

Characterizing post-dispersal seed predation in the matrix of a connected landscape: spatial, temporal and species-specific variation and its effect on biodiversity spillover

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Michael Craig
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ABSTRACT

By improving connectivity between patches, corridors have been demonstrated to be an important conservation tool in addressing habitat fragmentation and loss, the gravest threats to biodiversity worldwide. Recent work suggests that the effect of corridors can extend beyond connected patches, as adjacent habitats also have greater diversity. This “spillover effect” could occur because either more seeds arrive in these areas, or fewer seeds are removed by seed predators. However, no studies have documented which of these mechanisms contributes to this increased diversity. I investigated seed predation by counting the number of remaining seeds in seed depots placed in the matrix of a landscape-level, highly replicated corridor system. Spatial, temporal, and species-specific variation in seed predation were examined and related to observed patterns in biodiversity spillover. My results show that patch type did not significantly affect matrix seed removal, suggesting that increased spillover around connected patches is not driven by seed predation. However, matrix seed removal of small-seeded *Carphephorus bellidifolius* and *Anthaenantia villosis* was significantly higher than that of large-seeded *Phytolacca americana*. This species-specific removal, in conjunction with the dispersal mode (wind, unassisted, and avian, respectively) and subsequent expected deposition rates of each seed species, could determine the composition of the spillover community. Similarly, documented temporal variation in seed removal, whereby removal in the summer was significantly greater than that in the fall, could differentially affect seed species based on time of dispersal. Matrix seed removal was also significantly higher at 50 m from the patch edge than at the patch edge, a trend that could partially explain the observed decay of biodiversity spillover. These findings have strong implications for the conservation of fragmented landscape, and serve as a foundation for further research into the determinants of biodiversity spillover.

INTRODUCTION

25 Habitat destruction poses one of the greatest threats to biodiversity (Wilcove et al. 1998). Subsequent habitat fragmentation further endangers biodiversity by various mechanisms, including microclimate alteration and population isolation (Saunders et al. 1991). To alleviate the negative effects of habitat fragmentation, corridors may be promising tools. Corridors, or strips of land that connect two isolated patches of habitat, theoretically increase connectivity and

30 thereby facilitate gene flow, demographic stability, recolonization, and heterozygosity (Rosenberg et al. 1997). Recent landscape-scale studies have demonstrated that corridors positively affect plant communities by increasing seed dispersal and pollination (Tewksbury et al. 2002) and species richness (Damschen et al. 2006). Other studies, however, have suggested corridors may not promote connectivity (Beier and Noss 1998) and could also foster the spread

35 of invasive species (Simberloff and Cox 1987) and disease (Hess 1994). As a result, the actual conservation value of corridors has been debated (Haddad et al., *in press*, Gilbert-Norton et al. 2010, Simberloff et al. 1992, Simberloff and Cox 1987). Adding to the potential positive effects of corridors, Brudvig et al. (2009) recently documented a “spillover” effect, whereby an increase in species richness within patches connected by corridors led to an increase in plant species

40 richness in the surrounding matrix, or the intervening habitat between two patches of similar habitat (Ricklefs 2008). The increase in species richness within connected patches, and subsequently in the surrounding matrix, has been shown to vary by dispersal mode, for species with higher seed mobility (dispersal) can travel farther and in greater quantities, leading to increased seed deposition (Brudvig et al. 2009, Damschen et al. 2008). Yet, seed predation as

45 well as deposition can drive the seed limitation of species (Turnbull et al. 2000), but it is unclear which factor, or even an interaction between the two, underlies biodiversity spillover, a seed-

limited community. Consequently, disentangling the roles of seed predation and deposition would help determine which of the two limits the spread of plant species into non-target habitat surrounding connected patches. By using a highly-replicated fragmented landscape of longleaf pine savannah, one of the most endangered ecosystems in the United States (Noss et al. 1995), I was able to quantify matrix seed predation not only at a scale rarely used in conservation studies (Harrison and Bruna 1999), but also at the same spatial scale as biodiversity spillover, thereby facilitating comparisons between the two. Ultimately, I aim to better understand the determinants of the spillover effect, and therefore increase its predictability.

Seed predation by rodents and arthropods significantly affects plant communities (e.g. Paine and Beck 2007, Hulme 1997, Brown and Heske 1990). Temporal, spatial, and species-specific variation in seed predation (e.g. Plucinski and Hunter 2001; Manson and Stiles 1998; Brown and Heske 1990) can create a mosaic of predation across a landscape that results in differential predation on seed species (Plucinski and Hunter 2001, Whelan et al. 1990); it is therefore necessary to quantify spatiotemporal variation in seed predation across species to address broad questions of interest, e.g. whether seed limitation in biodiversity spillover is driven by seed predation or dispersal (Clark et al. 1999, Hyatt 1998, Hulme 1997). Due to seed predation's influential role in ecosystems, much work has already been done to characterize it within corridor systems. For instance, Orrock et al. (2006) demonstrated that the abundance of *Phytolacca americana*, an early successional plant, across a landscape was determined by seed predation, not dispersal. Also, while corridors have been shown to not alter total seed predation, they can also lead to different shifts, based on seed size, in seed predation by rodents and arthropods (Orrock and Damschen 2005, Orrock et al. 2003). Yet, despite extensive work within corridors, seed predation has not been characterized in the surrounding matrix, although many

70 experiments have assessed seed predation in forest interiors relative to that of edges in other
landscapes, yielding contrasting results. For instance, Plucinski and Hunter (2001) found no
difference in seed predation by both rodents and arthropods between intact forest and forest gaps.
However, Wolf and Batzli (2004) showed seed predation by *Peromyscus leucopus* is higher in
forest interiors than at edges, which they attributed to the edge-averse behavior of rodents (see
75 Orrock et al. 2005, Manson and Stiles 1998), whereas Meiners and LoGiudice (2003)
documented seed predation by *P. leucopus* to be higher at edges than in either forest interiors or
old fields. The importance of determining the gradient of seed predation across edges and forest
interiors was underscored by work done in conifer forests in the Pacific Northwest, where
fragmented forest edges and interiors were found to harbor higher densities of granivorous mice
80 than unfragmented forest interiors, which led to negative demographic changes in trillium
(Tallmon et al. 2003). Similar ecosystem-wide effects may be affected by corridors and could
underlie spillover (Staddon et al. 2010).

For the first time, I quantified seed predation in the matrix of a highly replicated
landscape-level corridor system in order to investigate seed predation's role in determining
85 biodiversity spillover. Both spatial, temporal and size-specific variation in seed predation were
investigated by measuring seed predation of three longleaf pine savannah species along a
gradient from patch edge to matrix interior around connected and unconnected patches in the
summer and fall. The spatial gradient allowed for the observation of any sharp changes in seed
predation proximal to the patch edge where spillover rapidly decays and where both patch- and
90 matrix-dwelling granivores may forage, while still quantifying seed predation at the distal edge
of spillover. The summer (average temperature, average precipitation; 73.4 °F, 2.99") and fall
(44.6 °F, 7.58") sampling periods captured both climactic and ecological variation (e.g. longleaf

95 pines setting seed) (The Southeast Regional Climate Center 2010, Boyer 1990). Patterns of
variation in seed predation were linked to dispersal ability and seed size, a factor in both
dispersal and predation (Mendoza and Dirzo 2007, Venable and Brown 1988), and used to better
understand biodiversity spillover. I predict that matrix seed predation will (1) not vary by patch
100 type, given previous work within corridors (Orrock et al. 2003); (2) be highest at intermediate
distances to the patch, where both patch- and matrix-dwelling granivores may forage, and lowest
at the edge, due to the edge aversion of rodents; and (3) be greater on wind- than avian-dispersed
species, per higher spillover of avian- than wind-dispersed species.

METHODS

Experimental Site

105 Experiments were conducted within eight 12 ha blocks at the Savannah River Site, a
200,000 acre National Environmental Research Park south of Aiken, South Carolina. In each
block, five open patches were created by clear-cutting the existing mature pine forest,
predominantly *Pinus palustris* (Longleaf Pine) and *Pinus taeda* (Loblolly Pine). After prescribed
burns, longleaf pine savannah, one of the most endangered ecosystems in the United States (Noss
et al. 1995), was established within each patch. This savannah contrasts to the sparsely-covered
110 floor of the surrounding forest, creating a marked edge around patches. Each block contains five
patches oriented in a cross, with a peripheral patch located 150 m from each edge of the central
patch (Figure 1). A 150 m x 25 m corridor connects the central patch to a peripheral
("connected") patch, each measuring 100 m x 100 m. The three other patches are either "winged"
(100 m x 100 m square with two 75 m x 25 m wings off opposite sides) or "rectangular" (100 m
115 x 137.5 m); in each block, there is a duplicate winged or rectangular patch.

The different patch types within each block allow us to test for the three possible mechanisms by which corridors may affect matrix seed predation: increasing patch connectivity (corridor effects), funneling organisms into a patch (drift-fence effects), and altering the shape of a patch (area effects). Winged and rectangular patches have equal area to the connected patch and corridor combined, thereby controlling for effects of larger patch size (e.g. Wilson and Taylor 1967). If corridors function only via corridor effects, matrix seed predation should be dissimilar around connected and unconnected patches (connected patches \neq winged patches; connected patches \neq rectangular patches). Drift-fence effects would lead to a difference between winged and connected patches and rectangular patches, which are dissimilarly shaped (rectangular patches \neq winged patches; rectangular patches \neq connected patches), but not between winged and connected patches, which have similar habitat protrusions that may divert organisms (winged patches = connected patches). If area effects occur, matrix seed predation would vary according to patch shape, which is approximated by the area to perimeter ratios of the different patch types: 22.62 for connected, 19.64 for winged, and 28.95 for rectangular. For edge-loving organisms, seed predation would be expected to be higher around winged and connected patches than around rectangular patches, particularly closer to the patch edge. For edge-averse organisms, the reverse would be expected, or higher seed predation around rectangular patches than around winged and connected patches.

The seeds of three herbaceous species were used to quantify matrix seed predation: *Phytolacca americana* (American Pokeweed, 2.5 mm diameter, 90.2 mg mass), *Carphephorus bellidifolius* (Sandywoods Chaffhead, 5 mm length, 27.9 mg mass), and *Anthraenantia villosis* (Green Silkscale, 3 mm diameter, 23.6 mg mass) (Figure 2). *P. americana* has previously been shown to be seed limited in this landscape (Orrock et al. 2006), while *C. bellidifolius* and *A.*

villosis both inhabit early successional habitats and are thus also likely to be seed limited (Clark
140 et al. 2007, Turnbull et al. 2000). All three species are native to longleaf pine savannahs, the
latter two being coastal plain endemics, and are dispersed via different mechanisms (avian, wind,
and unassisted, respectively). Consequently, I was able to observe how seed predation in the
matrix varied with respect to dispersal mode, which correlates with the magnitude of species-
specific spillover from corridors (Brudvig et al. 2009). Seeds were collected from SRS between
145 2007 and 2009. Before use in predation experiments, I determined the apparent viability of *A.*
villosis and *C. bellidifolius* seeds by gently squeezing them; those that resisted pressure were
considered viable (Ball and Miller 1990). *P. americana* seeds were extracted from berries; for all
species, seeds were presented as though they were naturally dispersed.

Seed Predation Experiment

150 Seed predation was investigated in the non-target pine forest surrounding a connected,
winged, and rectangular patch in each block using seed removal depots (Figure 1). The central
patch and one randomly selected duplicate peripheral patch were not used in my experiments.
Around all selected patches, I laid a line transect extending 50 m into the matrix from each
corner. Transects were set equidistantly from the two proximal patch edges and bisected the
155 grids used to quantify spillover by Brudvig et al. (2009). At 0, 15, and 50 m from the patch on
each transect, I set three clear plastic seed removal depots, spaced 1 m apart perpendicularly to
the transect. Depots had a 2.5 cm circular opening in two adjoining sides, which were oriented
into the matrix, and a tight fitting lid, assuring no seeds were lost to wind, rain, or other non-
predation events. No exclosures were employed, allowing both arthropods and rodents access to
160 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; all three seed species were used at

all distances. This number of seeds per depot is similar to that used in previous seed predation studies both within (Orrock and Damschen 2005) and outside (Meiners and LoGiudice 2003) the experimental system. Seed removal trials were conducted at all locations over two twenty day periods in 2009, from 18 August to 7 September (summer) and 12 November to 2 December (fall).

Data Analysis

Trays that were tipped during field experiments were excluded from data analysis, as were two transects due to the proximity of non-experimental clear cuts. The number of remaining seeds containing endosperms was tallied for each tray. Seeds not present in the tray at the end of each twenty-day trial were assumed to have been consumed by seed predators. The number of fecal pellets and empty hulls found in each tray were also recorded as evidence of rodent predation, for rodents typically consume seeds at the site of discovery, leaving empty hulls behind, whereas insects often remove the entire seed. Hull data was only applicable to *C. bellidifolius* and *A. villosis*, since *P. americana* has no removable seed coat. I used a linear mixed effects model to establish whether seed removal (proportion of seeds removed) and evidence of predation (number of empty hulls per seed removed) varied by patch type, distance from the patch edge, species, season, or any interaction therein. My experiment was a multi-level split-plot design, where patch type was the main plot and transect, distance, species, and season were all subplots. Block number was included as a random effect in my model to control for variation between sites. The number of seeds remaining and number of empty hulls were summed across transects in each patch for a given species, distance, and season before calculating the proportion of seeds removed and number of empty hulls per seed removed, although trays with no seed removal were excluded from hull analyses. The proportions of seeds removed were arcsine-root

185 transformed to improve normality (Quinn and Keogh 2002), and both data sets were modeled as normal distributions. A linear mixed effects model, including all main effects, all interaction terms, and block number as a random effect, was then separately fit to each data set by running PROC MIXED in SAS 8.1 (SAS Institute 2000).

190 RESULTS

Across both the summer and fall, 9,698 of approximately 31,000 seeds (10,333 seeds per species) were removed from 996 of the 1,546 depots placed in the field. Most of the fixed effects tested in the linear model did not significantly affect seed removal, particularly all three and four way interaction terms. Patch type as a main effect did not affect seed removal ($F_{2,14} = 1.43$, $p = 0.2712$) (Figure 3). Furthermore, no interactions including patch type had a significant effect on seed removal ($p \geq 0.3818$). Conversely, seed removal was significantly affected by species ($F_{2,315} = 173.90$, $p < 0.0001$), distance ($F_{2,42} = 4.41$, $p = 0.0183$), and season ($F_{1,315} = 227.92$, $p < 0.0001$) as main effects. Two interaction terms were significant: season by species ($F_{2,315} = 11.08$, $p < 0.0001$) and season by distance ($F_{1,315} = 5.36$, $p = 0.0051$); all other interaction terms, including higher order terms, did not have a significant effect on seed removal ($p \geq 0.1377$). The involvement of season in both significant interaction terms is most likely due to the magnitude of its main effect on seed removal, which decreased 60.1% from the summer (0.444 ± 0.037) to the fall (0.177 ± 0.037) when summed across all patch types, distances, and species (Figure 4).

Removal by Seed Species

205 Seed removal, summed across all patch types, distances, and seasons, was significantly different between all pairwise comparisons of species ($p < 0.0001$) (Figure 5). Removal was highest for small-seeded *C. bellidifolius* (wind-dispersed) (mean \pm 1 S.E., 0.48 ± 0.04), lowest

for the large-seeded *P. americana* (avian-dispersed) (0.10 ± 0.04), and intermediate for small-seeded *A. villosis* (unassisted) (0.36 ± 0.04). This same ordering of species by removal also emerged when seed removal data was divided by season (Figure 6). In the summer, *C. bellidifolius* (0.63 ± 0.04) removal was significantly higher than *A. villosis* (0.55 ± 0.04 ; $p < 0.0001$), which was removed significantly more than *P. americana* (0.16 ± 0.04 ; $p < 0.0001$). Similarly, in the fall, *C. bellidifolius* (0.33 ± 0.04) was removed significantly more than both *A. villosis* (0.16 ± 0.04 ; $p < 0.0001$) and *P. americana* (0.04 ± 0.04 ; $p < 0.0001$), and *A. villosis* was also removed significantly more than *P. americana* ($p < 0.0001$). Furthermore, removal for each species decreased significantly from the summer to fall (all $p < 0.0001$). Specifically, removal of *P. americana* decreased 75.4% between seasons, the most of all three species, although *A. villosis* removal decreased a similar amount (70.2%). *C. bellidifolius* removal, on the other hand, decreased much less (47.6%).

220 *Removal by Distance*

Distance into the matrix from the patch edge had a significant effect on seed removal both across and within seasons. For both seasons combined, removal at 50 m (0.59 ± 0.05) was significantly higher than that at 0 m (0.50 ± 0.05 ; $p = 0.0050$), but removal at 15 m (0.54 ± 0.05) did not significantly differ from that at either 0 m ($p = 0.1933$) or 50 m ($p = 0.1083$) (Figure 7). Although the fixed effect of species by distance was statistically insignificant ($F_{4,315} = 1.29$, $p = 0.2744$), further examination shows that removal of *C. bellidifolius* did differ significantly by distance ($F_{2,242} = 4.33$, $p = 0.0142$), although *A. villosis* ($F_{2,242} = 2.69$, $p = 0.0700$) and especially *P. americana* ($F_{2,242} = 0.03$, $p = 0.9723$) did not. When seed removal was separated by season, distance had a significant effect on removal in the summer ($F_{2,145} = 9.65$, $p = 0.0001$) but not in the fall ($F_{2,145} = 0.10$, $p = 0.9030$) (Figure 8). In the summer, seed removal rates at all three

distances were significantly different than one another: removal at 50 m (0.51 ± 0.04) was significantly higher than that at 15 m (0.45 ± 0.04 ; $p = 0.0413$) and 0 m (0.37 ± 0.04 ; $p < 0.0001$), and removal at 15 m was significantly higher than that at 0 m ($p = 0.0211$). Conversely, no pairwise comparisons of removal between distances in the fall were significant ($p \geq 0.6554$), which could be due to the significant decline in seed removal at all distances from the summer to fall (all $p < 0.0001$). Removal at 15 and 50 m both decreased approximately 63%, whereas removal at 0 m decreased slightly less (52.4%).

Evidence of Predation

The number of fecal pellets and empty hulls left in trays with seeds removed served as evidence of seed predation, rather than simply removal. Of the 996 trays with seeds removed, 173 trays (17.4%) contained an average of 1.87 feces per tray, whereas 560 trays (56.2%) contained an average of 7.33 empty hulls per tray. Further analysis was performed on the number of empty hulls per seed removed, which is roughly proportional to the amount of seed predation by rodents relative to that of arthropods. Seed species ($F_{1,63} = 14.86$, $p = 0.0003$), species by season ($F_{1,121} = 6.81$, $p = 0.0102$), and species by season by distance ($F_{2,121} = 3.82$, $p = 0.0246$) all had significant effects on the frequency of empty hulls (Figure 9). Across all patch types, distances, and seasons, the frequency of empty hulls for *C. bellidifolius* (0.52 ± 0.03) was significantly higher than that for *A. villosis* (0.39 ± 0.03 ; $p = 0.0003$) (Figure 10); in other words, *C. bellidifolius* was most likely consumed by rodents significantly more than *A. villosis*. Dividing these results by season, in the summer *C. bellidifolius* (0.45 ± 0.04) did not have a significantly higher frequency of empty hulls than *A. villosis* (0.41 ± 0.04) ($p = 0.3772$), but did in the fall (0.58 ± 0.04 and 0.37 ± 0.04 , respectively; $p < 0.0001$) (Figure 11). Furthermore, the frequency of empty hulls of *C. bellidifolius* in the fall was significantly higher than that in the summer ($p =$

0.0057). Further dividing these results by distance, per the significant effect of species by season
255 by distance, allows us to investigate spatial patterns in the frequency of empty hulls, i.e. rodent
predation (Figure 11). Interestingly, all significant differences occurred at 15 and 50 m. For
instance, the aforementioned significant increase of *C. bellidifolius* empty hulls from summer to
fall occurs at 15 m (0.41 ± 0.06 to 0.61 ± 0.06 ; $p = 0.0187$) and 50 m (0.50 ± 0.06 to 0.67 ± 0.06 ;
 $p = 0.0496$), but not 0 m ($p = 0.6248$). Similarly, the significant difference among species in the
260 fall was significant at 15 m (*A. villosis*: 0.34 ± 0.06 ; $p = 0.0016$) and 50 m (*A. villosis*: $0.35 \pm$
 0.06 ; $p = 0.0002$), but not at 0 m ($p = 0.4388$). The frequency of empty hulls for *A. villosis* in the
summer also followed this trend, for the frequency at 0 m (0.29 ± 0.06) was significantly less
than that at both 15 m (0.46 ± 0.06 ; $p = 0.0365$) and 50 m (0.48 ± 0.06 ; $p = 0.0192$), while the
latter two distances did not significantly differ ($p = 0.7966$).

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DISCUSSION

As I hypothesized, patch type did not have a significant effect on seed predation within
the surrounding matrix (Figure 3), suggesting that corridors do not significantly affect matrix
seed predation by any of the three previously proposed mechanisms. Drift-fence effects were
270 shown to be negligible, since rectangular patches did not differ from winged or connected
patches. Additionally, area effects did not significantly affect matrix seed predation, for the
degree of edginess of patches had no effect on seed predation. Thirdly, connected patches did not
differ from either type of unconnected patch, demonstrating that corridor effects were not present.
The absence of corridor effects on matrix seed predation contrasts with the strong observed
275 corridor effects on biodiversity spillover, deduced from the greater species richness in the matrix
surrounding connected patches than unconnected patches (Brudvig et al. 2009). Thus, given that

seed limitation can be driven by seed deposition or predation (Turnbull et al. 2000), my results suggest that greater spillover in the matrix of connected patches is driven predominantly by increased seed deposition, rather than decreased seed predation.

280 The uniformity in seed predation in the matrix around all patch types mirrors previous work done on seed predation within the same landscape, in which Orrock et al. (2003) found no net effect of corridors on within-patch seed predation due to opposing effects on rodents and arthropods. A number of factors could contribute to a similar uniformity in seed predation in the matrix. First, within-patch granivores are not expected to create strong variability in matrix seed
285 predation by patch type. The dominant rodent granivores within the experimental landscape are *Peromyscus polionotus* (oldfield mouse), *Sigmodon hispidus* (cotton rat), and *Peromyscus gossypinus* (cotton mouse) (Brinkerhoff et al. 2005, Orrock and Danielson 2005, Mabry et al. 2003). *P. polionotus* is a specialist that inhabits early successional, i.e. within patch, habitat (Davenport 1964), while *P. gossypinus* and *S. hispidus* are habitat generalists and may inhabit
290 the surrounding pine matrix as well as the patches (Golley et al. 1965). Previous studies have shown the population densities of all three species to not vary by patch type (Brinkerhoff et al. 2005, Mabry et al. 2003), so they would not be expected to create differential matrix seed
295 predation by patch type. While *P. gossypinus* and *S. hispidus* may both inhabit the matrix, it is likely their populations in this habitat, as in the patches, are not affected by patch type either. The fact that patch type did not have a significant effect on the number of empty hulls per seed removed, which serves as a rough indicator of rodent seed predation, supports this claim.

 Unlike rodents, arthropods do respond to patch type via area effects, leading to increased species richness and abundance in rectangular patches relative to connected or winged patches (Orrock et al. *unpublished data*, Orrock et al. 2003). However, we would not expect arthropods

300 to exhibit differential matrix seed predation by patch type for two reasons: (1) within-patch
community variation among patch types should not arise in the surrounding matrix due to the
habitat limitation of most of the dominant patch-dwelling arthropods, and (2) patch-dwelling
arthropods are not expected to consume significant amounts of seeds past 0 m. The dominant
within-patch arthropod granivores, comprising approximately 80% of individuals, are, in
305 decreasing order of abundance, *Dorymyrmex* spp., *Solenopsis* spp., *Pheidole* spp.,
Pogonomyrmex badius, and *Crematogaster* spp., all of which are ants (Orrock et al., *unpublished*
data). The former four genera preferentially establish colonies in open, disturbed habitats, and
would thus rarely inhabit the matrix (Graham et al. 2008, Stiles and Jones 1998, Porter 1988,
Tschinkel 1988, Risch and Carrol 1982), which is partially corroborated by the absence of
310 *Dorymyrmex* spp. and *Pogonomyrmex badius* from pitfall traps set in the matrix (Resasco,
unpublished data). Although *S. invicta* and *Pheidole* spp. were found in matrix pitfall traps, both
genera forage mostly on high temperature soils associated with direct sunlight (Porter and
Tschinkel 1987, Whitford et al. 1981), and so would not be expected to frequently predate seeds
in the matrix. Thus, patch-dwelling arthropods will not induce patch type effects in matrix seed
315 predation, nor will rodents, as previously shown. These two facts, combined with absence of a
patch type effect on total seed predation, imply seed predation by matrix-dwelling arthropods
does not respond to patch type either. This group of granivores, which includes *Crematogaster*
spp., a genera of tree- and forest-dwelling ants (Palmer 2003, Jackson 1984), and various beetles,
may consume large amounts of seeds as do within-patch arthropods in patches (Orrock et al.
320 2003). The lack of differential matrix seed predation by patch type exhibited by matrix-dwelling
arthropods could be due to low penetration of or lack of edge and fragmentation effects (Davies
et al. 2001). Alternatively, varying responses of groups of arthropods, e.g. edge sensitive vs.

edge insensitive, may compensate for one another and thereby lead to no net changes in seed predation around different patch types (Didham et al. 1998).

325 Unlike patch type, the effect of distance on matrix seed predation could partially explain the observed decay of biodiversity spillover. Across all seasons, patch types, and species, seed predation was significantly highest at 50 m, but did not differ between 0 and 15 m (Figure 7). Given that seed predation has been shown to be one of many factors that influence a seed's survival post-dispersal (e.g. Schupp et al. 1989), higher seed predation would lead to decreased
330 seed survival and subsequent germination, adversely affecting both the species richness and abundance of the plant community. Surprisingly, seed predation did not peak at 15 m as we hypothesized. One explanation is that, as previously discussed, within-patch granivores were not expected to significantly contribute to matrix seed predation, thereby rendering our prediction of an overlap in foraging ranges of patch- and matrix-dwelling granivores invalid. Rather, if matrix
335 seed predation is driven predominantly by matrix-dwelling granivores, seed predation would be highest at 50 m, as is the case. Unfortunately, very little work has been done to characterize the matrix granivore community (but see Mabry and Barrett 2002, Golley et al. 1965), but the empty hull analyses do provide us with some means of differentiating seed predation by predator. An empty hull was left after the removal of approximately 52% of *C. bellidifolius* seeds and 39% of
340 *A. villosis* seeds, suggesting both rodents and arthropods significantly predate these seeds in the matrix (Figure 10). Interestingly, these same results, in conjunction with overall rates of seed removal by species, suggest that rodent granivores in the matrix may prefer *C. bellidifolius* (mean proportion of seeds removed \pm 1 S.E., 0.48 ± 0.04) and *A. villosis* (0.36 ± 0.04), the two smaller seeded species, to *P. americana* (0.10 ± 0.04) (Mendoza and Dirzo 2007, Dirzo et al.
345 2007). Rodents' preferences for certain seed species has been shown to significantly impact plant

communities, and to depend on a variety of characteristics including seed size, chemical composition, and seed coat thickness (Rey et al. 2002, Alcantara et al. 2000, Blate et al. 1998, Kollmann et al. 1998). It could therefore be the case that, due to the relatively flaccid seed coat of *A. villosis* and *C. bellidifolius* and the hardness of *P. americana* seeds, the former two species offer a better benefit-to-cost ratio despite their smaller size (Blate et al. 1998, but see Mittelbach and Gross 1984). Hull analyses also suggest that rodents consume more seeds at 15 and 50 m than at 0 m based on significantly higher seed removal at the former two distances on *A. villosis* in the summer and *C. bellidifolius* in the fall (Figure 12). Lower rodent seed predation at the edge is expected per the edge-averse behavior of rodents (Orrock et al. 2005, Manson and Stiles 1998), but no such trend consistently emerges across all combinations of species and season (Figure 9).

While the effect of distance on seed predation alone can partially account for the decay of biodiversity spillover, it is likely that this decay is driven by both increased seed predation and decreased seed deposition further in the matrix (Matias et al. 2009, Hyatt and Casper 2000). Movement of bird- and wind-dispersed seeds from fields into forests has been investigated in other ecosystems, in which avian-dispersed species were observed to move farther into the forest and at greater densities than wind-dispersed species (Gorchov et al. 1993, Willson et al. 1989). Supporting this finding is recent work by Baker et al. (2009) in this study's experimental landscape, where the mean terminal velocity, assuming no vertical air movement, of *C. bellidifolius* seeds was estimated at approximately 0.68 m/s (± 0.18 m/s); in other words, one seed would need to be airborne for approximately 22 and 70 seconds, both highly unlikely, to penetrate 15 and 50 m into the matrix, respectively. Of note, however, is that considerable variation in terminal velocities, and subsequent dispersal distance, does exist among wind-

dispersed species. In contrast, studies on avian-dispersed species have demonstrated birds
370 frequently move around and between patches, making dispersal of these seeds far into the matrix
possible (Levey et al. 2005). As my results show, seed predation by dispersal mode follows the
opposite trend: avian-dispersed (i.e. *P. americana*) seeds were predated significantly less than
wind-dispersed (i.e. *C. bellidifolius*) seeds for all combinations of distance, patch type, and
season, while unassisted (i.e. *A. villosis*) seeds were predated at intermediate levels.
375 Consequently, avian-dispersed species would be expected to exhibit the highest spillover species
richness, given that they are under the least predation and have the greatest dispersal. Conversely,
wind-dispersed species seem to be the most heavily predated seeds in the matrix, and, given
lower deposition rates, would thus be more seed-limited than avian-dispersed species. Gravity-
dispersed species are expected to be severely seed limited and therefore exhibit low levels of
380 spillover, due to their limited dispersal and heavy predation in the matrix. All three hypotheses
are vindicated by the patterns observed by Brudvig et al. (2009), lending significance to the idea
that both dispersal and predation, rather than just one or the other, contribute significantly to
biodiversity spillover.

Temporal variation had a significant effect on seed predation in the matrix, whereby
385 predation on all three species significantly decreased from summer to fall (Figure 4). This
temporal-induced shift could have strong implications for the composition of the spillover
community. Since seeds are most vulnerable to predation for a brief period after dispersal and
deposition (Plucinski and Hunter 2001), seasonal changes in seed predation could have
substantial effects on seed survival for a given species, depending on when its seeds disperse
390 (Kollman et al. 1998). In this study's landscape, the majority of *P. americana* fruits were ripe,
signifying the seeds were ready to be dispersed, by late summer, when the first predation trial

was conducted (*personal observation*). *A. villosis* and *C. bellidifolius*, on the other hand, mostly set seed in October and began to disperse their seeds in November (Stephanie Wagner, *personal observation*). Thus, *P. americana* seeds were at a greater risk of predation during peak seed
395 dispersal and deposition in the late summer. Conversely, when both *C. bellidifolius* and *A. villosis* seeds were dispersed in the fall, seed predation had decreased significantly compared to the summer, which could therefore increase their seed survival rates relative to *P. americana*. Due to lack of annual replication, I am unable to state whether this observed decrease in seed predation from summer to fall occurs every year. However, there are a number of explanations
400 for the aforementioned decrease that suggest my results illustrate an annual pattern. First, arthropods have been shown to decrease their foraging activity with decreasing temperature (Hulme 1997, Porter and Tschinkel 1987); the frequency of empty hulls per seed removed, which increased from summer to fall for both *A. villosis* and *C. bellidifolius*, supports this claim, signifying a greater percentage of rodent seed predation. Indeed, small mammals in this
405 ecosystem forage throughout the summer and fall (Martin et al. 1951), but they will shift their diets according to food availability (Whitaker and Hamilton 1998, Wolfe and Linzey 1977). In particular, *P. palustris* and *P. taeda* both set seed in October (Boyer 1990, Baker and Langdon 1990). Given that small mammals have been shown to consume and even prefer pine seeds (Boyer 1964, Stephenson et al. 1963), they may decrease their predation on smaller seeds, or
410 those that spill into the matrix from the patches. Thus, both rodent and arthropod granivores may decrease predation from the summer to fall on seeds dispersed from the patches, or target habitat, facilitating differential seed survival based on time of seed dispersal and deposition.

One limitation of my study is its inability to definitively differentiate seed predation by granivores, although the empty hull and fecal pellet data do provide some insight into this matter.

415 No exclosures were applied to the seed removal depots, thereby allowing all granivores access to
all depots. As a result, the documented seed removal quantifies total seed predation in the matrix.
Employing rodent exclosures at some seed depots would allow for the measurement of seed
predation by just arthropods, as well as arthropods and rodents. Furthermore, track plates could
be implemented to differentiate between rodents. Track plates are sheets of acetate that are
420 coated with a mixture of oil, graphite, and alcohol (Connors et al. 2005). These plates could be
secured to the ground in front of the openings in the seed removal depots and record the tracks of
small mammals when they walk over the plates. Consequently, I could determine which rodents
frequent the depots and, in conjunction with differential seed removal between seed depots with
and without exclosures, thereby better understand whether matrix- or patch-dwelling granivores
425 dominate seed predation in the matrix. Such insight is necessary for predicting how corridors
may alter matrix seed predation, and subsequently biodiversity spillover, via effects on the
primary seed consumers.

Our results have strong implications for the conservation of fragmented landscapes with
corridors around the world. One such highly fragmented ecosystem is longleaf pine savannah of
430 the Southeast United States, one of the most endangered ecosystems in the nation (Noss et al.
1995) and home to many endemic and threatened plant and animal species (Sorrie et al. 1996,
Hardin and White 1989, Ortego and Lay 1988). Very few pristine old-growth longleaf forest
remnants remain, estimated at approximately 0.00014% of old-growth longleaf forests' extent
before European settlement (Varner and Kush 2004), yet longleaf pine savannahs have continued
435 to decline in recent decades, such as by approximately 20% from 1985 to 1995 (Outcalt and
Sheffield 1996), due mainly to the development of lands (Martin et al. 1993). Thus, it is crucial
to not only protect and foster these remnants, but also to expand current longleaf pine savannah

habitat to compensate for concurrent losses. Corridors hold great promise in addressing both of these restoration goals, considering their demonstrated positive effects on longleaf pine savannah communities (Damschen et al. 2006, Levey et al. 2005) and their potential role in promoting biodiversity spillover into non-target habitat (Brudvig et al. 2009). My work has suggested that this spillover depends more on seed dispersal (and deposition) than predation, particularly in longleaf pine savannahs where this study was conducted. Fortunately, longleaf pine savannahs have been shown to be fairly uniform in composition across most of their range, Southern Florida being a notable exception (Martin et al. 1993). As a result, dispersal and predation of seeds, and therefore biodiversity spillover, would be anticipated to be similar across savannahs, regardless of their location. However, even if seed predation was to differ among longleaf savannahs, my results suggest that spillover would still most likely occur, albeit to varying extents for different species based on patterns of variation in seed predation and seed life history traits, such as size and time of deposition. Corridors, though, are not restricted to conserving just this habitat, but rather have been employed in many fragmented ecosystems and landscapes (Beier 1993, Newmark 1993, Land Conservation Council 1989). By partially unraveling the mechanisms determining the spillover effect, its occurrence, or lack thereof, can be better compensated for and modeled over all types of landscapes, making corridors even more appealing for conservation.

The improvement of non-target habitat, i.e. the matrix, surrounding patches connected by corridors via the spread, or spillover, of plant species was recently discovered in this study's experimental landscape (Brudvig et al. 2009). My results show that seed predation in the matrix was not significantly affected by patch type, and therefore does not drive the larger biodiversity spillover observed around connected relative to unconnected patches. However, seed predation

did vary temporally, spatially, and by seed species, which could have strong impacts on the composition and size of the plant spillover community. This work serves as a foundation for better understanding the underlying mechanisms of the spillover effect, which is necessary in order to predict and model its occurrence. Given the monetary constraints conservation projects are often faced with, it is crucial to utilize funds in the most efficient manner possible.

Harnessing the improvement of non-target habitat surrounding connected patches would greatly improve the utility and effectiveness of corridors, and should therefore be a target of future research.

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FIGURES

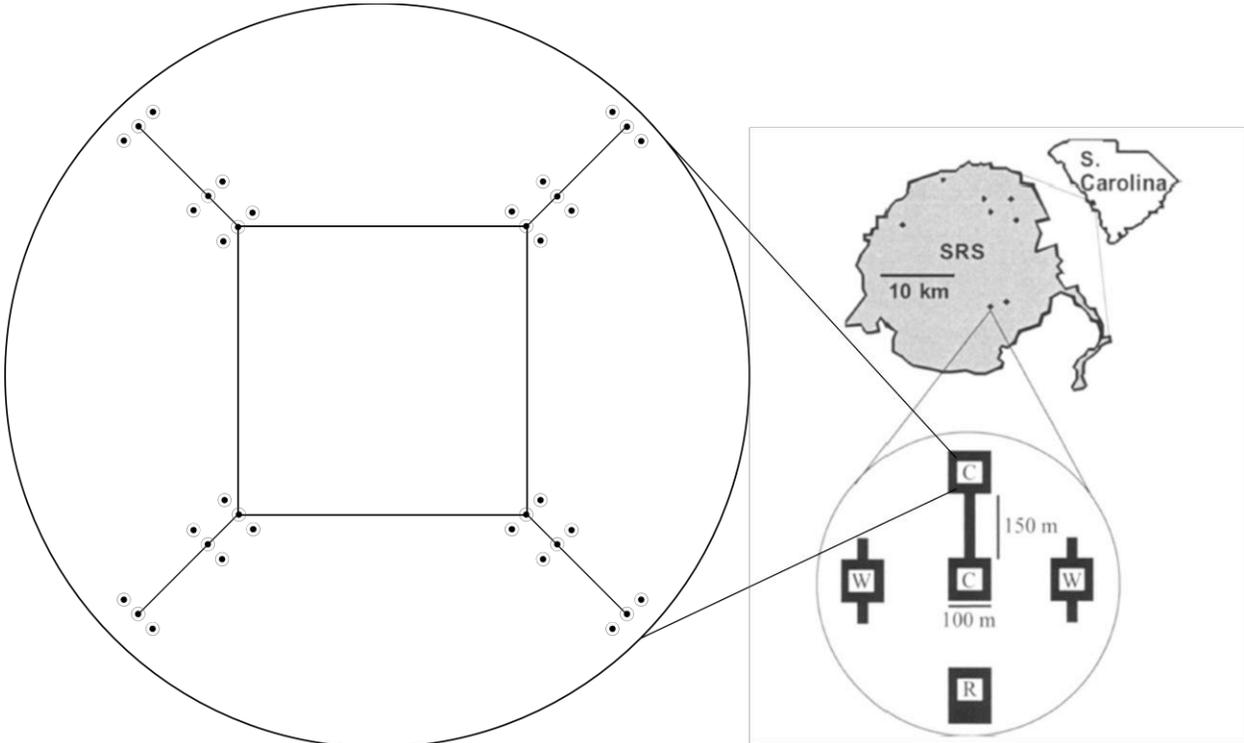


Figure 1: Location of Savannah River Sites in South Carolina, the position of the eight experimental blocks in SRS, and the five patches within each block. Enlarged at left are the four transects used for measuring seed predation, with each dot along the transects representing a single seed predation tray.



Figure 2: Images of seeds, compared to a dime. From left to right: *Phytolacca americana*, *Athaenantia villosis*, and *Carphephorous bellidifolius* (avian-, unassisted-, and wind-dispersed, respectively). The upper row shows each seed inside its hull as they were placed in the seed trays, while the lower row depicts the isolated seed.

Fixed Effect	Num DF	Denom DF	F-Value	Pr > F
Patch type	2	14	1.43	0.2712
Distance	2	42	4.41	0.0183
Patch type x Distance	4	42	0.33	0.8552
Species	2	315	173.90	<0.0001
Patch type x Species	4	315	0.67	0.6150
Distance x Species	4	315	1.29	0.2744
Patch type x Distance x Species	8	315	0.82	0.5885
Season	1	315	227.92	<0.0001
Patch type x Season	2	315	0.21	0.8146
Distance x Season	2	315	5.36	0.0051
Patch type x Distance x Season	4	315	0.84	0.4994
Species x Season	2	315	11.08	<0.0001
Patch type x Species x Season	4	315	1.05	0.3818
Distance x Species x Season	4	315	1.76	0.1377
Patch type x Distance x Species x Season	8	315	0.38	0.9293

Figure 3: All fixed effects included in our linear mixed effects model for the proportion of seeds removed. Highlighted rows indicate a significant effect.

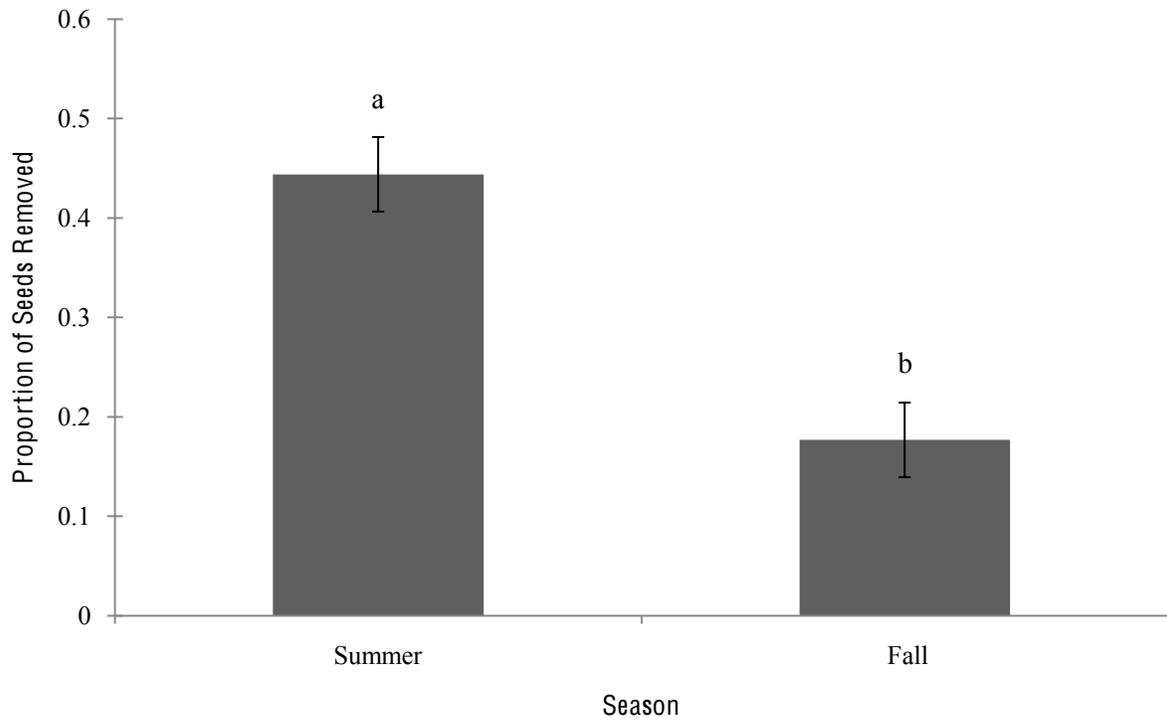


Figure 4: Mean (± 1 standard error) for untransformed proportion of seeds removed across all patch types, distances, and species for summer and fall. Letters denote statistical significance.

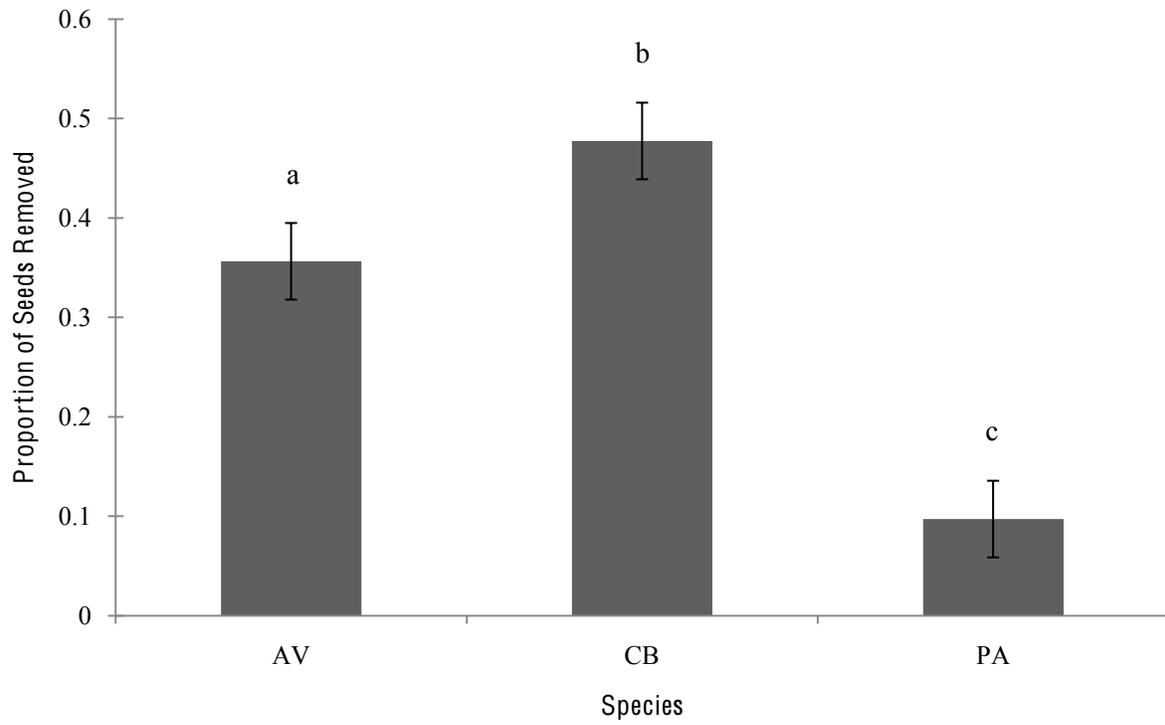


Figure 5: Mean (± 1 standard error) for untransformed proportion of seeds removed across all patch types, distances, and seasons for *A. villosis* (AV), *C. bellidifolius* (CB), and *P. americana* (PA). Letters denote statistical significance.

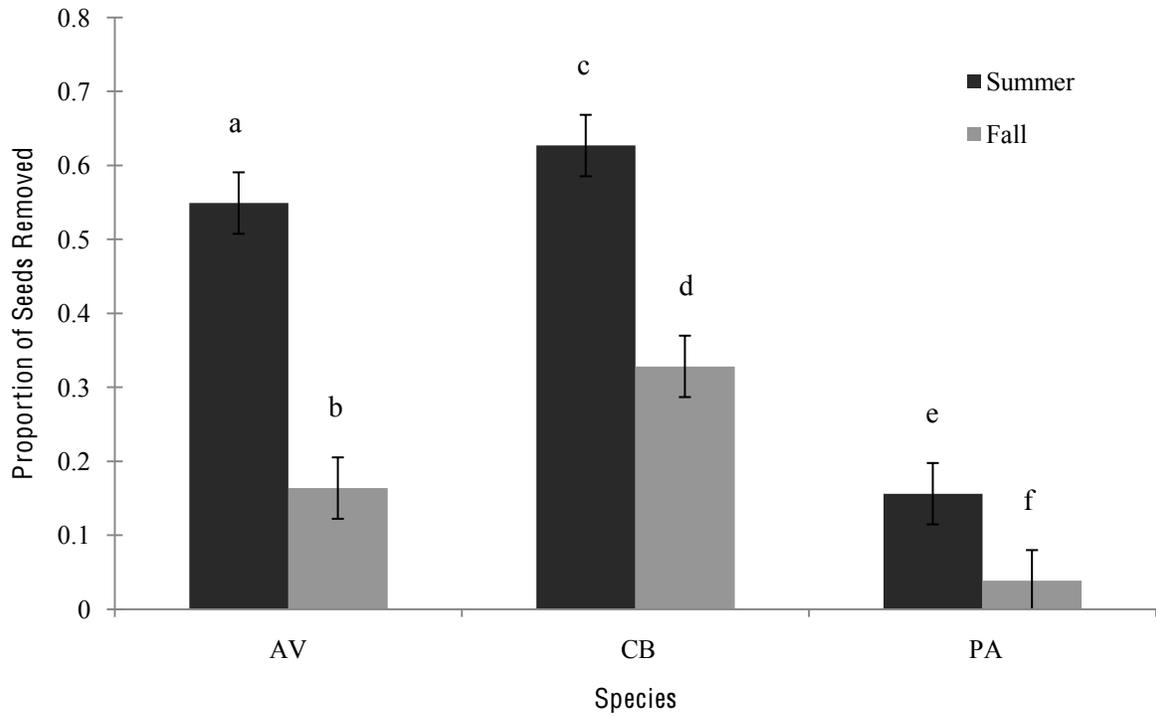


Figure 6: Mean (± 1 standard error) for untransformed proportion of seeds removed across all patch types and distances for *A. villosis* (AV), *C. bellidifolius* (CB), and *P. americana* (PA) in the summer and fall. Letters denote statistical significance.

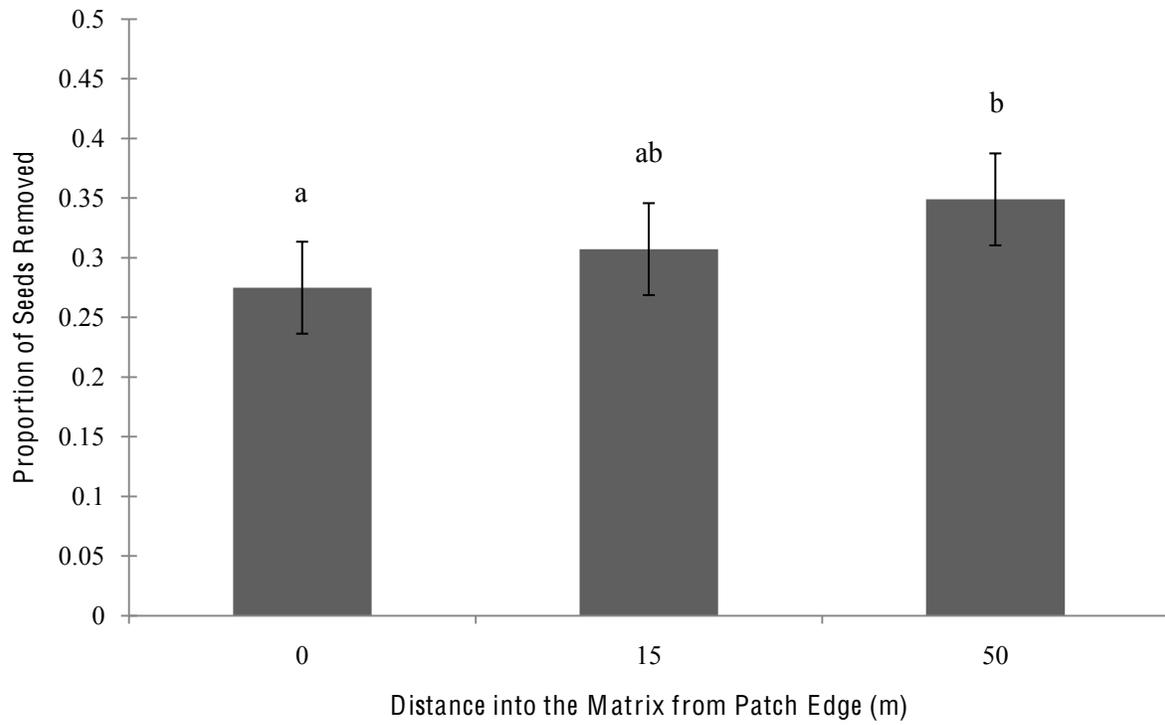


Figure 7: Mean (± 1 standard error) for untransformed proportion of seeds removed across all species, seasons, and patch types at 0, 15, and 50 m into the matrix from the patch edge. Letters denote statistical significance.

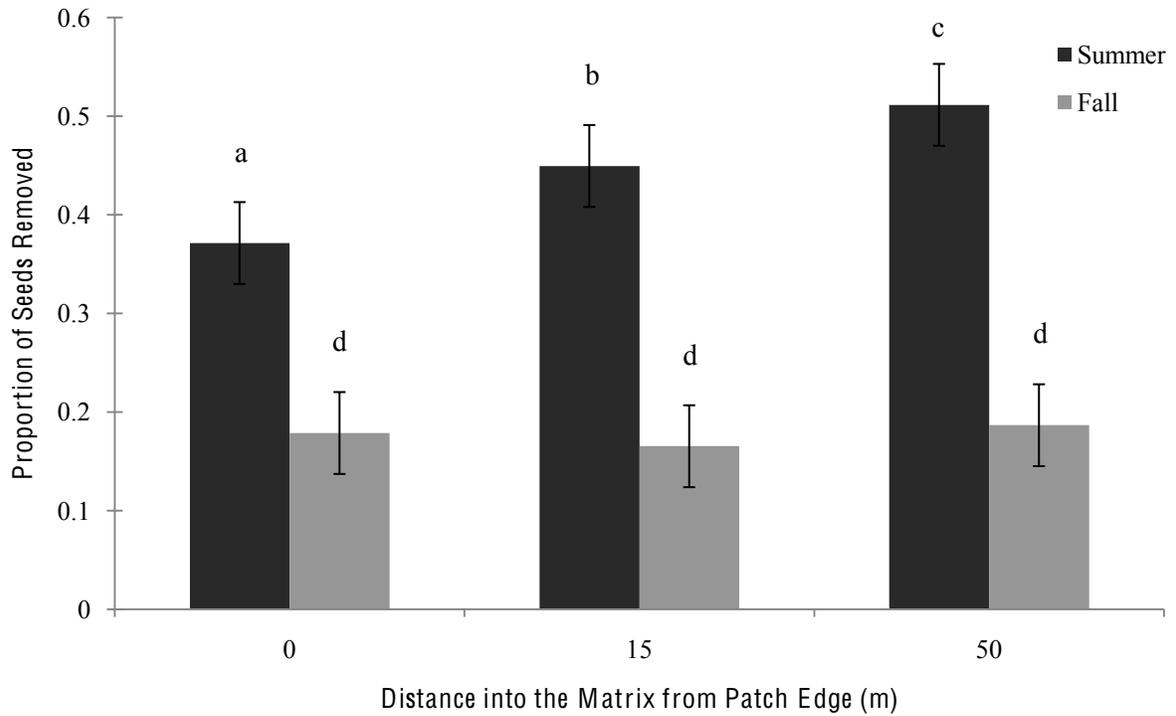


Figure 8: Mean (\pm 1 standard error) for untransformed proportion of seeds removed across all patch types and species at 0, 15, and 50 m into the matrix from the patch edge for summer and fall.

Fixed Effect	Num DF	Denom DF	F-Value	Pr > F
Patch type	2	14	0.83	0.4554
Distance	2	121	2.77	0.0669
Patch type x Distance	4	121	0.66	0.6222
Species	1	63	14.86	0.0003
Patch type x Species	2	63	0.09	0.9147
Distance x Species	2	121	0.41	0.6666
Patch type x Distance x Species	4	121	1.19	0.3177
Season	1	121	1.90	0.1705
Patch type x Season	2	121	0.22	0.8014
Distance x Season	2	121	0.34	0.7131
Patch type x Distance x Season	4	121	1.03	0.3950
Species x Season	1	121	6.81	0.0102
Patch type x Species x Season	2	121	0.62	0.5417
Distance x Species x Season	2	121	3.82	0.0246
Patch type x Distance x Species x Season	4	121	0.71	0.5843

Figure 9: All fixed effects included in our linear mixed effects model for number of empty hulls left per seed removed. Highlighted rows indicate a significant effect.

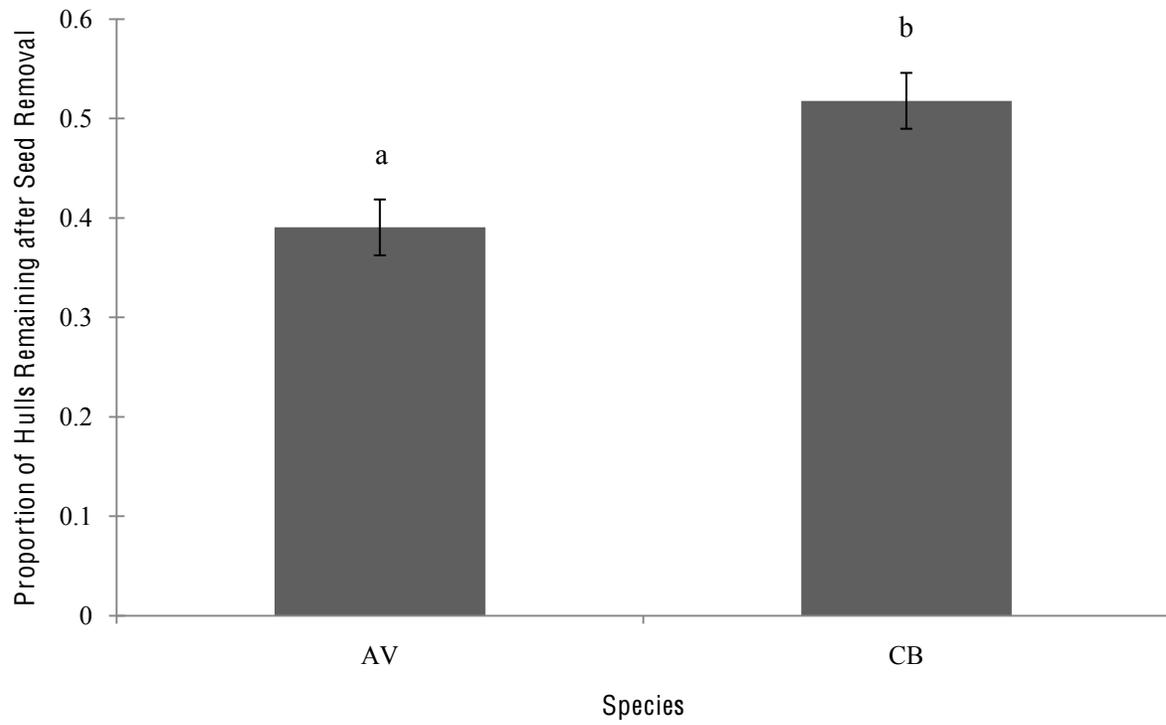


Figure 10: Mean (± 1 standard error) for number of empty hulls left per seed removed across all patch types, distances, and seasons for *A. villosis* (AV) and *C. bellidifolius* (CB). Letters denote statistical significance.

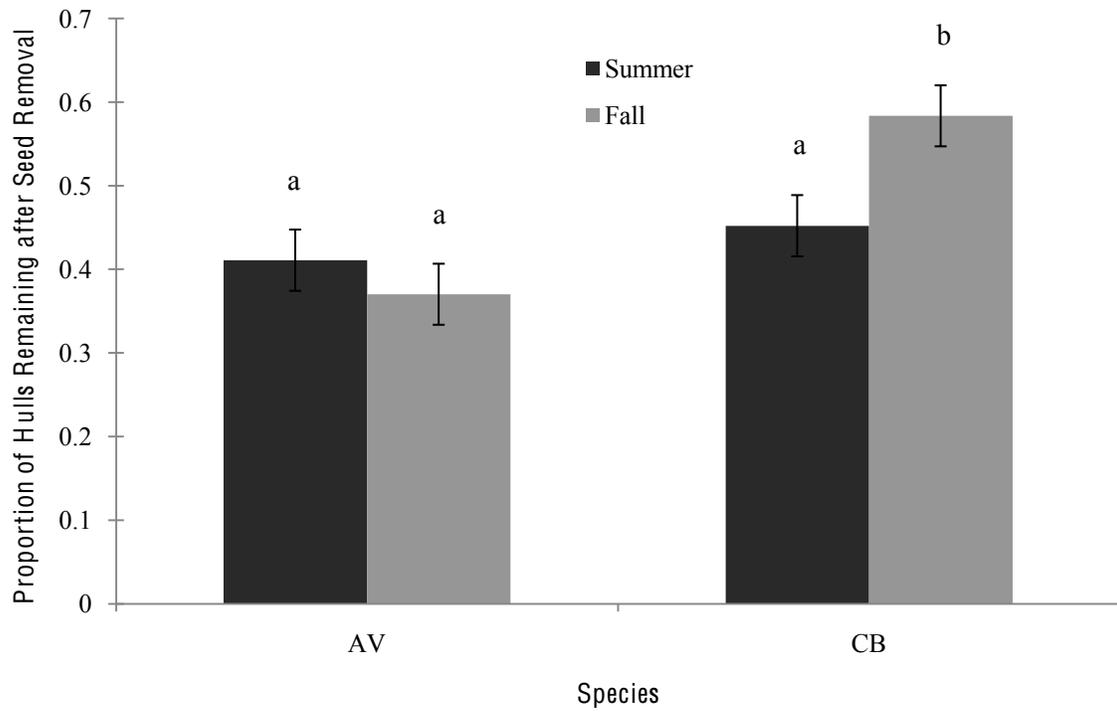


Figure 11: Mean (± 1 standard error) for number of empty hulls left per seed removed across all patch types and distances for *A. villosis* (AV) and *C. bellidifolius* (CB) in the summer and fall. Letters denote statistical significance.

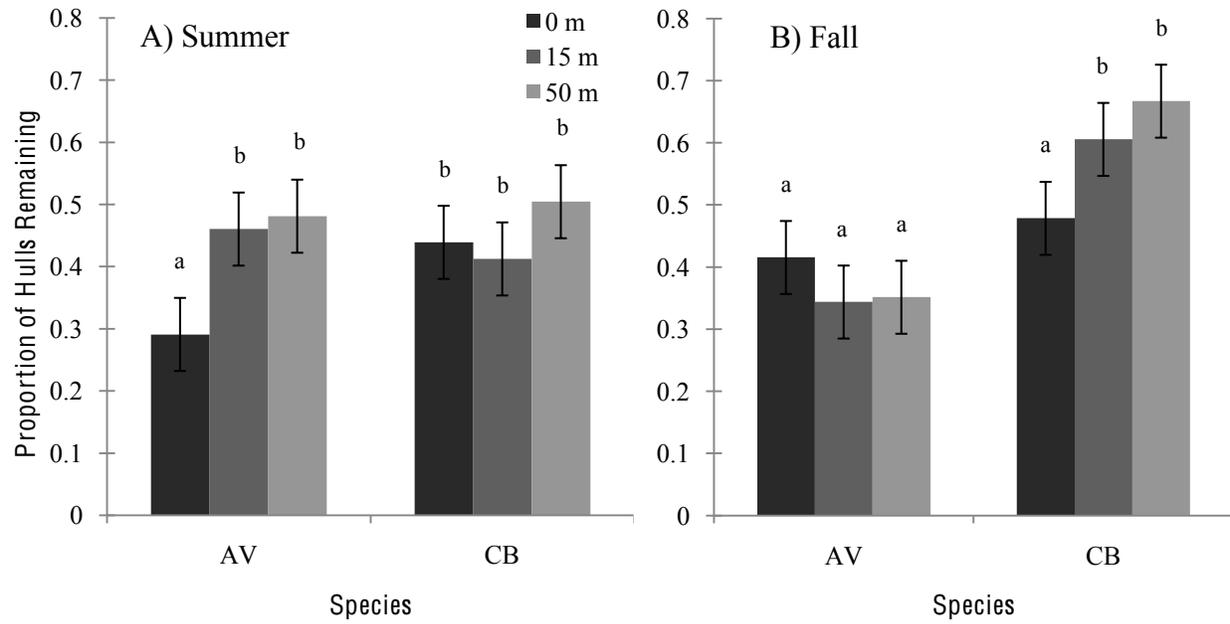
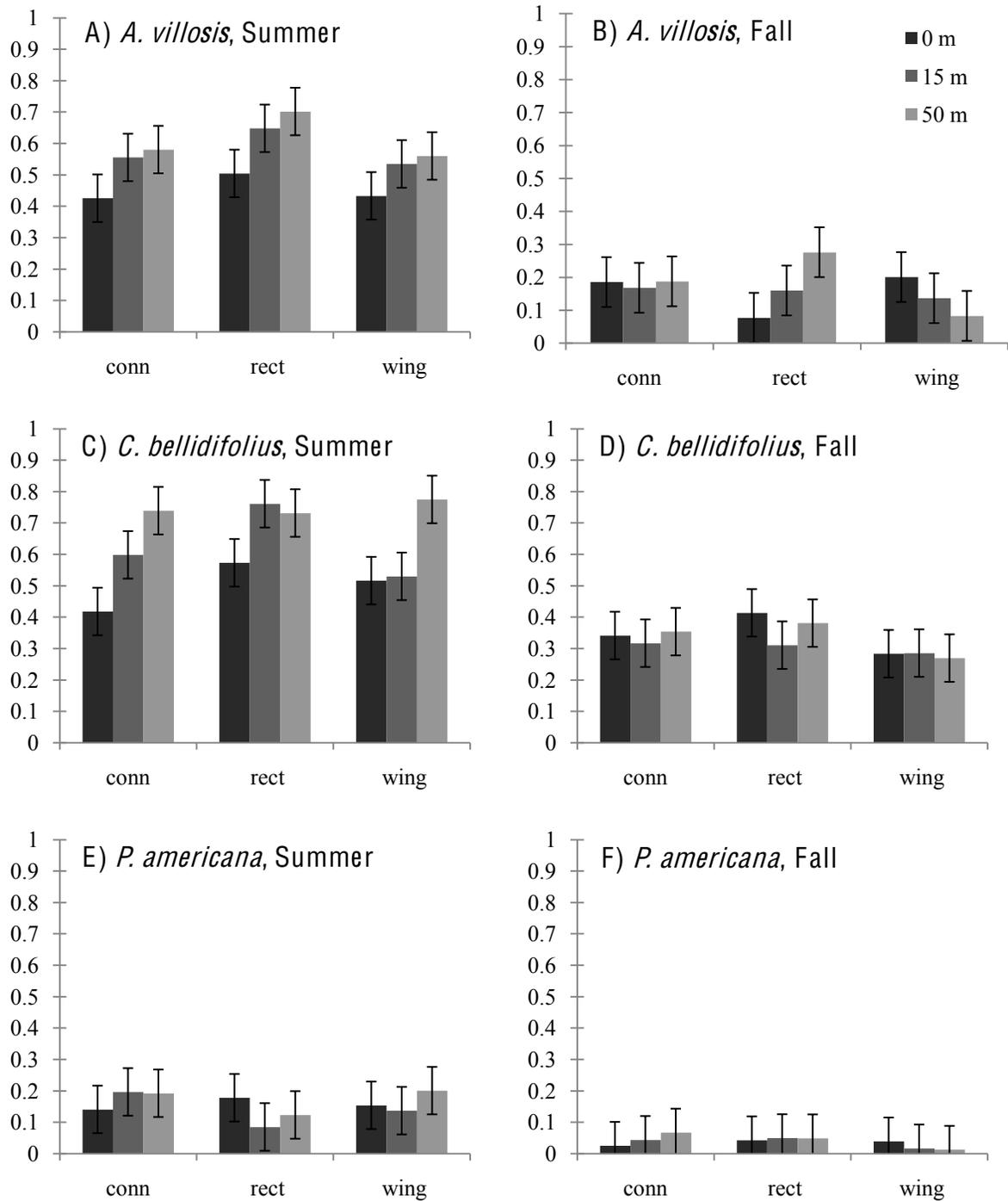
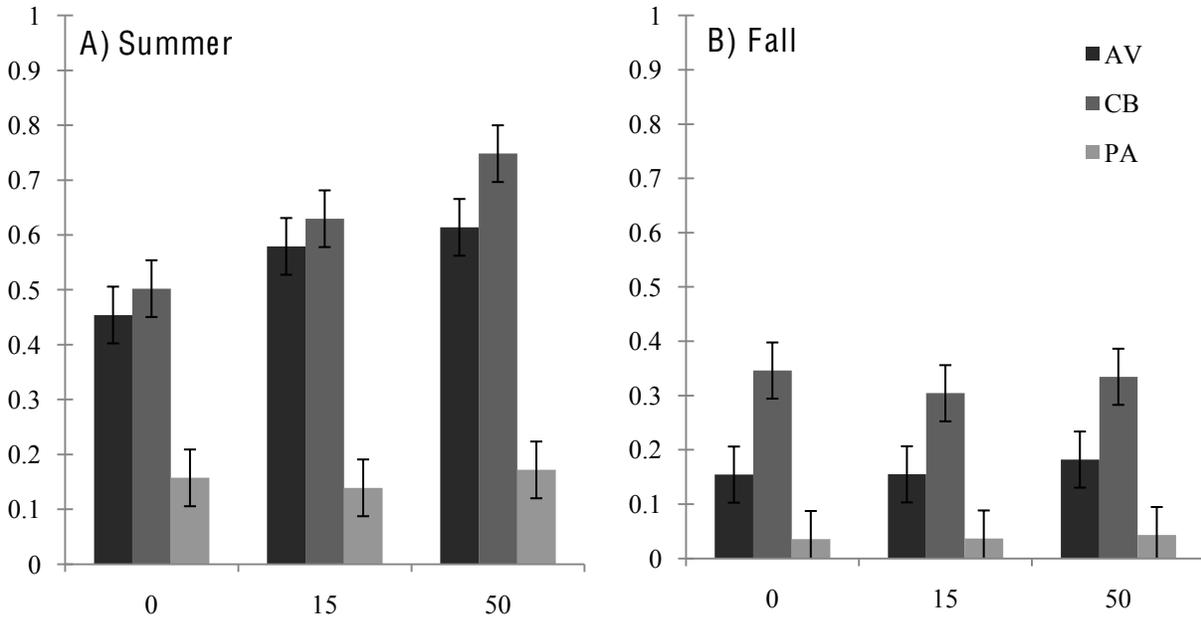


Figure 12: Mean (± 1 standard error) for number of empty hulls left per seed removed across all distances for *A. villosis* (AV) and *C. bellidifolius* (CB) in the summer (A) and fall (B) at 0, 15, and 50 m into the matrix from the patch edge. Letters denote statistical significance within each figure.

APPENDED FIGURES



Appendix A: Mean (± 1 standard error) for untransformed proportion of seeds removed in the A,C,E) summer and B,D,F) fall for A,B) *A. villosis*; C,D) *C. bellidifolius*; and E,F) *P. americana* at 0, 15, and 50 m.



Appendix B: Mean (± 1 standard error) for untransformed proportion of seeds removed summed across all patch types, due to its statistical insignificance, for *A. villosis* (AV), *C. bellidifolius* (CB), and *P. americana* (PA) at 0, 15, and 50 m in the A) summer and B) fall.

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