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CORRIDORS CAUSE DIFFERENTIAL SEED PREDATION

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Abstract. Corridors that connect disjunct populations are heavily debated in conservation, largely because the effects of corridors have rarely been evaluated by replicated, large-scale studies. Using large-scale experimental landscapes, we found that, in addition to documented positive effects, corridors also have negative impacts on bird-dispersed plants by affecting seed predation, and that overall predation is a function of the seeds' primary consumer (rodents or arthropods). Both large-seeded *Prunus serotina* and small-seeded *Rubus allegheniensis* experienced greater predation in connected patches. However, *P. serotina* experienced significantly less seed predation compared to *R. allegheniensis* in unconnected patches, due to decreased impacts of rodent seed predators on this large-seeded species. Viewed in light of previous evidence that corridors have beneficial impacts by increasing pollination and seed dispersal, this work demonstrates that corridors may have both positive and negative effects for the same plant species at different life stages. Moreover, these effects may differentially affect plant species within the same community: seeds primarily consumed by rodents suffer less predation in unconnected patches. By shifting the impact of rodent and arthropod seed predators, corridors constructed for plant conservation could lead to shifts in the seed bank.

Key words: connectivity; conservation; corridor; granivory; plant community; seed predation.

INTRODUCTION

Corridors are a controversial strategy for reducing the negative impacts of habitat fragmentation (see reviews in Rosenberg et al. 1997, Beier and Noss 1998, Tewksbury et al. 2002, Haddad et al. 2003). By connecting disjunct patches, corridors are thought to increase population persistence by promoting population rescue after local extinction, increasing gene flow, and by increasing abundance (Rosenberg et al. 1997). However, corridors have been criticized because mechanisms underlying purported corridor effects are unknown (Simberloff et al. 1992) and because of a lack of large-scale evidence that corridors have beneficial effects (but see Mech and Hallett 2001, Tewksbury et al. 2002, Haddad et al. 2003). Characterizing the impact of corridors is further complicated because corridors can affect populations in at least three ways: corridors can connect patches ("corridor effects"), corridors can serve to intercept organisms moving through the matrix

and direct them into a focal patch ("drift-fence effects"; Rosenberg et al. 1997), and corridors change the amount of area in a patch ("area effects"; Haddad and Baum 1999).

For plants, recent work suggests that corridors may have positive effects by increasing pollination and seed dispersal (Tewksbury et al. 2002, Haddad et al. 2003). However, corridors may also negatively impact plants at other life stages. For example, corridors may affect the impact of seed predators: rodents have been shown to consume more seeds of pokeweed, *Phytolacca americana*, in connected patches, whereas arthropods consumed more *P. americana* seeds in unconnected patches (Orrock et al. 2003). As such, corridors could lead to greater impacts on seeds primarily consumed by rodents (generally larger seeds; Brown and Heske 1990, Whelan et al. 1991) and reduced impacts on seeds consumed primarily by arthropods. If corridor-mediated shifts in seed predation affect some seeds but not others, using corridors for conservation could lead to unintended shifts in the plant community, similar to documented shifts in plant community composition following exclusion of specific seed predators (e.g., Brown and Heske 1990, Howe and Brown 2000, 2001).

We used a large-scale experimental landscape composed of clearcut patches within a matrix of mature

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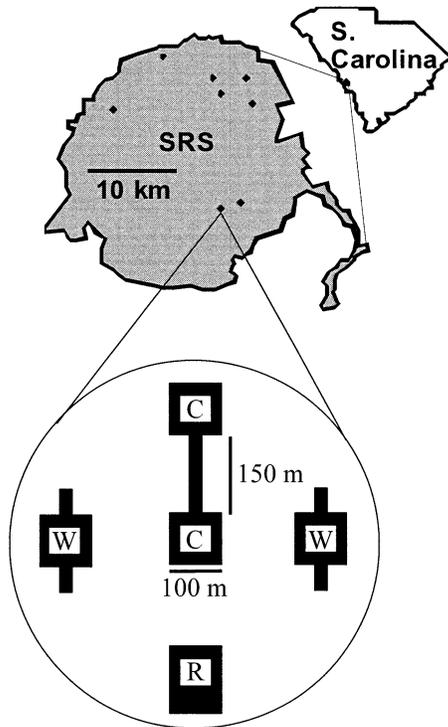


FIG. 1. The experiment was conducted in eight replicated blocks at the Savannah River Site (SRS), South Carolina, USA. Each block consisted of five patches created during the fall and winter of 1999 by clear-cutting mature pine forest (the matrix) followed by prescribed burning. In each block, there were three different patch types: connected (C), rectangular (R), and winged (W).

pine forest (Fig. 1) to determine if corridor-mediated changes in seed predation lead to differential impacts on two plant species that differ in their susceptibility to rodent and arthropod seed predators. Black cherry (*Prunus serotina*) and blackberry (*Rubus allegheniensis*) are common in recent clearcuts in the study area (Radford et al. 1968). Both species are dispersed by vertebrates, including birds (Smith 1975), and therefore are predicted to benefit from corridors (Tewksbury et al. 2003). The seeds of these two species differ substantially in size: *P. serotina* seeds are large (6.29–6.71 mm; 0.068–0.084 g; 95% CI, $n = 10$ seeds) and are consumed primarily by rodents (Whelan et al. 1991), whereas *R. allegheniensis* seeds are much smaller (2.29–2.62 mm; 0.002–0.003 g; 95% CI, $n = 10$ seeds), and are likely to be consumed by both arthropods and rodents (Smith 1975). Because corridors could influence seed predators by changing both patch connectivity and patch shape, the experimental landscape contained three different patch types, allowing us to distinguish the ways in which corridors can influence the impact of seed predators. Our objectives were to determine (1) if seed predation by rodents and arthropods differed with patch shape and connectivity, (2) if overall seed predation differed with patch shape

and connectivity, and (3) if patch shape and connectivity affected seed predation of one plant species more than the other.

METHODS

Study area and experimental landscape

The experiment was conducted in eight 12-ha replicated blocks created at the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina, USA (Fig. 1). Each block 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 block, there were three different patch types: connected, rectangular, and winged. Connected patches consisted of a 1-ha square patch joined by a 25 m wide corridor that was 150 m long. Rectangular patches consisted of a 1-ha square patch with 0.375 ha of additional area, representing the area added by the corridor. Winged patches consisted of a 1-ha square patch with two extending drift-fence sections, each 75 m long and 25 m wide. All patches were of similar area: connected patches were 1.19 ha, whereas winged and rectangular patches were 1.38 ha. Two connected patches were in each block. Four of the eight blocks had two rectangular patches and one winged patch, whereas the other four blocks had two winged patches and one rectangular patch, yielding a total of 12 winged patches, 12 rectangular patches, and 16 connected patches.

Use of three different patch types allowed us to determine if corridors influenced seed predation by changing patch connectivity (corridor effects), by serving to direct organisms into a focal patch (drift-fence effects), or by changing patch shape (area effects). If corridors affect seed predation by increasing connectivity alone, predation should differ between connected and unconnected patches (connected patches \neq winged and rectangular patches). If corridors affect seed predation by serving as a drift fence, foraging should be similar between connected and unconnected patches of the same shape (winged patches = connected patches; winged and connected patches \neq rectangular patches). If corridors affect seed predation by changing patch shape, the change in predation should depend upon how seed predators respond to patch edges, because patch types differed in the relative amounts of edge and core habitat, although area was similar among all patches. This is 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. Edge-loving seed predators should exhibit greatest activity in connected and winged patches (where the amount of edge relative to patch area is greatest). Conversely, edge-avoiding seed predators should exhibit greatest activity in rectangular patches. For seed predators that have no preference regarding edges, impact should be similar among all patch types because total

area is similar among all patch types (i.e., winged patches = connected patches = rectangular patches). The small difference in total area between connected and unconnected patches does not change the qualitative order of our predictions. Rather, if seed removal is greatest in connected patches despite the slightly reduced overall area of connected patches, we have a more conservative test for corridor effects.

Arthropod and rodent seed predation

To quantify seed predation, paired $27 \times 27 \times 11$ cm trays were placed next to one another along a random side of an 8-m square centered in each patch (80 total trays; Fig. 1). Each tray was filled with 1.5 L of sand, similar to the sandy soils of the study area. Trays had two 2.5-cm openings and were covered with tight-fitting lids. Lids eliminated seed loss due to rain and wind and served to exclude avian granivores, which have been shown to have negligible impacts relative to arthropods and rodents in this study area (Orrock et al. 2003). One tray (A) was open only to arthropods (tray openings were barred with metal fencing with 1.5-cm² mesh), whereas the other tray (AR) was open to arthropods and rodents (tray openings unbarred). We assume that seed removal is equivalent to seed predation. This assumption is supported by previous work in this system that shows a strong relationship between seed removal and recruitment of naturally occurring plants (Orrock et al. 2003), as well as frequent signs of depredation within foraging trays during the current experiment (hulls of depredated seeds were found in 38% of our observations).

In each tray, 20 seeds of each species were scattered on the surface of the sand, an amount representative of seed deposition (Smith 1975) and similar to densities used in other seed predation studies (Willson and Whelan 1990). Seeds were obtained from a commercial supplier (Sheffield's Seed Supply, Locke, New York, USA). *Rubus allegheniensis* seeds were chosen because they are located in the study area and are of intermediate size compared to the two other *Rubus* species in the study area: *R. cuneifolius* (2.42–2.60 mm; 95% CI, $n = 10$ seeds) and *R. argutus* (2.19–2.37 mm; 95% CI, $n = 10$ seeds).

Seed predation trials were conducted twice at all locations, from 30 July to 10 September 2002 and from 10 September to 7 October 2002. There was no difference between data collected during the two sessions within each patch type (paired t tests, all $P > 0.15$); data were pooled for analysis. Substrate and vegetation characteristics (which can affect seed removal; Orrock et al. 2003) were measured by a single observer (E. I. Damschen) in a 1-m radius around each pair of trays in late July 2002 by visually estimating the percent cover of downed woody debris, woody plants, herbaceous plants, bare soil, and leaf litter.

Statistical analyses

We used a mixed-model ANOVA (Quinn and Keough 2002) to determine if rodent and arthropod removal of *P. serotina* and *R. allegheniensis* differed due to connectivity or patch shape. Our split-plot design included block and patch type (connected, rectangular, or winged) as the main plot, with enclosure treatment (A or AR) as the small plot. Patch type and enclosure were fixed effects. Block was treated as a random effect (Quinn and Keough 2002). To determine whether overall seed removal (i.e., seeds removed from AR enclosures) differed due to patch shape or connectivity, we used a linear contrast. To determine if patch shape and connectivity affected overall removal of one species more than the other, we used the difference between the number of *R. allegheniensis* and *Prunus serotina* remaining in AR trays as the dependent variable in a mixed-model ANOVA with patch type as a fixed effect and block as a random effect.

Substrate and vegetation variables were examined as possible covariates in all three analyses: a split-plot ANOVA for each plant species, and the ANOVA for the difference between *P. serotina* and *R. allegheniensis* in A and AR enclosures. All analyses were performed with SAS Version 8.1 (SAS Institute 2000). The number of *R. allegheniensis* seeds remaining was square-root transformed to improve normality (Quinn and Keough 2002). Although their inclusion does not change the qualitative outcome of our analyses, observations from two patches are not used in the analyses due to disturbance by feral pigs. Estimates are presented with 95% confidence intervals to provide an estimate of the effect sizes observed in our study and to allow readers to interpret the biological significance of our findings (Johnson 1999).

RESULTS

Seed removal differed among connected, rectangular, and winged patches and also differed depending upon which predators were allowed access (Fig. 2A, B). Due to the interaction between patch type and enclosure treatment, strong predator- and patch-specific patterns led to a marginally significant main effect of patch type for *Rubus allegheniensis* (Table 1). This occurred because allowing rodents access to *R. allegheniensis* seeds significantly increased seed removal in connected and winged patches, but not in rectangular patches (Table 1, Fig. 2B). Arthropods rarely removed *Prunus serotina* seeds, and allowing rodents access to *P. serotina* seeds always led to significantly greater seed removal regardless of patch type (Table 1, Fig. 2A). When overall seed removal was examined (AR enclosures), removal of both *P. serotina* and *R. allegheniensis* seeds differed among patch types (Table 1), with greater removal of *P. serotina* (linear contrast, $F_{1,35} = 12.44$, $P < 0.01$) and *R. allegheniensis* (linear contrast, $F_{1,35} = 5.76$, $P = 0.02$) seeds in connected patches compared

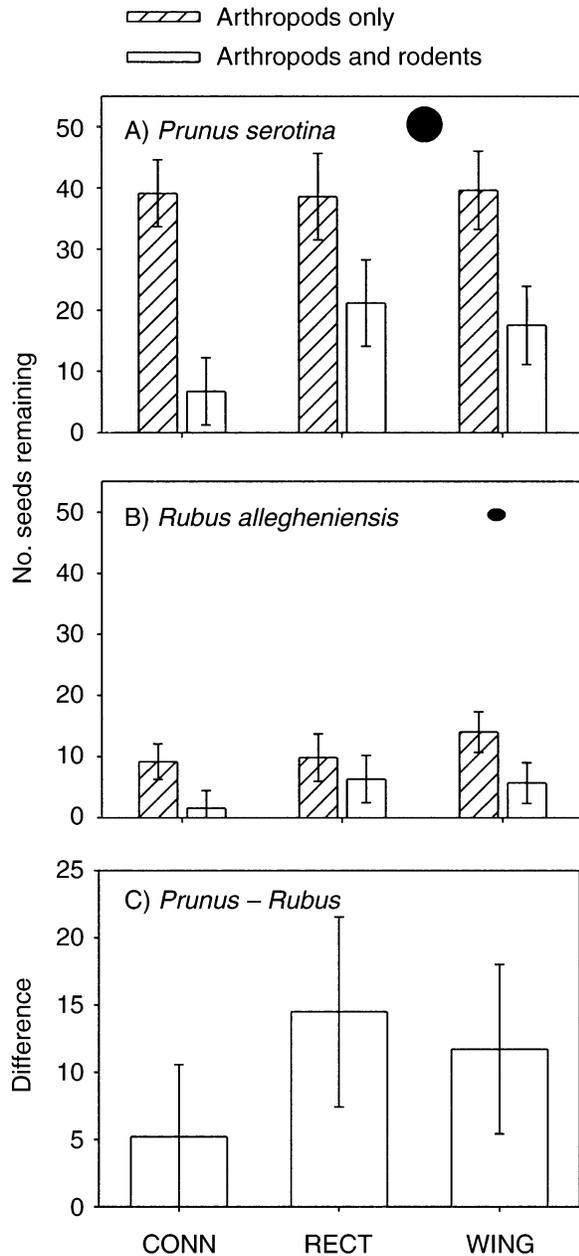


FIG. 2. Mean number (and 95% confidence intervals) of (A) *Prunus serotina* seeds and (B) *Rubus allegheniensis* seeds left by arthropods or arthropods and rodents in connected (CONN), rectangular (RECT), and winged (WING) patches. Black shapes after each species name in (A) and (B) depict the actual size and shape of a typical seed of that species. (C) The difference between *P. serotina* and *R. allegheniensis* in the number of seeds remaining in exclosures open to both rodents and arthropods. Forty seeds of each species were available for removal over the course of the experiment.

to winged and rectangular patches (Fig. 2A, B). Arthropod removal of *R. allegheniensis* seeds was positively related to the amount of bare soil around exclosures (coefficient = -2.24 ± 2.27 , mean and 95% CI; $F_{1,27} = 3.99$, $P = 0.06$). Removal of *P. serotina* and

the difference between *R. allegheniensis* and *P. serotina* seed removal were not related to substrate and vegetation features (all $P > 0.15$).

In winged and rectangular patches, more *R. allegheniensis* were removed compared to *P. serotina*; i.e., the difference between *P. serotina* and *R. allegheniensis* was significantly different from zero (Fig. 2C; $t > 3.80$, $df = 28$, $P < 0.01$). In connected patches, the difference was marginally significant (Fig. 2C; $t = 1.08$, $df = 28$, $P = 0.06$). The main effect of patch type on the difference between the number of *R. allegheniensis* and *P. serotina* removed by both arthropods and rodents was also marginally significant ($F_{2,28} = 2.66$, $P = 0.09$). As suggested by the overall patterns of seed removal (Fig. 2), there was a smaller difference in connected patches compared to winged and rectangular patches (linear contrast, $F_{1,28} = 5.14$, $P = 0.03$); i.e., removal of both species was most equal in connected patches (Fig. 2C).

DISCUSSION

Our findings indicate that corridors can have negative impacts on bird-dispersed plants via seed predation (Orrock et al. 2003), and that these effects may be a function of seed size and susceptibility to particular seed predators (Fig. 2). As such, the impact of corridors on plants may be species and life-stage specific: seeds that are primarily consumed by rodents may suffer less predation in unconnected patches, but seeds that survive in connected patches may later benefit from greater pollination and seed dispersal (Tewksbury et al. 2002, Haddad et al. 2003).

Our findings support other evidence that corridor effects are more important than drift-fence or area effects in affecting overall rodent seed predation (Orrock et al. 2003). Several potential mechanisms might contribute to greater rodent seed predation in connected patches, and explanations are not mutually exclusive. It seems likely that shifts in seed predation are not due to corridor-mediated changes in rodent abundance *per se*, because previous work has shown that the overall abundance of two common rodent seed predators, cotton mice (*Peromyscus gossypinus*) and cotton rats (*Sigmodon hispidus*) was unaffected by corridors in a similar experimental landscape (Danielson and Hubbard 2000, Mabry et al. 2003). Likewise, Mabry et al. (2003) found that another common seed predator, the oldfield mouse (*Peromyscus polionotus*) was equally abundant in connected and unconnected patches in two years, and less abundant in connected patches in the third year, further suggesting that rodents are not more abundant in connected patches.

Rather than shifting abundance, corridors may alter seed predation by changing movement, habitat use, and population structure of rodent species such as *P. polionotus* and *S. hispidus*, which are found almost exclusively within early-successional habitats (Danielson and Hubbard 2000, Mabry et al. 2003). *Sigmodon his-*

TABLE 1. Summary of mixed-model ANOVA analyses of removal of *Rubus allegheniensis* and *Prunus serotina* seeds by arthropods (A) and arthropods and rodents (AR) in three different patch types (connected, rectangular, and winged).

Effect	<i>Prunus</i>			<i>Rubus</i>		
	F	df	P	F	df	P
Patch type	3.10	2, 28	0.06	3.53	2, 27	0.04
Exclosure	89.66	1, 35	<0.01	26.88	1, 35	0.01
Patch type × exclosure						
Arthropod removal (A) equal among patch types	0.02	2, 35	0.98	2.65	2, 35	0.09
Arthropod and rodent removal (AR) equal among patch types	6.37	2, 35	<0.01	3.13	2, 35	0.06
A and AR removal equal in connected patches	71.58	1, 35	<0.01	20.37	1, 35	<0.01
A and AR removal equal in rectangular patches	12.92	1, 35	<0.01	1.91	1, 35	0.18
A and AR removal equal in winged patches	24.98	1, 35	<0.01	12.11	1, 35	<0.01

Note: The interaction between patch type and exclosure treatment is dissected into planned linear contrasts to determine how patterns of removal vary among and within patch types.

pidus is more likely to leave patches via a corridor (Bowne et al. 1999, Haddad et al. 2003), and *P. polionotus* and *S. hispidus* are more likely to move between connected patches compared to *P. gossypinus* (Mabry and Barrett 2002, Haddad et al. 2003). More male than female *S. hispidus* and *P. polionotus* were found in unconnected patches (Danielson and Hubbard 2000), suggesting that connected patches may represent qualitatively different habitats. Corridors may also increase the patch residency time of female oldfield mice, *Peromyscus polionotus* (Danielson and Hubbard 2000), which could contribute to the greater seed removal by rodents in connected patches. At least for *P. polionotus*, patch shape may also be important. *Peromyscus polionotus* activity is greatest in the center of connected and winged patches (Mabry et al. 2003; Orrock and Danielson, *in press*). Increased activity near the patch center (where we measured seed predation; Fig. 1), when coupled with greater residency times in connected patches, could contribute to the greater levels of rodent seed predation that we observed in connected patches.

The interplay between arthropod and rodent seed predators may also be important in determining how connectivity and patch shape affect overall seed predation of *Rubus allegheniensis*. Allowing rodent seed predators access to seeds resulted in significant increases in seed removal in connected and winged patches (Table 1). However, arthropods alone were just as effective as both arthropods and rodents in rectangular patches (Table 1, Fig. 2B). This patch-specific shift in the relative importance of arthropod vs. rodent seed predation may be magnified in natural situations, where seeds may escape predation by being buried by wind or rain (because our design used covered trays to exclude avian granivores, seeds could not be buried by wind or rainfall events). Rodents will exhume and consume large buried seeds, whereas arthropod seed predators generally only consume seeds on the soil surface (Reichman 1979, Hulme 1994). As such, burial would be expected to lead to even greater overall survival of *R. allegheniensis* seeds in rectangular patches, because

R. allegheniensis is more likely to be buried due to its smaller size (Bekker et al. 1998), and burial would provide safety from arthropods. In connected and winged patches, *R. allegheniensis* would be less likely to escape consumption via burial, because rodents are significant seed predators in these patches (Fig. 2B).

Overall predation on *Prunus serotina* seeds was significantly less than predation on *R. allegheniensis* seeds in rectangular and winged (i.e., unconnected) patches due to the reduced impact of rodent seed predators (Fig. 2). The magnitude of the difference was significant between connected and unconnected patches: on average, remaining *P. serotina* seeds were more than twice as abundant as *R. allegheniensis* seeds in unconnected patches compared to connected patches (Fig. 2). Although more research is required to understand whether these differences in seed survival are sufficient to produce changes in the relative abundance of established *P. serotina* and *R. allegheniensis*, the crux of our findings is that corridors can cause differential seed predation that favors a large-seeded species (*P. serotina*) in unconnected patches. Because seed size may determine the risk of consumption by rodent granivores, our work predicts that, all else being equal, small-seeded plant species will form a larger portion of the plant community in connected patches, because rodent granivory will more effectively suppress large-seeded species (e.g., Brown and Heske 1990). Conversely, large-seeded species will perform better in unconnected patches, where rodent granivory is reduced. Given evidence that rodent foraging is sensitive to patch geometry (Bowers and Dooley 1993; Orrock and Danielson, *in press*), edge (e.g., Bowers and Dooley 1993, Ostfeld et al. 1997), and connectivity (Fig. 2), and that these effects can translate into landscape-level changes in plant recruitment (Tallmon et al. 2003), a greater understanding of how patch shape and connectivity affect rodent consumers may be critical for predicting the impacts of anthropogenic habitat alteration on plant communities.

Corridors have beneficial effects that make them useful for conservation (Rosenberg et al. 1997, Gonzalez

et al. 1998, Mech and Hallett 2001, Tewksbury et al. 2002, Haddad et al. 2003). However, our results demonstrate that corridors also may affect predators that subsequently impact prey: both *P. serotina* and *R. allegheniensis* experienced greater overall seed predation in connected patches (Fig. 2), and more *R. allegheniensis* were consumed in unconnected patches relative to *P. serotina*. Ultimately, our results indicate that understanding the impact of corridors on the survival of a particular plant species will require understanding how corridor benefits at one life stage may be offset by negative effects of corridors (e.g., as mediated through corridor effects on granivores) on another life stage. Other work has demonstrated that plant community composition can shift following the manipulation of rodent granivores (Brown and Heske 1990, Howe and Brown 2000, 2001); our work suggests that corridors affect the impact of seed predators, and thus could lead to impacts on plant communities.

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