Ecology, 93(5), 2012, pp. 1016–1025

Habitat patch shape, not corridors, determines herbivory and fruit production of an annual plant

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Abstract. Habitat corridors confer many conservation benefits by increasing movement of organisms between habitat patches, but the benefits for some species may exact costs for others. For example, corridors may increase the abundance of consumers in a habitat to the detriment of the species they consume. In this study we assessed the impact of corridors on insect herbivory of a native plant, *Solanum americanum*, in large-scale, experimentally fragmented landscapes. We quantified leaf herbivory and assessed fruit production as a proxy for plant fitness. We also conducted field surveys of grasshoppers (Orthoptera), a group of abundant, generalist herbivores that feed on *S. americanum*, and we used exclosure cages to explicitly link grasshopper herbivory to fruit production of individual *S. americanum*. The presence of corridors did not increase herbivory or decrease plant fruit production. Likewise, corridors did not increase grasshopper abundance. Instead, patches in our landscapes with the least amount of edge habitat and the greatest amount of warmer "core" area had the highest levels of herbivory, the largest cost to plant fruit production as a result of herbivory, and the most grasshoppers. Thus habitat quality, governed by patch shape, can be more important than connectivity for determining levels of herbivory and the impact of herbivory on plant fitness in fragmented landscapes.

Key words: connectivity; conservation planning; insect herbivory; Orthoptera; plant–animal interactions; plant fitness; Solanum americanum.

Introduction

Habitat fragmentation is a leading cause of population decline and species extinction (Wilcove et al. 1998, Collinge 2009). Isolation of organisms in small habitat patches can reduce migration and gene flow, decreasing species diversity and population viability (MacArthur and Wilson 1967, Hanski 1999). The most popular strategy to mitigate the negative effects of fragmentation is the creation and maintenance of habitat corridors, which increase the movement of many species (Beier and Noss 1998, Crooks and Sanjayan 2006, Gilbert-Norton et al. 2010). By facilitating movement, corridors provide a mechanism for population rescue, bolstering populations that would otherwise decline (Hanski 1999). Although corridor studies traditionally have focused on vertebrates (Debinski and Holt 2000, Haddad and Tewksbury 2006), corridors also benefit a wide range of other taxa, with effect sizes similar to those for vertebrates (Gilbert-Norton et al. 2010). Thus corridors enjoy broad popularity as a conservation strategy (Crooks and Sanjayan 2006, Hilty et al. 2006, Krosby et al. 2010).

Nonetheless, the wholesale endorsement of corridors has been criticized because evidence substantiating broad positive effects of corridors is not evenly divided among taxa, with relatively few studies examining corridor impacts on plants (Beier and Noss 1998, Haddad and Tewksbury 2006, Gilbert-Norton et al. 2010). In addition, the popular endorsement of corridors as a management tool may overlook the fact that corridors increase the amount of edge habitat in fragmented landscapes (Simberloff et al. 1992, Haddad et al. 2011), and edges can profoundly alter habitat quality by changing abiotic conditions such as light, moisture, and temperature in patch fragments (Laurance et al. 2002, Collinge 2009). Several studies have shown clear benefits of corridors for plants, e.g., by increasing pollination, seed dispersal, and community diversity, and edge effects accompanying corridors do not negate these positive impacts (Haddad et al. 2011). But there are far fewer studies assessing how corridors may alter ecological interactions that can reduce plant fitness, and these results are more difficult to generalize. For example, corridors can increase seed predation by rodents (Orrock et al. 2003, Orrock and Damschen 2005) and insect gall parasitism of plants (Sullivan et al. 2011), but seed predation by invertebrates (Orrock et al. 2003, Orrock and Damschen 2005) and the development of plant fungal disease (Johnson and Haddad 2011) are more strongly influenced by habitat patch shape, which

Manuscript received 8 April 2011; revised 2 November 2011; accepted 4 November 2011. Corresponding Editor: E. E. Crone.

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determines the ratio of interior "core" area to patch edges.

Connectivity and edge effects are the two most important drivers of plant–animal interactions in fragmented habitats, but no study to date has explicitly compared their influence on herbivory and its consequences for plant fitness. Herbivores consume ~18% of terrestrial plant primary productivity (Cyr and Pace 1993, Agrawal 2011); herbivory can severely limit plant fitness (Louda 1984, Marquis 1984, Crawley 1985, Hawkes and Sullivan 2001, Wise and Abrahamson 2005); and two recent reviews suggest disparate effects of fragmentation on herbivory, likely because different herbivore taxa respond differently to connectivity and edge effects (Tscharntke and Brandl 2004, Collinge 2009). In this study, we tease apart the impacts of corridors and edge effects (mediated by habitat patch shape) on insect herbivory, and we explicitly assess the consequences for plant fitness, in experimentally fragmented landscapes at the Savannah River Site (SRS), in South Carolina, USA. When we began this work, the evidence both within and beyond our study system either suggested strong positive corridor effects on insect herbivores or was conflicting. Thus we test two alternative hypotheses, as follows.

First, we test the hypothesis that corridors increase herbivory and decrease plant fruit production. Consistent with predictions of island biogeography and metapopulation models (MacArthur and Wilson 1967, Hanski 1999), connectivity in fragmented landscapes increases diversity and abundance of a variety of insect taxa (Rathcke and Jules 1993, Kruess and Tscharntke 1994, Collinge 2000, Tscharntke et al. 2002, Baum et al. 2004, Ockinger et al. 2010). In the experimental landscapes at SRS, practically all previous studies of insects show that corridors increase dispersal and abundance (Haddad et al. 2011; but see Orrock et al. 2011); among butterflies, for example, which are common herbivores in the landscapes, three out of four species are more abundant in connected patches, and the fourth does not differ by patch type (Haddad and Baum 1999). If patches connected by corridors have a greater abundance of insect herbivores, herbivory should increase in those patches.

Second, we test the hypothesis that habitat patch shape is a more important determinant of herbivory and plant fruit production than the presence of a corridor. This alternative to our first hypothesis is based on the recognition that changes in abiotic conditions created by habitat edges, especially gradients in light, moisture, and temperature, strongly influence the abundance of many insect populations in fragmented habitats (Laurance et al. 2002, Ries et al. 2004, Collinge 2009). For insects, the length of habitat edges relative to the amount of interior core area in a patch, and the resulting variance in abiotic conditions, may be the most important landscape determinants of habitat quality and population size (Deans et al. 2005, Cook and Holt 2006). Thus insect herbivores that thrive in conditions along edges should be more abundant and consequently increase herbivory in edgier patches; species that thrive in core habitat and avoid edges should be more abundant and increase herbivory in patches with more core area.

We test each of these hypotheses at SRS by focusing on a plant species native to the southeastern United States, *Solanum americanum*, and herbivory by grasshoppers (Orthoptera), which are common generalist herbivores in the experimental landscapes. To explore a potential abiotic mechanism underlying grasshopper abundance and herbivory, we also evaluate temperature distributions in the landscapes as a function of patch shape and distance from edges.

METHODS

Experimental landscape configuration

Eight replicated landscape blocks were created in 1999 and 2000 by clear-cutting habitat patches from mature pine plantation forest. The forest matrix of each landscape remains intact while habitat patches have had hardwoods removed and have been burned four times since 1999 to promote longleaf pine (*Pinus palustris*) savannah restoration. Thus patches and corridors of predominantly savannah habitat are set within a matrix of mature pine forest. Each landscape replicate is ~50 ha, including forested buffer area, and has a total of five patches of approximately equal area. Within each landscape are three different patch types: connected, rectangular, and winged (Fig. 1A). Connected patches consist of a 1 ha square patch joined by a 25 m wide corridor that is 150 m long. Rectangular patches consist of a 1.375-ha patch, with the additional 0.375 ha representing the area of the corridor. Winged patches consist of a 1 ha square patch with two dead-end "wings" that are 25 m wide and 75 m long; these wings are on opposite sides of the winged patches and have a combined area of 0.375 ha (Fig. 1A). Thus rectangular and winged patches are 1.375 ha; connected patches are each effectively 1.1875 ha (each has a 1 ha square patch plus one-half of the corridor that connects them). The different shapes of the three patch types produce different ratios of interior to edge habitat. Connected and winged patches have less interior area and more edge habitat (area to perimeter ratios of 22.62 and 19.64, respectively); rectangular patches have more interior area and less edge habitat (area to perimeter ratio of 28.95) (Orrock and Damschen 2005).

This design makes it possible to test the effects of corridors and patch shape on herbivory, plant fruit production, and herbivore abundance. If connectivity via corridors is the most important landscape determinant of herbivory, for instance, then plants in connected patches should have more herbivory than plants in winged and rectangular patches (connected > winged and rectangular). If patch shape is more important, then either edgy patches with less core area will have more herbivory (winged and connected > rectangular), or

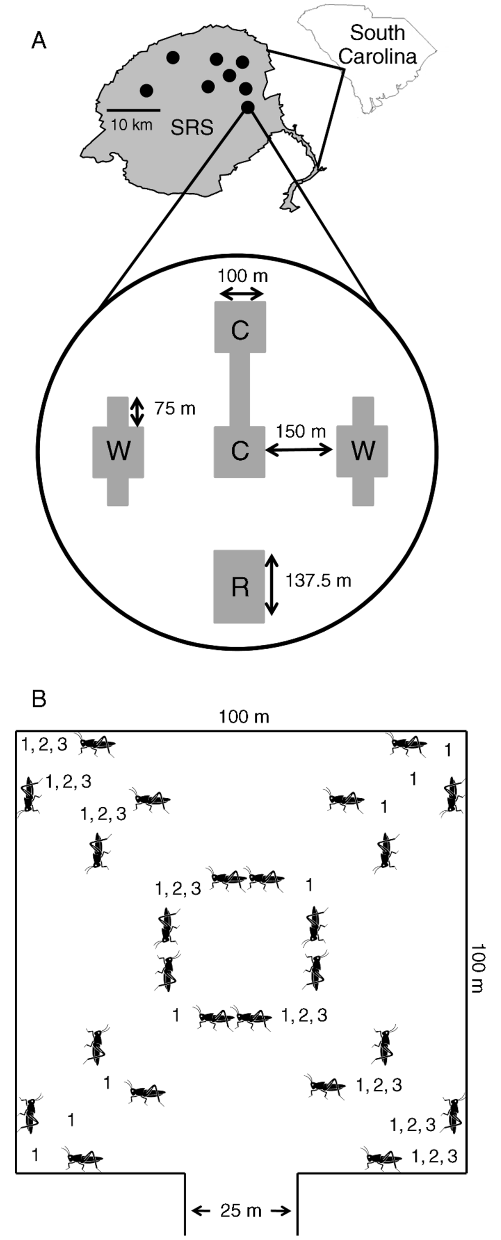

FIG. 1. (A) Map of eight replicated landscape blocks at the Savannah River Site (SRS), South Carolina, USA, with the insert showing the patch configuration of one landscape. Each landscape has two connected patches joined by a 150-m corridor. Four landscapes have two winged patches and one rectangular patch, as shown; the other four have two rectangular patches and one winged. (B) Diagram of one experimental patch showing locations of all study plants and grasshopper surveys. The number 1 indicates plant locations for experiment 1 (2008), comprising four transects per patch; 2 indicates plant locations for experiment 2 (2009), comprising two randomly selected transects per patch; 3 indicates plant locations for experiment 3 (2009 exclosure experiment), adjacent to experiment 2 plants. Each grasshopper symbol represents a 10-m grasshopper survey transect (2009).

patches with more core area and less edge habitat will have more herbivory (rectangular > connected and winged). The small difference in area between connected and unconnected patches in the landscapes does not change the order of our predictions. If herbivory, for instance, is greatest in connected patches despite the slight reduction in area, we have a more conservative test for corridor effects.

Focal species and planting design

Solanum americanum is a fast-growing annual that can thrive in our experimental patches. Although it is not found in the patches except where planted, it is common in nearby areas. In good conditions, *S. americanum* can produce >100 fruits per plant in a single growing season. It also self-pollinates readily, and it can fruit prolifically in the absence of pollinators. Finally, *S. americanum* is commonly eaten by grasshoppers in the southeastern United States, and grasshoppers are the primary herbivores that consume *S. americanum* in our experimental landscapes at SRS (D. M. Evans and N. E. Turley, *personal observations*).

Plants used for this study originated from diverse populations ranging between Miami, Florida, and Aiken, South Carolina. Seeds were collected from the source populations and, to minimize maternal and genetic differences among individuals in each population, grown and self-pollinated in a greenhouse for one generation. Seeds from these self-pollinated plants were then germinated in a greenhouse prior to planting in the field. During May and June of 2008 and 2009, equal numbers of seedlings from each source population were randomly interspersed and planted in every patch along transects to ensure good spatial coverage in the patches; each transect consisted of four planting locations at discrete distances from patch edges: 1, 10.5, 20, and 37 m. Seedlings were planted in these transects in 2008 and 2009 for three experiments (Fig. 1B) to assess the effects of connectivity and patch shape on herbivory and fruit production.

In experiment 1, conducted May–August 2008, seedlings (~10 cm tall) were planted along four transects in each patch (16 plants per patch, 640 plants total; Fig. 1B). Experiment 2, conducted June–August 2009, repeated experiment 1 except that only two randomly selected transects per patch were planted (eight plants per patch, 320 plants total; Fig.1B). Experiment 3, also conducted June–August 2009, was an herbivore exclosure experiment designed to explicitly link grasshopper herbivory to plant fruit production. Plants used for experiment 3 were planted in the same general locations as the plants for experiment 2 (Fig. 1B), but there were two plants per location (320 pairs), and each plant was covered with a wire mesh cage. Cages were ~1.2 m tall and 0.5 m in diameter, with small enough mesh size (2.7-mm gaps) to exclude most grasshoppers. One cage in each pair protected plants from grasshopper herbivory; the other cage was a control. Control cages shaded plants to the same extent as exclusion cages (~25% light reduction), but each control cage had six to seven openings cut along the bottom and sides (each opening ~15 cm^2) to allow access by grasshoppers. This paired design permits us to assess the impact of grasshopper herbivory on fruit production by comparing, at each location, the number of fruits produced in the exclosure cage to the number produced in the open cage.

All plants were watered three to four times per week, receiving approximately the same amount of water each time. Watering commenced on the day of planting for each experiment and continued until herbivory measurements were taken in late August each year.

Assessing herbivory, fruit production, and plant mortality

For plants in experiments 1 and 2, the percentage of leaf area missing due to chewing damage by insect herbivores was visually estimated on all leaves. Each leaf of every plant was counted and placed into a damage category (0%, 1–10%, 11–25%, 26–50%, 51–75%, 76–100%). During summer 2009, we also opportunistically collected grasshoppers ($N = 30$) in the patches, to identify the species most commonly observed consuming *S. americanum*.

The number of ripe fruits produced by each plant was recorded in all three experiments. *Solanum americanum* commonly fruits throughout the summer in South Carolina. Fruit monitoring began in late June 2008 for experiment 1 and early July 2009 for experiments 2 and 3. We counted the number of ripe fruits produced by each plant weekly until late August for experiments 1 and 2 and biweekly until mid-September for experiment 3. Each time we visited plants to count fruits we removed all ripe fruits (by clipping their pedicels) and all fruits that were on the ground. For plants in experiments 1 and 2, we also removed open, exposed bracts, which indicate fruits taken by birds. Total fruit production was calculated for each plant by summing the number of fruits we removed, fruits on the ground, and fruits removed by birds.

At the end of each study period we also tallied the total number of plants that died and the number of small plants that herbivores chewed off at the main stem. These "clipped" plants usually died; when they survived they produced few leaves or fruits. We removed dead and clipped plants from all analyses of herbivory and fruit production, with the following numbers remaining: experiment 1, 363 plants; experiment 2, 291 plants; experiment 3, 262 pairs of plants. Because experiment 3 had a paired design, we removed both plants in a pair from analysis if either plant died or was clipped. We separately analyzed the influence of patch type on mortality and small plants being clipped in all three experiments (Appendix A).

Assessing herbivore abundance

In 2009, we conducted visual surveys for grasshoppers in each patch five times between mid-June and late August. Grasshoppers also occasionally occur in the surrounding forest matrix, but they are much less common in the matrix; we surveyed only in the patches (savannah habitat) because our aim was to assess grasshopper abundance in the different patch types. Surveys were conducted between 10:00 and 18:00 hours along transects placed 1, 20, and 37 m from patch edges (Fig. 1B). Starting at these distances, surveyors walked 10 m in a direction parallel to one of the patch edges, then returned to the starting point (without counting) and walked 10 m parallel to the other nearby patch edge. While walking the transects, surveyors counted all grasshoppers observed regardless of species and regardless of whether grasshoppers remained stationary, jumped, or flew away. Most grasshoppers that jumped or flew moved <15 m, and surveyors avoided counting them more than once. All patches in a landscape were surveyed on the same day; the landscapes were surveyed in a random rotation during each survey period.

Measuring landscape effects on temperature

We measured temperature in all patches to assess a potential link among grasshopper abundance and abiotic differences between patch types. During June and July of 2008 and 2009, we rotated 80 Hobo temperature loggers (model UA-002-08; Onset Corporation, Bourne, Massachusetts, USA) through the eight landscapes as follows: all loggers were deployed in a single landscape simultaneously, with one logger at each planting location along each transect in every patch (four locations per transect × four transects per patch × five patches per landscape); loggers were positioned ~0.3 m above the ground and recorded temperature every 10 minutes for four consecutive days in each landscape before being moved to the next landscape. The landscapes were sampled in random rotation.

Statistical analyses

We assessed how levels of leaf herbivory varied by patch type using plants from experiments 1 and 2. These plants were in the open, not shaded by cages or protected from herbivores. Levels of herbivory were assessed in three ways. First, we evaluated the influence of patch type on the proportion of damaged plants per patch, considering a plant damaged if it had any leaf damage at all. We treated the proportion of damaged plants in each patch as the response variable in a generalized linear mixed-effects (GLME) model with a binomial distribution. Patch type was a fixed effect; year (2008 or 2009) and landscape (1–8) were random effects.

We also evaluated the influence of patch type on the proportion of damaged leaves per plant. As before, we treated this proportion as the response in a GLME model with a binomial distribution. Patch type was treated as a fixed effect; year (2008 or 2009) was treated as a random effect. Landscape (1–8), patch number (1–40), and plant number (1–654) were nested random effects, which avoids artificially inflating degrees of freedom.

The third herbivory analysis focused on whether and how patch type influenced the proportion of severely damaged leaves among plants that experienced at least some herbivory. We used this approach, in addition to the herbivory models described previously, to include in our binomial modeling framework an assessment of whether patch type influenced the amount of leaf area missing. We considered only plants in experiments 1 and 2 that had at least one damaged leaf, and we defined severe damage as leaves with >10% area missing. We considered >10% damage "severe" because, among all plants in experiments 1 and 2 that had at least one damaged leaf ($N = 527$), the median amount of damage was in the 1–10% category. Among these damaged plants, 302 plants had at least one leaf severely damaged (>10%); 32% of all damaged leaves (826/2601) were severely damaged. Thus we treated the proportion of leaves (per damaged plant) with >10% damage as the response variable in a GLME model with a binomial distribution. Patch type was a fixed effect; year (2008 or 2009) was a random effect; landscape (1–8), patch number (1–40), and plant number (1–527) were nested random effects.

We used two more GLME models to evaluate the relationship between herbivory and fruit production for plants in experiments 1 and 2. Each model used one of the herbivory metrics described before (proportion of damaged leaves among all plants, proportion of severely damaged leaves among damaged plants) as a predictor of fruit production. The response variable in each model was the number of fruits produced, with a Poisson distribution; herbivory was a fixed effect; year (2008 or 2009) and landscape (1–8) were random effects.

We assessed the impact of grasshopper herbivory on fruit production (experiment 3) for each pair of caged plants by subtracting the total number of fruits produced by the plant exposed to herbivory (in the control cage) from the number of fruits produced by the adjacent plant protected from herbivory (in the exclosure cage). We then used this difference in fruit production as the response variable in a linear mixed-effects (LME) model to compare, by patch type, the cost in fruit production associated with herbivory. Patch type was a fixed effect; landscape (1–8) and patch number (1–40) were nested random effects.

To determine the influence of patch type on grasshopper abundance, we used a GLME model with a Poisson distribution. The response variable was the total number of grasshoppers detected in each patch during each survey; patch type was a fixed effect; survey period (1–5) and landscape (1–8) were random effects.

We used temperature data to determine whether differences in grasshopper abundance among patch types could be explained by patch shape effects on daytime temperatures. Prior to analyzing temperature data, nighttime temperatures were removed, and all daytime temperatures recorded by each data logger were averaged to produce one mean daytime temperature (sunrise to sunset) for each logger deployment (80 temperature means for each landscape in 2008 and 2009). To assess edge effects on temperature, we used these data in a LME model in which distance from the patch edges, patch type, and their interaction were fixed effects; year (2008 or 2009) and landscape (1–8) were random effects. We used the same data (from 2009) to correlate temperature with grasshopper abundance, which was sampled only in 2009. Since temperature loggers were deployed only once at each grasshopper sampling location in 2009 (1, 20, and 37 m from edges on all transects), we used the mean number of grasshoppers (taken from the five survey periods) at each location as the response variable in a GLME model with a Poisson distribution; temperature was a fixed effect; landscape (1–8) was a random effect.

Finally, we assessed how patch shape influenced the distribution of daytime temperatures in the landscapes as follows: Starting with the mean daytime temperatures recorded by each logger (at 1, 10.5, 20, and 37 m on all transects) we used nonlinear regression to estimate temperature as a continuous function of distance from edge to center in each patch separately (80 regressions; 40 patches in 2008 and 2009). After inspecting the temperature data (following Crawley [2007]) and recognizing that temperature increased consistently from edge to center in all patches (see *Results*), we chose a single function to describe temperature as it varied with distance in each patch: temperature $\sim Y \times D^Z$ (where Y is an estimate of the temperature at patch edges; D is the distance to the nearest edge, between 1 and 37 m from the edges; and Z is a constant estimated individually for each patch). We then used the predicted values for temperature between 1 and 37 m from the edges in each patch to calculate how much interior core area of each patch, each year, was warmer than the mean temperature of the landscape in which the patch resided. (Estimating temperature only between 1 and 37 m from patch edges was sufficient to calculate how much interior area of each patch had above average temperatures. In every patch, each year, temperatures 1 m from the edges were below the patch's landscape mean; temperatures 37 m from the edges were above the patch's landscape mean; and temperatures increased with distance.) We used a LME model to assess the influence of patch type on the proportion of total area in each patch that had above average temperatures. Patch type was a fixed effect; year (2008 or 2009) and landscape (1–8) were random effects.

All analyses were fit using the statistical program R (R Development Core Team 2010) and the lme4 package (Bates and Sarkar 2010). We assessed the significance of individual factors, e.g., "patch type," with likelihood ratio tests (LRT; following Crawley [2007]), comparing full models to null models that were exactly similar except that the factor of interest, e.g., patch type, was

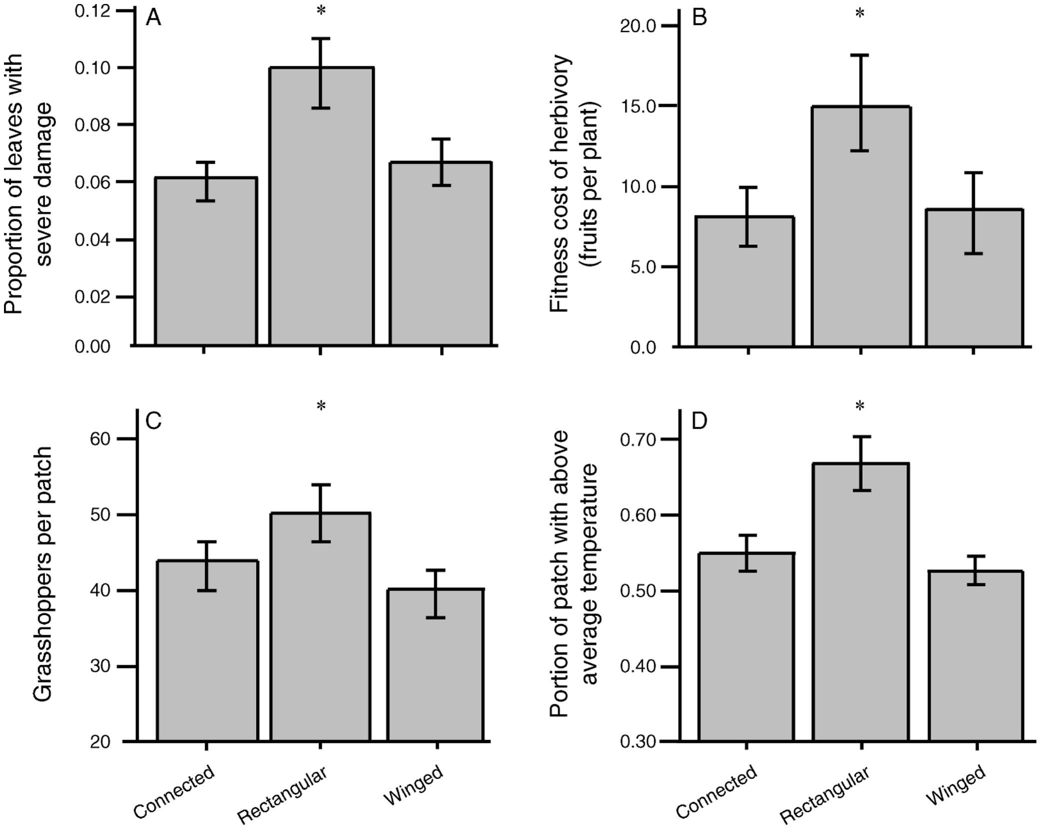

FIG. 2. Effect of patch type on (A) severe leaf herbivory, (B) the reduction in plant fruit production as a result of herbivory, (C) grasshopper abundance, and (D) temperature in the patches. All panels show patch means ± SE. Regarding effect sizes for Fig. 2B (experiment 3, paired design): on a per-plant basis, the average reduction in fruits due to grasshopper herbivory was 8.0 fruits in connected, 15.1 fruits in rectangular, and 8.3 fruits in winged patches. The average number of fruits produced by the plants protected from grasshoppers was 31.6 fruits in connected, 38.8 fruits in rectangular, and 32.9 fruits in winged patches. Thus the percentage by which grasshopper herbivory reduced plant fruit production for each patch type was 25.3% in connected (8.0/31.6), 38.9% in rectangular (15.1/38.8), and 25.2% in winged patches (8.3/32.9). Asterisks indicate significance when $P \leq 0.5$.

removed. We assessed differences between levels of categorical factors using the multcomp package (Hothorn et al. 2010) and the Westfall procedure for assigning *P* values (following Westfall [1997]; Bretz et al. 2010). This resampling-based procedure is suitable for normal, binomial, and Poisson distributions (Westfall and Troendle 2008, Oden et al. 2010).

RESULTS

Grasshoppers accounted for >99% of all insects observed consuming *S. americanum* leaves at our sites (based on 300 hours of video recordings and >4000 person-hours in the field). Leaf miners and fire ants also were occasionally observed consuming *S. americanum* leaves. We observed seven grasshopper species from five genera consuming *S. americanum*: *Melanoplus impudicus*, *Melanoplus sanguinipes*, *Melanoplus scudderi*, *Pardalophora phoenicoptera*, *Psinidia fenestralis*, *Schistocerca americana*, and *Trimerotropis* sp.

The results that follow are summarized in Appendix B. Patch type had no influence on the proportion of plants that died or were clipped at the main stem by herbivores (Appendix A). Patch type also had no influence on the proportion of plants per patch that experienced herbivory (LRT, $\chi^2 = 0.85$, df = 2, $P = 0.66$) or the proportion of damaged leaves per plant (LRT, $\chi^2 = 3.063$, df = 2, $P = 0.22$). Among plants that experienced herbivory, patch type did have a significant influence on severe herbivory, i.e., the proportion of leaves with >10% damage (LRT, $\chi^2 = 11.31$, df = 2, $P < 0.01$; Fig. 2A). Plants in rectangular patches had significantly more severe leaf damage than plants in connected patches ($z = 3.69$, $P < 0.01$) and winged patches ($z = 2.67$, $P < 0.01$); the amount of severe leaf damage on plants in connected and winged patches was not different ($z = 0.88$, $P = 0.38$).

A strong correlation between herbivory and fruit production in experiments 1 and 2 confirmed that the proportion of damaged leaves per plant had a significant, negative effect on fruit production ($z = 22.6$, $P < 0.01$), as did the proportion of severely damaged leaves per damaged plant ($z = 20.10$, $P < 0.01$). Each 0.1 increase in the proportion of damaged leaves per plant corresponded with a 13% decrease in fruits. The strength

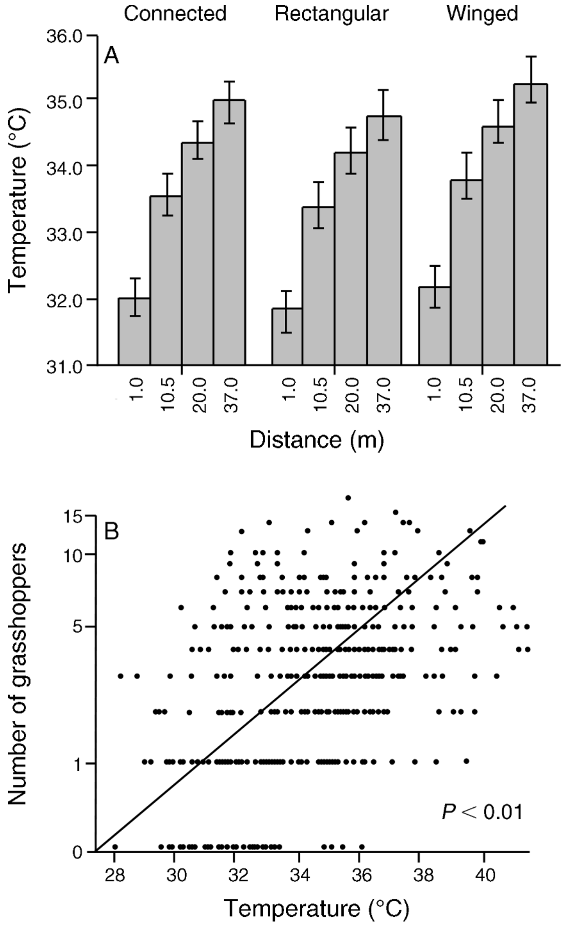

FIG. 3. (A) Edge effect on temperature (means ± SE) and (B) correlation between temperature and grasshopper abundance. In panel A, distances are from the habitat patch edges. Note the log scale for grasshopper abundance in panel B.

of this relationship nearly doubled when considering the proportion of severely damaged leaves per damaged plant; each 0.1 increase corresponded with a 22% decrease in fruits.

The negative relationship between herbivory and fruit production was explicitly linked to grasshoppers in the different patch types in experiment 3. Plants exposed to grasshopper herbivory produced fewer fruits, on average, than plants protected from grasshoppers in all patch types (Fig. 2B), but patch type was also a significant factor determining the amount by which fruit production was reduced (LRT, $\chi^2 = 6.32$, df = 2, $P = 0.04$). The reduction in fruits associated with grasshopper herbivory was significantly greater in rectangular patches than in connected ($z = 2.34$, $P = 0.05$) and winged patches ($z = 2.04$, $P = 0.05$); the reduction in fruits in connected and winged patches was not different ($z = 0.09$, $P = 0.93$).

Patch type was also a significant factor determining grasshopper abundance (LRT, $\chi^2 = 21.02$, df = 2, $P < 0.01$; Fig. 2C). There were more grasshoppers in rectangular patches than in connected ($z = 3.51$, $P < 0.01$) and winged patches ($z = 4.34$, $P < 0.01$); grasshopper abundance in connected and winged patches was not different ($z = 1.30$, $P = 0.19$).

Mean daytime temperatures increased significantly with distance from the edges (LRT, $\chi^2 = 644$, df = 9, $P < 0.01$; Fig. 3A), and there was no interaction between distance and patch type (LRT, $\chi^2 = 1.86$, df = 6, $P = 0.93$). There was also a significant positive correlation between temperature and grasshopper abundance ($z = 16.48$, $P < 0.01$; Fig. 3B). For every 1°C increase, there was a 27% increase in grasshoppers. The 80 nonlinear models describing rates of temperature increase for each patch in each year also consistently had significant parameter estimates (Y, in all cases, $P < 0.01$; Z, in all cases, $P < 0.03$).

Finally, patch type was a significant factor determining how much area in a patch was warmer than the average temperature of the landscape in which the patch resided (LRT, $\chi^2 = 19.76$, df = 2, $P < 0.01$; Fig. 2D). Rectangular patches had a larger portion of area with above average temperatures compared to connected ($z = 3.59$, $P < 0.01$) and winged patches ($z = 4.41$, $P < 0.01$); the amount of area with above average temperatures in connected and winged patches was not different ($z = 1.13$, $P = 0.26$).

DISCUSSION

The corridor hypothesis

Our results provide no support for the hypothesis that corridors increase herbivory and decrease plant fruit production. Leaf herbivory did have a significant, negative impact on *S. americanum* fruit production, but plants in patches connected by corridors did not have higher levels of herbivory than plants in isolated rectangular or winged patches. Nor did plants in connected patches experience a greater reduction in fruits as a result of herbivory. It is important to note that connected and winged patches had equivalent levels of herbivory and reduction in fruits as a result of herbivory. Because connected and winged patches have both similar area and similar shape, winged patches are appropriate controls for assessing potential corridor effects. Our corridor hypothesis was based on theoretical and empirical evidence that connectivity in fragmented habitats can increase insect abundance (MacArthur and Wilson 1967, Rathcke and Jules 1993, Kruess and Tscharntke 1994, Haddad and Baum 1999, Hanski 1999, Collinge 2000, Tscharntke et al. 2002, Baum et al. 2004, Haddad et al. 2011). But grasshoppers, the primary consumers of *S. americanum* in our landscapes, were not more abundant in connected patches.

The lack of a corridor effect in our study may be explained by considering the habitat requirements, movement behavior, and dispersal abilities of the grasshopper species we observed consuming *S. americanum*. The impact of corridors on plants will depend largely on how plant mutualists and antagonists (pollinators, seed dispersers, disease agents, and herbivores) respond to fragmentation and connectivity. It is well established that corridors increase movement and abundance of many species. But several studies indicate that corridors may have little impact on habitat generalists and species that move readily through matrix areas separating patch fragments (Didham et al. 1996, Rosenberg et al. 1997, Haddad 1999, Hudgens and Haddad 2003, Ockinger et al. 2010), and recent reviews call for additional studies to assess how corridors impact species with different degrees of habitat specialization and dispersal ability (Chetkiewicz et al. 2006, Gilbert-Norton et al. 2010). Among the seven grasshopper species we observed consuming *S. americanum*, three of the most abundant in our landscapes (*Melanoplus sanguinipes*, *Pardalophora phoenicoptera*, *Schistocerca americana*) are active fliers as adults and known to disperse long distances (Kuitert and Connin 1952, Capinera et al. 2004). Two of these (*M. sanguinipes*, the "migratory grasshopper," and *S. americana*, the "American locust") are also habitat generalists that feed on a variety of grasses and herbaceous plants (Fielding and Brusven 1992, Smith and Capinera 2005). *Melanoplus sanguinipes* is one of the most pervasive crop pests in the United States (Capinera et al. 2004), and *S. americana* is found in almost every habitat in the state of Florida (Squitier and Capinera 2002). Three of the other species (*Melanoplus impudicus*, *Melanoplus scudderi*, *Psinidia fenestralis*) are also abundant and wide-ranging in the eastern United States (Capinera et al. 2004). These generalist herbivores appear to be unaffected by the connectivity provided by corridors in our landscapes.

This result contributes to a growing body of evidence that connectivity does not pose a threat to plants by bolstering populations of antagonistic species in fragmented landscapes (Simberloff et al. 1992, Haddad et al. 2011). To the contrary, we found that the "edginess" of connected patches (a consequence of the linear corridor) resulted in relatively less herbivory, lower cost to plant fitness as a result of herbivory, and fewer grasshoppers.

The patch shape hypothesis

We found strong support for the hypothesis that habitat patch shape is a more important determinant of herbivory and plant fruit production than the presence of a corridor. In rectangular patches, which have higher area/perimeter ratios, plants had significantly more severe herbivory than plants in connected or winged patches. Plants in rectangular patches also had a greater reduction in fruit production as a result of herbivory. We based the "patch shape hypothesis" on the recognition that gradients in abiotic variables, e.g., light, moisture, and temperature, created by habitat edges can profoundly alter the abundance and distribution of insects in fragmented landscapes (Laurance et al. 2002, Ries et al. 2004, Collinge 2009). Indeed, we found strong positive relationships between distance from edge and temperature in the patches and also between temperature and grasshopper abundance. We further found that rectangular patches, which have more core area far from edges, had a significantly larger portion of area with above average temperatures, and rectangular patches had more grasshoppers.

These results, taken together, suggest that grasshoppers in rectangular patches were more abundant, created more severe leaf damage, and had a greater negative impact on plant fitness because rectangular patches have relatively more area with above average daytime temperatures. Other studies have also found strong positive correlations between temperature and both grasshopper abundance and foraging activity (Harrison and Fewell 1995, Lactin and Johnson 1996, Ritchie 2000, Gilman et al. 2008). Because most grasshopper species are heliotherms, they commonly move within habitats to maintain a high diurnal body temperature (reviewed in Uvarov [1977] and Chapman and Joern [1990]). One review found that most grasshopper species prefer temperatures between 35° and 42°C (Chapman and Joern 1990), which is warmer than the mean daytime temperatures in all of our landscapes in 2008 and 2009 (2008, 33.1°C; 2009, 34.4°C).

Our finding that rectangular patches have more area with high temperatures also helps explain two previous studies of insects at SRS. Orrock et al. (2011) found a greater abundance of thermophilic ants and beetles in rectangular patches. Orrock et al. (2003) also detected higher levels of invertebrate seed predation in rectangular patches and originally suggested that these patches provide more high-quality habitat to heat-loving taxa. Thus our results, along with these earlier studies, highlight a trade-off between habitat quality and connectivity that will often be faced by landscape managers. The relatively small differences in area–perimeter ratios in our patches show that fairly small changes in habitat quality can trump potential corridor effects, with significant plant fitness consequences.

Finally, our study points to a new explanation for the previously demonstrated positive impacts of corridors on plants: Whether corridors confer benefits for plants will often depend on a balance of fitness trade-offs mediated by interactions with mobile organisms. In the landscapes at SRS, corridors increase pollination, seed dispersal, and plant community diversity (Haddad et al. 2011), yet our study shows no accompanying herbivory cost to plants in habitats connected by corridors.

ACKNOWLEDGMENTS

We thank the U.S. Department of Agriculture Forest Service–Savannah River and especially Chris Hobson, Jim Segar, John Blake, and Ed Olson for creating and maintaining our experimental landscapes. We are indebted to Hamilton Boyce, Caitlin Graff, Lindsey Fenner, Anna Kramer, Rachel Malinen, Heather Nycum, and Elizabeth Smith for field assistance. Thanks also to Cesar Nufio for assistance identifying grasshoppers. Funds were provided by the Department of Energy–Savannah River Operations to the Department of Agriculture through the U.S. Forest Service, Savannah River, under Interagency Agreement DE-AI09–00SR22188; to D. M.

Evans by the National Science Foundation, Sigma Xi, the Society for Integrative and Comparative Biology, and the University of Washington; to N. E. Turley by the National Science Foundation, the Mary Gates Foundation, and the University of Washington.

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Supplemental Material

Appendix A

Analysis of plant mortality and clipping in relation to patch type (*Ecological Archives* E093-088-A1).

Appendix B

Summary of statistical tests and results (*Ecological Archives* E093-088-A2).