to NONE treatments, but invertebrates did not remove a significant number of seeds in connected patches ($t = 1.38$, df = 15, $P = 0.19$). Univariate ANCOVA on the difference between treatments I and IR found significant effects due to patch type ($F_{2,15} = 8.59$, $P < 0.01$; Fig. 2b). In rectangular patches, 36% more seeds were removed from treatment I relative to treatment IR ($t = -2.38$, df = 15, $P = 0.01$), suggesting that seed predation by invertebrates increases with area, specifically as the amount of area relative to perimeter increases (Table 1). In connected patches, rodents and invertebrates removed 33% more seeds than invertebrates alone ($t = 3.72$, df = 15, $P < 0.01$), suggesting that rodents are responding to corridor effects (Table 1). Rodents and invertebrates did not remove more seeds than invertebrates alone in winged patches ($t = 1.50$, df = 15, $P = 0.15$). Regardless of patch type, allowing birds access to seeds did not result in a significant increase in seed removal, i.e., the difference between treatments IR and ALL did not differ due to patch type ($F_{2,15} = 0.09$, $P = 0.91$; Fig. 2b), and was not different from zero ($t < 0.25$, df = 15, $P > 0.81$ for all patch types). However, rodents, birds, and invertebrates (ALL) combined to remove significantly more seeds than invertebrates alone in winged patches (paired t test, $t = 2.52$, df = 11, $P = 0.03$; Fig. 2a).

TABLE 3. Effect of patch type (connected, rectangular, winged) and experimental unit (EU) on three different metrics of seed predation.

Metric of predation	Factor	Pillai's trace	F	df	P
Field germination 2000	patch type	0.06	0.23	4, 32	0.91
	EU	0.80	1.52	14, 32	0.16
	patch type × EU	0.89	0.91	28, 32	0.59
Field germination 2001	patch type	0.13	0.57	4, 32	0.69
	EU	0.67	1.15	14, 32	0.34
	patch type × EU	0.92	0.98	28, 32	0.52
Number of seeds remaining	patch type	0.21	0.89	4, 30	0.48
	EU	0.82	1.50	14, 30	0.17
	patch type × EU	2.18	1.04	28, 30	0.41
	woody debris	0.05	0.35	2, 14	0.71
Viability of remaining seeds	patch type	0.28	1.51	4, 30	0.33
	EU	0.84	1.55	14, 30	0.15
	patch type × EU	1.16	1.47	28, 30	0.15
	leaf litter	0.44	5.44	2, 14	0.02

Notes: Each metric of predation is composed of two dependent variables representing data from NONE and ALL exclosures collected in connected (Conn), rectangular (Rect), and winged (Wing) patches. If significant in the previous MANCOVA model, covariates describing microhabitat in a 1-m radius around exclosures were included (e.g., woody debris).
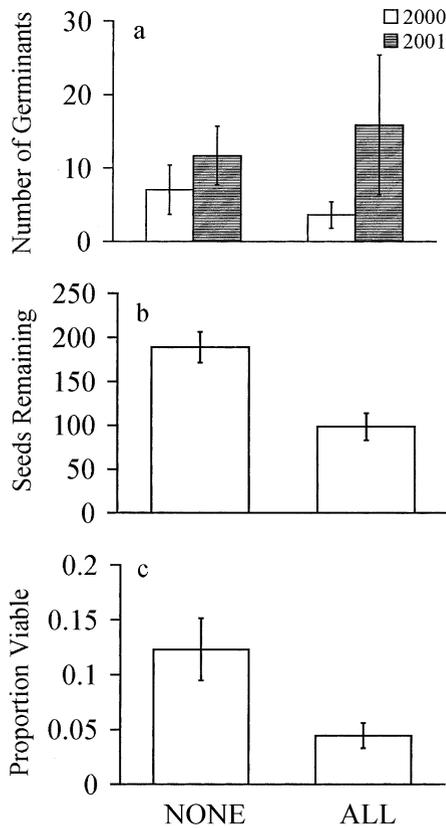
FIG. 3. Mean effects (and 95% confidence intervals) of seed predators across all patch types as measured by exclosure treatments allowing access by no seed predators (NONE) or access by invertebrate, rodent, and bird seed predators (ALL). Effects of seed predators are measured using (a) the number of *P. americana* seeds germinating in the field in 2000 and 2001, (b) the number of *P. americana* seeds remaining in experimental exclosures, and (c) the proportion of remaining *P. americana* seeds that were viable.

Corridors and overall seed predation.—Although corridors affected predator-specific seed removal, corridors did not change the overall impact of seed predators on *P. americana*: there was no effect of patch type on overall seed predation (Table 3, Fig. 2). Regardless of patch type, seed predation significantly re- duced the number and viability of remaining seeds, and reduced the number of field germinants in 2000 ($t = 2.33$, df = 39, $P = 0.03$; Fig. 3a), but not the number of field germinants in 2001 ($t = 0.13$, df = 39, $P = 0.89$; Fig. 3a). Averaged across all patch types, seed predators removed 49% of the available *P. americana* seeds ($t = 8.00$, df = 39, $P < 0.001$; Fig. 3b), and remaining seeds were only 36% as viable as seeds from NONE treatments not available to predators ($t = 5.46$, df = 39, $P < 0.001$; Fig. 3c).

Seed predation and the distribution of P. ameri- cana.—The number of *P. americana* plants was neg- atively related to seed removal by invertebrates, ro- dents, and birds (Table 4). Changes in viability and the number of germinants in 2000 were not retained in the final model. Standardized partial regression coeffi- cients suggest that seed removal by rodents was most related to reduced abundance of naturally recruiting *Phytolacca americana*, followed by seed removal by invertebrates and seed removal by birds (Table 4). Col- linearity did not affect the selection or interpretation of the final model, as the largest condition index value was 4.31, below the value of 30 indicative of collin- earity (Hair et al. 1998).

DISCUSSION

Corridors altered large-scale predator–prey interac- tions in a manner most consistent with area effects, and perhaps corridor effects (for rodents), rather than drift- fence effects. However, there was no net effect over the entire landscape because the effects of corridors on predator taxa were antagonistic: when corridors led to increased rodent seed predation, this was accompanied by reduced invertebrate seed predation, and vice versa (Table 3, Fig. 2). We suspect that there was no net corridor effect on prey (seeds) because *P. americana* seeds are readily consumed by both insects (Hyatt 1998) and mammals (McDonnell et al. 1984, Hyatt 1998). Overall seed removal from exclosures and the abundance of naturally occurring *P. americana* plants in the same patch were negatively correlated, suggest- ing that seed predators may affect the distribution of

TABLE 4. Relationship between the total number of *P. americana* plants (after log transfor- mation) found in each patch and seed predation in each of 40 patches.

Source	df	MS	Partial correlation coefficient	F	R^2	P
Model	3	12.93		8.22	0.41	<0.001
Invertebrate seed removal	1	20.18	−0.54	12.83	0.26	<0.001
Rodent seed removal	1	35.44	−0.79	22.53	0.38	<0.001
Bird seed removal	1	15.76	−0.48	10.02	0.22	0.003
Error	36	1.57				

Notes: Independent variables for each predator type were derived by subtracting treatments with the predator from treatments without the predator. Values of F and R^2 for individual predator effects are partial values that describe the effects of each predator while accounting for all others in the model. Adjusted R^2 for the entire model was 0.36.

P. americana in the landscape by reducing the number of available seeds (Table 4).

Corridors and seed predation by invertebrates, rodents, and birds.—Corridors did not influence the number of *P. americana* germinants or the viability of remaining seeds, but corridors did affect patterns of seed removal (Tables 2 and 3, Fig. 2). Moreover, seed removal and viability were significantly related to the amount of woody debris and leaf litter within a 1-m radius, emphasizing the importance of local microhabitat characteristics in affecting seed risk (Reader and Beisner 1991, Hulme 1997, Manson and Stiles 1998).

Patterns of seed removal by invertebrates were consistent with the hypothesis that invertebrate seed predators avoid edges and are affected by corridors primarily as area effects (Tables 1 and 2, Fig. 2). The shape of rectangular patches yields the most amount of core habitat relative to the amount of edge habitat, even though overall area is nearly equal among rectangular, connected, and winged patches (see *Methods*, Fig. 1). The increased core habitat in rectangular patches may represent increased high-quality habitat for early successional invertebrate seed predators. For example, fire ants (*Solenopsis* spp.) only establish in habitats where direct sunlight reaches the soil (Stiles and Jones 1998). Moreover, colony growth, abundance, and foraging are positively related to soil temperature and insolation (Porter and Tschinkel 1987, Porter 1988). The occurrence and abundance of carabid beetles and harvester ants (*Pogonomyrmex* spp.) also respond to changes in temperature, edge, and core area (Didham et al. 1998, Crist and Ahern 1999, MacMahon et al. 2000, Davies et al. 2001). Gonzalez et al. (1998) found that corridors promote population rescue for moss-dwelling arthropods. Our data suggest that the distribution of invertebrate seed predators may be limited more by habitat quality and availability than by the ability of invertebrates to colonize a patch, and support the conclusion of Collinge (2000) that corridor effects per se may be weak or nonexistent for ground-dwelling invertebrates.

Greater seed removal by rodents in connected and winged patches may arise because corridors affect rodent movement and behavior. Old-field mice (*Peromyscus polionotus*) and cotton mice (*P. gossypinus*) were the primary rodent species in our experimental patches (R. J. Brinkerhoff et al., *unpublished manuscript*), and both consume a variety of seeds (Gentry and Smith 1968, Cothran et al. 1991). Corridors may increase patch residency time of female *P. polionotus* (Danielson and Hubbard 2000), and may also serve as movement conduits for *P. polionotus* (Haddad et al. 2003; R. J. Brinkerhoff et al., *unpublished manuscript*); both effects could increase seed removal by *P. polionotus* in connected patches.

We found no evidence that corridors affect avian seed predation. The most common avian granivores in our system were Mourning Doves (*Zenaida macroura*), Dark-eyed Juncos (*Junco hymenalis*), Chipping Sparrows (*Spizella passerina*), White-throated Sparrows (*Zonotrichia albicolis*), Northern Cardinals (*Cardinalis cardinalis*), and Eastern Towhees (*Pipilo erythrophthalmus*) (P. Champlin, *personal communication*). We suspect that seed predation by avian granivores did not exhibit a corridor effect in our study due to the scale of our experimental patches. Avian granivores forage over relatively large areas, concentrating on high-density patches of seeds (Thompson et al. 1991). As such, although birds contributed to the removal of seeds (Fig. 2), the small scale of our experimental patches relative to the scale of foraging by avian granivores probably precluded any corridor effects on avian seed removal. Moreover, the nested design of our exclosure treatments may have made corridor effects more difficult to detect for avian granivores because rodents and ants also had access to ALL treatments that allowed bird access. If rodents and invertebrates compensate for corridor-mediated changes in avian seed predation, such changes may not be readily detected by measuring the number of remaining seeds. However, the significant partial correlation between bird seed removal from our experimental exclosures and the abundance of naturally recruiting *P. americana* plants (Table 4) suggests that there was a detectable "signal" of avian foraging after accounting for seed losses to invertebrates and rodents. Thus, although corridors may be important short-term foraging conduits for frugivorous birds (Tewksbury et al. 2002), corridors do not appear to affect the impact of avian granivores on *P. americana* seeds in the long term.

Corridors and overall seed predation.—Corridors led to changes in the efficacy of invertebrate and rodent seed predators (Fig. 2), but corridors did not affect total seed predation when all predators had access to seeds (Table 3, Fig. 2). Overall, seed predators significantly reduced the number of *P. americana* germinants in 2000, reduced the number and viability of remaining seeds, but did not affect the number of germinants in 2001 (Fig. 3).

The similar levels of overall seed removal among patches contrast with predator-specific patterns caused by patch shape (Fig. 2), and suggest that compensation occurs between seed predators, primarily rodents and invertebrates, as has been noted in other studies (Brown and Davidson 1977, Reichman 1979). Moreover, the difference between connected and rectangular patches provides evidence that patch shape may affect interactions between seed predators. In rectangular patches, invertebrates removed a significant amount of seeds when they had exclusive access to seeds. When rodents were also allowed access, seed removal was no longer significantly different from NONE treatments (Fig. 2a). This suggests that some reciprocal interaction was occurring, at least in rectangular patches. If invertebrates negatively affected rodents, but not vice versa, seed removal should have been equal in I and IR exclosures

in rectangular patches, which it was not (Fig. 2a). Although we cannot be certain of the mechanism, the potential for corridor-mediated interactions exists: invertebrates can alter rodent foraging (Holtcamp et al. 1997) and intraguild predation can occur between rodents and invertebrates (Gentry and Smith 1968, Danielson and Hubbard 2000). Although additional studies are required to determine if corridors affect competition in time and space, our data provide evidence that there may be little truly "predator-free" space from the perspective of *Phytolacca americana*.

Why were significant reductions in viability and the number of seeds reflected in the number of germinants in 2000 but not 2001? Several mechanisms may be at work. First, we may have failed to detect germinants that were lost to desiccation or herbivory between our sampling sessions. However, the lack of evidence of herbivory in the field (e.g., clipped seedlings) and the consistency of germination among all treatment types (Table 2, Fig. 3) do not support this explanation. Second, *P. americana* germination may have been affected by precipitation differences between 2000 and 2001. However, this explanation is not supported by field data, as there was no significant difference in precipitation during the study in 2000 and 2001 (t test, $t = 0.72$, df $= 233$, $P = 0.48$). Third, *P. americana* seedlings may exhibit density-dependent germination inhibition via allelopathy, as extracts from mature *P. americana* are known to inhibit germination (Edwards et al. 1988), and seedlings may become microsite limited when many emerge during pulses of germination (Maron and Simms 1997). Although we removed germinants as soon as we found them, our rate of removal may not have been sufficient to avoid germination inhibition of remaining seeds. Because *P. americana* germination is expected to be greatest during the spring (Baskin and Baskin 2001), density-dependent allelopathic effects would be most likely to occur during the spring phase of our study (i.e., in 2001), in agreement with the greater number of germinants we observed from March to July 2001 compared to June–September 2000 (see *Methods*, Fig. 3a).

Seed predation and the distribution of P. americana.—We observed a significant negative relationship between the abundance of naturally recruiting *P. americana* and seed removal from our experimental exclosures. It is possible that the relationship between the number of seeds remaining and the number of naturally recruiting *P. americana* is spurious, because we surveyed plants in 2000, but collected seed-removal and viability data in 2001. However, the strength of the relationship between seed removal and naturally recruiting plants was strong, as seed removal explained 41% of the variance in *P. americana* abundance (Table 4).

Although seed removal by rodents was most related to the overall abundance of *P. americana* plants, removal by invertebrates and birds was also important (Table 4). Rodent seed predators may have more influence on *P. americana* than invertebrate seed predators because rodents detect and exhume buried seeds (Reichman 1979, Abramsky 1983). Because avian seed predators forage across large scales and target high-density seed patches, their impact may be to reduce spatial variation in seed density rather than dramatically reduce total seed density (Thompson et al. 1991). Moreover, each experimental unit may receive a fraction of foraging by avian granivores compared to invertebrate and rodent granivores because the latter forage almost exclusively within each experimental unit. Although avian seed predators generally removed fewer seeds than rodents and invertebrates (Fig. 2), the significant relationship between seed removal by birds and the abundance of naturally occurring *P. americana* (Table 4) suggests that avian granivores may still have important effects on *P. americana* recruitment.

Corridors, predators, and prey.—Corridors may have several beneficial effects that make them amenable to conservation (Rosenberg et al, 1997, Haddad 1999, Tewksbury et al. 2002). However, our results demonstrate that corridors also affect multiple species in different ways within a given trophic level. Generally, our results suggest that corridors are most likely to alter predator–prey interactions when predators differ greatly in their response to corridors and in their impacts on prey. For example, seeds that are consumed only by a particular predator type would be more likely to exhibit a net effect due to corridors. Hence, large-seeded, early successional species, such as *Prunus* spp., that are primarily consumed by rodents (Whelan et al. 1991), may benefit from lower predation in rectangular patches, whereas the converse may be true for seeds primarily consumed by invertebrates. Moreover, by mediating interactions among seed predators, corridors could differentially affect seed banks in fragmented landscapes and thus shape the resulting plant community.

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