

AN EXPERIMENTAL TEST OF WHETHER HABITAT CORRIDORS AFFECT POLLEN TRANSFER

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Abstract. Negative effects of habitat fragmentation are thought to be diminished when habitat patches are joined by a corridor. A key assumption is that corridors facilitate exchange rates of organisms between otherwise isolated patches. If the organisms are pollinators, corridors may be important for maintaining genetically viable populations of the plants that they pollinate. We tested the hypothesis that corridors increase the movement of insect pollinators into patches of habitat and thereby increase pollen transfer for two species of plants, one pollinated by butterflies (*Lantana camara*) and the other by bees and wasps (*Rudbeckia hirta*). We worked in an experimental landscape consisting of 40 \geq 1-ha patches of early-successional habitat in a matrix of forest. Within each of eight experimental units, two patches were connected by a corridor (150 \times 25 m), and three were not. Patch shape varied to control for the area added by the presence of a corridor. Differences in patch shape also allowed us to test alternative hypotheses of how corridors might function. The Traditional Corridor Hypothesis posits that corridors increase immigration and emigration by functioning as movement conduits between patches. The Drift Fence Hypothesis posits that corridors function by “capturing” organisms dispersing through the matrix, redirecting them into associated habitat patches. Using fluorescent powder to track pollen, we found that pollen transfer by butterflies between patches connected by a corridor was significantly higher than between unconnected patches (all values mean \pm 1 SE: 59% \pm 9.2% vs. 25% \pm 5.2% of flowers receiving pollen). Likewise, pollen transfer by bees and wasps was significantly higher between connected patches than between unconnected patches (30% \pm 4.2% vs. 14.5% \pm 2.2%). These results support the Traditional Corridor Hypothesis. There was little support, however, for the Drift Fence Hypothesis. To generalize our results to a larger scale, we measured the probability of pollen transfer by butterflies as a function of distance along a 2000 \times 75 m corridor. Pollen transfer probability exponentially declined with respect to distance and successfully predicted pollen transfer probability on the scale of our previous experiment. These results suggest that corridors facilitate pollen transfer in fragmented landscapes.

Key words: corridor experiment; drift fence hypothesis; habitat corridor; habitat fragmentation; insect pollinators; landscape ecology; *Lantana camara*; plant–animal interaction; pollen transfer; pollination; *Rudbeckia hirta*.

INTRODUCTION

Habitat fragmentation is frequently cited as one of the most serious threats to biodiversity (Wilcove et al. 1998). Precipitating this threat are alteration of habitat within fragments and isolation of populations (Fahrig and Merriam 1994, Harrison and Bruna 1999). Of these two mechanisms, isolation has generated much attention because metapopulation ecologists view it as a defining element of landscapes (Hanski 1998) and because conservation biologists view it as a tractable problem (Rosenberg et al. 1997, Beier and Noss 1998). Both groups generally tout corridors (i.e., strips of habitat that connect patches of similar habitat) as a means

of maintaining populations in otherwise isolated patches of habitat. Corridors are hypothesized to diminish negative effects of fragmentation by increasing the exchange rate of organisms between habitat patches. Recent studies provide support for the ability of corridors to increase immigration and emigration, stem inbreeding depression, lower extinction rates, lessen demographic stochasticity, and generate higher population densities (Gilbert et al. 1998, Gonzalez et al. 1998, Aars and Ims 1999, Haddad and Baum 1999, Mech and Hallett 2001).

Corridors remain controversial, nonetheless. Not all studies support corridor theory (Rosenberg et al. 1998, Bowne et al. 1999, Collinge 2000, Danielson and Hubbard 2000, Andreassen and Ims 2001). More fundamentally, controversy has arisen because potentially negative impacts of corridors are often overlooked, because mechanisms of corridor function are often surmised, and because alternative hypotheses are rarely explored (Simberloff et al. 1992, Beier and Noss 1998).

Manuscript received 10 September 2003; revised 5 June 2004; accepted 25 June 2004; final version received 19 July 2004. Corresponding Editor: E. S. Menges.

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Equally troublesome are issues of study design (Rosenberg et al. 1997, Nicholls and Margules 1991, Holt and Debinski 2003). In particular, because most corridor studies are based on correlative data, the underlying cause of observed patterns remains speculative. Among the handful of experimental studies, those that are well replicated tend to be on laboratory microcosms or on small spatial scales (reviewed in Holt and Debinski 2003), leading to disagreement about relevance to landscape-level processes (Beier and Noss 1998, Haddad et al. 2000). A final methodological shortcoming is that corridors are often viewed solely as connectors, even though the presence of a corridor almost always generates increased patch area and edge habitat relative to patches without corridors (Rosenberg et al. 1997). This oversight is problematic because edge and area effects are well known to have population and community impacts (Murcia 1995, Bender et al. 1998, Davies et al. 2001, Steffan-Dewenter 2003). Perhaps movement into patches connected by corridors is elevated compared to unconnected patches because the former have greater overall area, not because of their connectivity. Such a distinction is far from trivial, especially for those charged with deciding whether to focus limited resources on preserving habitat area or connectivity.

We report an experimental test of whether corridors affect insect pollination of two open-habitat plant species. We focused on plants because relatively little is known about how corridors affect their biology (Spira 2001, Kirchner et al. 2003) and because their sessile nature often makes them dependent on animal mutualists for gene flow. Given that animal movement is influenced by landscape structure, plant pollination may be as well. Our study was large scale (>400 ha, including matrix and buffer areas), well-replicated (based on a power analysis), controlled for area effects, and tested two non-mutually exclusive hypotheses of corridor function: (1) the *Traditional Corridor Hypothesis*, which posits that corridors function as movement conduits, channeling dispersing organisms between connected habitat patches (Rosenberg et al. 1997, Beier and Noss 1998); and (2) the *Drift Fence Hypothesis*, which posits that corridors function as drift fences, "intercepting" organisms as they disperse through matrix habitat and redirecting them into habitat patches attached to the corridor (Anderson and Danielson 1997, Haddad and Baum 1999). Because different types of pollinators are likely to differ in behavior, we attempted to generalize our results by running parallel experiments on one species pollinated primarily by butterflies and one by bees and wasps. Finally, to extrapolate our results to a larger scale, we measured the distance that butterflies at our site carried pollen down pre-existing corridors that were an order of magnitude larger than corridors in our experimental landscapes.

METHODS

Study site.—The experiment was conducted at the Savannah River Site (SRS; 33.20° N, 81.40° W), a National Environmental Research Park, near Aiken, South Carolina, USA. We worked in mature (>40-year-old) forest dominated by loblolly (*Pinus taeda*) and slash pine (*Pinus elliotii*). The vegetation of SRS is described in Workman and McLeod (1990). Experimental patches and corridors were created in the winter of 1999–2000 by harvesting trees, removing them without damaging the matrix canopy, and burning several months later. At the time of our experiments in the summers of 2000 and 2001, the patches were dominated by herbs (e.g., *Aristida tenuifolia*, *Pityopsis graminifolia*, *Lespedeza stuevei*), shrubs (e.g., *Vaccinium arboreum*, *Crataegus flava*), and small trees (e.g., *Prunus serotina*, *Quercus nigra*, *Sassafras albidum*, *Diospyros virginiana*).

Eight experimental units each consisted of five patches, a central *source* patch (100 × 100 m) surrounded by four equidistant *receiver* patches, 150 m away (Fig. 1). A buffer zone, extending 100 m from the outside edge of all receiver patches, consisted of generally homogenous forest. The number of experimental units was based on a power analysis, using data on butterfly movement between patches in a similar system at the same site (Haddad 1999). Adopting standard values of alpha (0.05) and beta (0.80), a sample size of eight assured detection of significant differences with effect sizes (difference in means/standard deviation of differences) >0.96.

Each experimental unit had one each of three types of receiver patches: *connected*, *winged*, and *rectangular* (Fig. 1). In addition, four experimental units had a second winged patch and four had a second rectangular patch, allowing estimation of variance within experimental units for those patch types. The position of receiver patches relative to the source patch was determined randomly for each experimental unit. A 25 m wide corridor connected each source patch with one receiver patch, the connected receiver. The other three receiver patches in each experimental unit were not connected to the source patch, but were equal in area to the connected receiver plus the corridor, thereby allowing us to decouple corridor and area effects on pollen transfer between patches. Rectangular receiver patches had the area of the corridor added to their side farthest from the source patch, creating a rectangle. Winged receiver patches had the area of the corridor added as two blind, 25 × 75 m "pseudocorridors" extending from the patches' sides. As pollinators dispersed from the source patch and flew toward the winged patch, these pseudocorridors were perpendicular to their flight path.

Comparisons of pollen transfer from the source patch to the connected patch vs. to unconnected receiver patches tested the Traditional Corridor Hypothesis, which predicts higher pollen transfer to connected than

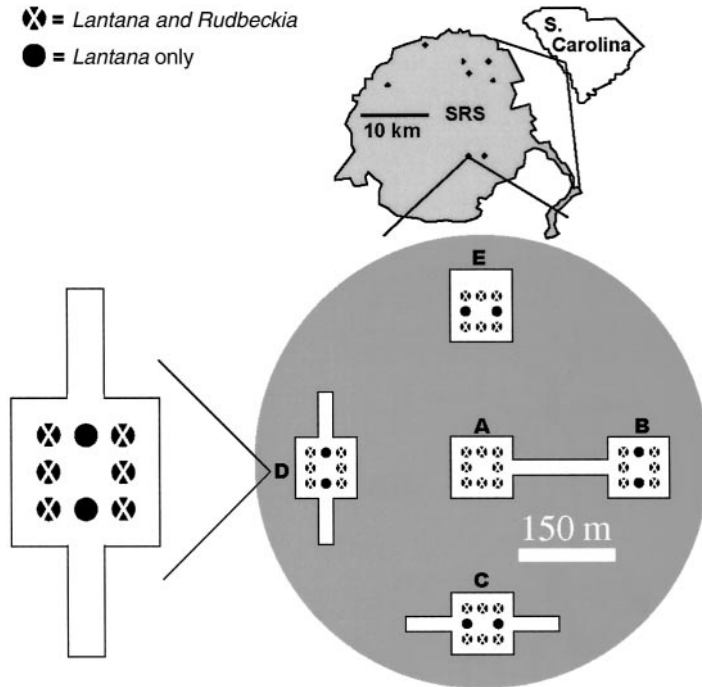


FIG. 1. Location of Savannah River Site (SRS) in South Carolina, USA, and locations of eight experimental landscapes within the site. One experimental landscape is enlarged to show: Patch A, source patch; Patch B, connected receiver patch; Patches C and D, winged receiver patches; and Patch E, rectangular receiver patch. Orientation and identity of receiver patches was determined randomly (with the proviso that each experimental landscape had at least one of each patch type). Four of the landscapes had two winged patches, and four had two rectangular patches. Circles mark locations of flowering plants used in the experiment. Eight *L. camara* were planted in every patch in the same configuration, whereas only six bouquets of *R. hirta* were planted in all patches (except the source patch, which had eight).

unconnected patches. Comparisons of pollen transfer from the source patch to winged vs. rectangular receiver patches tested the Drift Fence Hypothesis, which predicts lower pollen transfer to rectangular than to winged patches.

Pollen transfer by butterflies.—Because all naturally occurring species of butterfly-pollinated plants were highly variable in abundance among patches, it proved infeasible to standardize their densities. Thus, we selected a study species that did not occur in the patches, but met the following criteria: (1) it had naturally occurring congeners in the region and in the same type of habitat; (2) it was visited by the most common butterfly species visiting similar flowers in the patches; (3) it was not commonly visited by other pollinators; and (4) it was commercially available, affordable, and easily transplanted. *Lantana camara* (Verbenaceae) met all of these criteria (see Plate 1; see also Appendix). Fluorescent powder (Day-Glo Color Corporation, Cleveland, Ohio, USA) was used to estimate pollen movement among patches. It is widely used by pollination biologists because it is easily detectable in minute quantities and because powder transfer is strongly and positively correlated with pollen transfer (Dudash 1991, Kearns and Inouye 1993). Hereafter, we refer to powder as “pollen.”

In June 2000, eight *L. camara* plants 30–50 cm in height were transplanted into each patch ($n = 320$ plants) in three rows, 33 m from their nearest neighbor and 17 m from the nearest edge (except for plants 71 m from the back edge of rectangular patches; Fig. 1). In September 2000, we randomly selected one to two

experimental units for trials on a given day. We repeated each experimental unit a minimum of three times, depending on weather. The time interval between trials in a given experimental unit was greater than *L. camara* flower longevity. This interval and afternoon thundershowers eliminated pollen contamination from one trial to the next. Powder was applied before 10:00 hours to all flowers in source patches. That night, an ultraviolet lamp was used to look for pollen on flowers in surrounding receiver patches. To minimize assumptions about pollen carryover, we did not count the grains of pollen per inflorescence, but rather recorded the presence or absence of powder on each inflorescence, as suggested by Handel (1983).

Pollen transfer by bees and wasps.—*Rudbeckia hirta* is most frequently pollinated by bees and wasps, although butterflies visit it occasionally (P. Townsend, *personal observation*). It occurs naturally at SRS, but was not in any of our experimental patches. In July 2001, six *R. hirta* flowers with 30–40 cm stems (hereafter “bouquets”) were placed in water-filled jugs in all patches (Fig. 1). In the source patch, eight bouquets were placed identically to *L. camara* plants. In the receiver patches, six bouquets were positioned in the same manner as with *L. camara*, except that there were no bouquets in the middle row because we did not have enough flowers.

Methods of tracking pollen were identical to those for *L. camara*, with the following exceptions. We placed cages (1 × 1 cm hardware cloth) over all *R. hirta* flowers in the source patches to eliminate transfer of pollen by butterflies. These cages did not appear to



PLATE 1. A gulf fritillary (*Agraulis vanillae*) nectaring from *Lantana*. Photo credit: P. Townsend.

influence visitation by bees and wasps. If no pollen was found on the flowers in the receiver patches on the first night of an experiment, flowers were rechecked the following night. Trials in each experimental unit were repeated from two to four times, with most of the experimental units having three trials. We used new sets of flowers in each trial.

Pollen transfer along larger corridors.—To determine how far butterflies transport pollen along larger corridors, we placed potted *L. camara* plants in four power-line rights-of-way. All power lines were straight and had continuous forest on both sides for at least 3000 m, thereby simulating a long corridor. At one end of each power line, six *L. camara*, 30–50 cm height, were placed in two rows, ~12 m apart. These “source” plants and were dusted with powder before 10:00 hours on trial days. Four “receiver” plants were placed in two rows, ~12 m apart at distances of 200, 450, 700, and 1050 m from the source plants. Data on pollen transfer were collected in the same manner as previously described. A pilot run in June 2001 revealed that pollen was frequently transported 1050 m. Thus, the distances between source and receiver plants were increased to 500, 1000, 1500, and 2000 m. This experiment was repeated at least six times per power line in June and September of 2001. Source plants were alternated between opposite ends of the power line to control for directional effects.

Data analysis.—All proportions were arcsine square-root transformed to meet assumptions of normality and homogeneity of variance. We analyzed pol-

len transfer frequency with mixed linear models (PROC MIXED Version 8.1; SAS Institute 1990), treating the two experiments (*L. camara* and *R. hirta*) separately. Patch type was the independent unit and experimental landscape (a set of five patches) and connectivity (connected vs. unconnected) were main effects, with patch shape of unconnected patches (winged or rectangular; $n = 12$ patches of each) nested within connectivity. This model provides a test of connectivity effects based on combined effects of the two types of unconnected patches (the Traditional Corridor Hypothesis), allows a direct comparison of winged and rectangular patches (the Drift Fence Hypothesis), and is consistent with previous analyses of data from our experimental landscapes (Tewksbury et al. 2002), allowing a direct comparison of results with those studies.

For the *L. camara* experiment, fixed effects were connectivity, patch shape, and average number of flowers on the plant (to control for variation in display size to pollinators). Random effects were experimental landscape and interaction of experimental landscape and connectivity. Covariance parameter estimates for random effects were generated with the COVTEST command of PROC MIXED. The proportion of inflorescences with pollen for each plant was averaged for each patch and was used as the dependent variable.

For the *R. hirta* experiment, we could tightly control the number of flowers (each bouquet always had six); thus it was unnecessary to include flower number as a covariate. In all other respects, the analysis was identical to that of *L. camara*.

We also compared pollen transfer from the source patch to the front vs. back of receiver patches (i.e., we compared plants in the rows nearest and farthest from the source patch). For both *L. camara* and *R. hirta*, the proportion of flowers with pollen for each plant in the front row was averaged for each patch and compared to the average for the back row, using a standard ANOVA. These comparisons were made for all three types of receiver patches.

For the power-line experiment, we used a repeated-measures ANOVA in which the proportion of inflorescences on each plant within each power line was the dependent variable (“within factor”). We averaged the data for each of three time steps, June, early September, and late September.

RESULTS

Pollen transfer by butterflies.—Transformed data met assumptions of normality (Shapiro-Wilk = 0.98, $P = 0.68$), and examination of residuals revealed no pattern of unexplained variation. Differences in pollen transfer of *Lantana camara* among patches were influenced by random effects of experimental landscape, although this influence was nonsignificant ($P = 0.107$; Table 1A).

Corridors significantly increased pollen flow between source and connected patches, relative to pollen

TABLE 1. Tests of fixed and random effects from mixed linear models for (A) *Lantana camara* and (B) *Rudbeckia hirta*.

| Effects, by species | Estimate | 1 SE | 95% CI | Numer- ator df | Denom- inator df | F or Z† | P |
|---------------------------------------|----------|-------|---------------|-------------------|---------------------|------------|-------|
| A) <i>Lantana camara</i> | | | | | | | |
| Fixed effects | | | | | | | |
| Connectivity‡ | 0.360 | 0.064 | 0.222, 0.498 | 1 | 7 | 31.73 | 0.001 |
| Patch type§ | -0.085 | 0.058 | -0.210, 0.039 | 1 | 13 | 2.19 | 0.163 |
| No. flowers | | | | 1 | 13 | 2.74 | 0.122 |
| Random effects | | | | | | | |
| Experimental landscape | 0.022 | 0.018 | | | | 1.24 | 0.107 |
| Experimental landscape × connectivity | 0.004 | 0.010 | | | | 0.42 | 0.336 |
| B) <i>Rudbeckia hirta</i> | | | | | | | |
| Fixed effects | | | | | | | |
| Connectivity‡ | 0.163 | 0.040 | 0.077, 0.249 | 1 | 7 | 16.54 | 0.005 |
| Patch type§ | -0.039 | 0.035 | -0.114, 0.035 | 1 | 14 | 1.28 | 0.378 |
| Random effects | | | | | | | |
| Experimental landscape | 0.000 | 0.003 | | | | 0.12 | 0.453 |
| Experimental landscape × connectivity | 0.002 | 0.003 | | | | 0.63 | 0.263 |

Note: The dependent variable is the proportion of flowers in a receiver patch receiving pollen from a source patch.

† For fixed effects, the statistic is *F*; for random effects, the statistic is *Z*.

‡ Tests the Traditional Corridor Hypothesis: pollen is transported from a source patch to connected patches more frequently than to unconnected patches.

§ Tests the Drift Fence Hypothesis: pollen is transported from a source patch to rectangular patches less frequently than to winged patches.

flow between source and unconnected patches ($P < 0.001$; Table 1A). An average of $59\% \pm 9.2\%$ (mean ± 1 SE) of *L. camara* flowers in connected patches received pollen from the source patch, compared to an average of $25\% \pm 5.2\%$ in the rectangular and winged patches, combined (Fig. 2A). This result was consistent across all eight experimental landscapes (experimental landscape \times connectivity interaction term nonsignificant; $P = 0.34$; Table 1A). There was only a marginal difference in the amount of pollen transferred from the source patch to rectangular and winged patches ($P = 0.163$; Table 1A). This result provides only weak evidence for a drift fence effect, although the difference was in the predicted direction: flowers in rectangular patches received 7.4% less pollen from the source patch than flowers in winged patches (Fig. 2A). Flowers in receiver patches positioned along the edge nearest (N) to the source patch were no more likely to receive pollen from the source patch than were flowers along the edge most distant (D) to the source patch (P values > 0.10 ; connected N = 0.55 ± 0.43 , D = 0.56 ± 0.43 ; rectangular N = 0.21 ± 0.30 , D = 0.26 ± 0.33 ; winged N = 0.24 ± 0.34 , D = 0.23 ± 0.31 ; ANOVA table not shown).

Pollen transfer by bees and wasps.—Again, transformed data met assumptions of normality (Shapiro-Wilk = 0.98, $P = 0.81$), residuals showed no pattern of unexplained variance, and effects of experimental unit were negligible ($P > 0.45$; Table 1B). Corridors significantly increased the amount of *Rudbeckia hirta* pollen transferred by bees and wasps between the source patch and connected patches relative to unconnected patches ($P < 0.005$; Table 1B). An average of $30\% \pm 4.2\%$ of *R. hirta* flowers in connected patches

received pollen from the source patch, vs. $14.5\% \pm 2.2\%$ in rectangular and winged patches (Fig. 2B). As with *L. camara*, the experimental landscape \times connectivity interaction term was nonsignificant ($P = 0.26$; Table 1B). Pollen transfer from the source patch to rectangular patches was 2.9% less than to winged patches, providing little support for a drift fence effect ($P = 0.378$; Table 1B, Fig. 2B). Likewise, pollen transfer from the source patch did not differ between flowers near to (N) and distant from (D) the source patch in a given type of receiver patch (P values > 0.10 ; connected N = 0.23 ± 0.35 , D = 0.34 ± 0.34 ; rectangular N = 0.14 ± 0.23 , D = 0.11 ± 0.23 ; winged N = 0.17 ± 0.28 , D = 0.16 ± 0.26 ; ANOVA table not shown).

Pollen transfer along larger corridors.—The proportion of *L. camara* flowers receiving pollen from other flowers along the same power line decreased with distance from those flowers ($F_{3,56} = 19.72$, $P < 0.001$; Fig. 3). This effect was consistent among power lines, although it differed in magnitude ($F_{3,56} = 3.28$, $P = 0.027$). Pollen transfer probability showed a decreasing exponential relationship with respect to distance: $y = 1952x^{-1.58}$, $R^2 = 0.85$. This equation predicts fairly well the proportion of pollen transfer observed in the experimental landscapes. For example, the distance from the nearest plant in source patches to the nearest plant in the connected patches was 183 m. The equation predicts 52% of the flowers with pollen transfer at this distance, compared to the observed average of 56% measured at an equivalent distance in the experimental landscapes.

DISCUSSION

Corridors clearly facilitated transfer of pollen between otherwise isolated habitat fragments. Flowers in

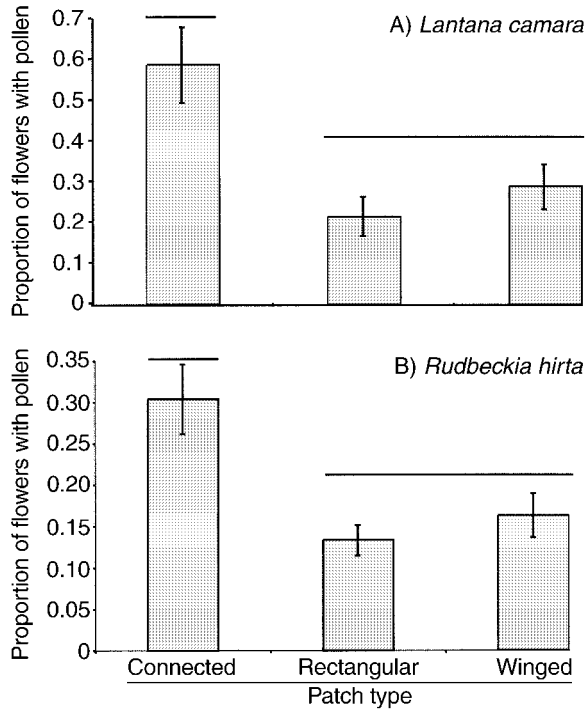


FIG. 2. Proportion (mean \pm 1 SE) of flowers of (A) *Lantana camara* and (B) *Rudbeckia hirta* with pollen, in relation to patch type. More flowers in connected patches received pollen from the source patch than did flowers in either type of unconnected patch (rectangular or winged), thereby supporting the Traditional Corridor Hypothesis. Flowers in rectangular and winged patches did not significantly differ in the proportion of their flowers receiving pollen from the receiver patch, a result that undermines a key prediction of the Drift Fence Hypothesis. These results were consistent for butterfly-pollinated plants (*L. camara*) and bee- and wasp-pollinated plants (*R. hirta*). Different horizontal bars denote significant ($P < 0.05$) differences between (but not within) the bars under them.

patches connected by a corridor were approximately twice as likely to receive pollen from an adjacent patch than were flowers in isolated patches. Because patch areas were equal, this difference in pollen transfer is directly attributable to the presence of corridors. Blind-ended pseudocorridors had a lesser impact on the probability of pollen transfer, which indicates that corridors

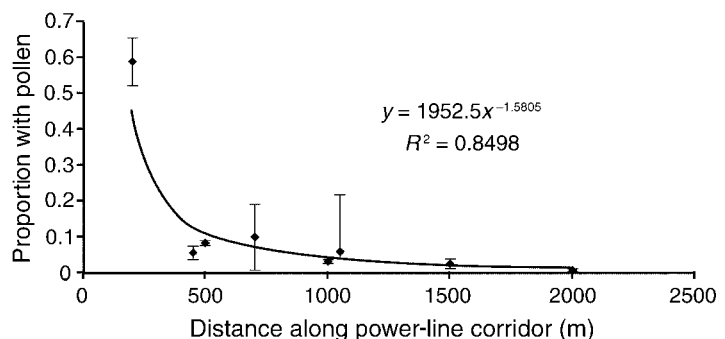
may not be effective at redirecting movement of pollinators dispersing through the matrix (Drift Fence Hypothesis). Results were in the predicted direction, with rectangular patches receiving less pollen than winged ones. These results were consistent for plant species pollinated by two disparate taxa, Lepidoptera and Hymenoptera. Thus, our study supports the Traditional Corridor Hypothesis: corridors increase movement of organisms into habitat patches by directing their movement out of adjacent patches connected by corridors. Although these results are restricted to the scale of our experiment (150-m corridors), they can probably be extrapolated by an order of magnitude because butterflies predictably transfer pollen as far as 2000 m along power-line corridors.

Previous experiments on corridor function.—Numerous studies have concluded that corridors increase interchange of individuals between otherwise isolated habitat patches (reviewed in Rosenberg et al. 1997, Beier and Noss 1998, Debinski and Holt 2000). The vast majority of these studies are descriptive and subject to differing interpretations (Nicholls and Margules 1991, Simberloff et al. 1992). We therefore focus attention on field experiments designed to test corridor function.

In a large-scale study of northern bird communities, fragmentation had less impact on species richness of forest patches connected by corridors than on unconnected patches (Schmiegelow et al. 1997). However, the difference was small and could be attributed to the larger area of patches with corridors. Creation of the patches resulted in increased movement through areas that became corridors, but only for juveniles (Machtans et al. 1996). Several experiments on voles, in landscapes of mown and unmown grassland, have demonstrated preferential use of corridors by one sex for dispersal (La Polla and Barrett 1993, Aars and Ims 1999, Aars et al. 1999, Andreassen and Ims 2001). In all these studies, many animals moved independently of corridors and population-level effects were often small or nonexistent.

There are vast differences in how different organisms respond to corridors. Because salamanders move readily through hostile matrix habitat, corridors did not

FIG. 3. Proportion (mean \pm 1 SE) of *L. camara* flowers with pollen in relation to distance from the source patch. Pollinators transported pollen along much larger corridors than in our five-patch experimental landscapes. The proportion of *L. camara* flowers receiving pollen along power-line corridors was negatively affected by distance ($F_{3,56} = 19.72$, $P < 0.001$; repeated-measures ANOVA). The negative projection of the standard error bar for $x = 1050$ m is not shown.



have a consistent positive effect on their immigration into habitat patches (Rosenberg et al. 1998). Individuals showed compensatory behavior when in the matrix, moving more quickly than in corridor habitat. In a grassland system, corridors had no effect on arthropod diversity or overall rate of patch colonization (Collinge 2000). Of three species studied intensely, only one preferred to move via corridors. In contrast, arthropods in moss patches on boulders were clearly influenced by the presence of corridors (Gonzalez et al. 1998). As predicted by theory, declines in abundance and diversity as a result of fragmentation were reduced by the presence of corridors, which presumably increased exchange among patches (Gilbert et al. 1998, Gonzalez et al. 1998, Collinge 2000).

Finally, in a landscape similar to ours, corridors had little effect on colonization ability or population density of most rodent species, despite their nonrandom use of habitat (Bowne et al. 1999, Danielson and Hubbard 2000). In the same landscape, however, densities and interpatch movement of most butterfly species were enhanced by the presence of corridors (Haddad 1999, Haddad and Baum 1999). A more recent experiment at the same site found support for the Traditional Corridor Hypothesis but not for the Drift Fence Hypothesis (Tewksbury et al. 2002).

Landscape type and scale.—Corridors are usually pictured as strips of primary habitat in a denuded matrix. Our experimental landscapes were the opposite: patches and corridors of early-successional growth surrounded by forest. Their key feature, however, was a sharp contrast between the two types of habitat. This issue of fragmentation and corridor studies is often downplayed relative to issues of connectivity, edge, and area. Yet the matrix matters, and studies such as ours need to be interpreted in that context (Davies et al. 2001, Ricketts 2001, Steffan-Dewenter et al. 2002, Steffan-Dewenter 2003). We suggest one reason that several other field experiments have failed to find strong or consistent corridor effects is their more subtle contrast between habitat patches and matrix (e.g., La Polla and Barrett 1993, Collinge 2000, Andreassen and Ims 2001). For example, in Collinge's system, the mown areas (matrix) contained vegetation similar to that of the unmown areas. The main difference between the two was vegetation height (65% shorter in mown), which may have been relatively unimportant from the perspective of the insect species studied.

Disturbances caused by such processes as fire, insect outbreaks, wind, disease, and landslides typify most forests, creating natural patches of early-successional vegetation. Many plants and animals rely on these patchy habitats and face the challenge of finding them via dispersal through matrix habitat. At our site, numerous species of flowering herbaceous plants and their insect pollinators are found in early-successional areas and presumably fit this pattern of habitat use and dispersal, at least historically. Thus, despite our inverse

design, the corridor effect that we observed reflects a natural situation and probably holds for other species in the same habitat.

More generally, connectivity is a dual function of landscape structure and the scale at which an organism perceives that landscape (Beier and Noss 1998, Tischendorf and Fahrig 2000). Thus, the same landscape may be fragmented for some species and highly connected for others. Specialized species with limited dispersal capabilities are thought to typify the former group, whereas highly vagile generalists typify the latter (Collinge 2000, Thomas 2000, Steffan-Dewenter and Tschardtke 2002). Assuming that insect pollinators of *Lantana camara* and *Rudbeckia hirta* were vagile generalists, the strong corridor effect that we observed is perhaps surprising and suggests that more specialized species might show even stronger effects (see Steffan-Dewenter 2003).

Pollinators.—At our site, *R. hirta* flowers were most commonly visited by several species of bees and wasps (e.g., *Campsomeris pluipis*, *Xylocopa virginica*, *Cerceris fumipennis*, *Polistes* sp.), which were similar or identical to those observed on other flowering plants in the patches. *Lantana camara* flowers were most commonly visited by gulf fritillaries (*Agraulis vanillae*), but variegated fritillaries (*Euptoieta claudia*), buckeyes (*Junonia coenia*), clouded sulfurs (*Colias philodice*), black swallowtails (*Papilio polyxenes*), and spicebush swallowtails (*P. troilus*) were also frequent visitors. All of these butterfly species are generalists in terms of nectar sources and at least three are known to disperse through forested matrix at our site, one (*P. troilus*) extensively (Haddad 1999). Consequently, the nonrandom pattern of pollination that we observed may have been generated by pollinators that dispersed via corridors and matrix, but preferred corridors. Alternatively, they may have been caused by one abundant taxon of pollinators dispersing primarily via corridors and other less common taxa dispersing primarily via matrix. We suspect the former explanation because all pollinators studied via mark-release-recapture techniques at our site move through both corridor and matrix habitats (reviewed in Haddad et al. 2003).

A limitation of our study is that we lack movement data for individual pollinators. Thus it was impossible to determine the number of independent pollen transfer events: perhaps all pollen found on receiver plants on a given day was transferred by a single pollinator. This is a statistical issue, though. What is probably most important from a plant population perspective is the number of flowers receiving pollen from a distant source.

Habitat fragmentation and pollination.—Unfortunately, we lack data on how differences in pollination affected the reproductive success of our species. We could not document fitness consequences of different pollination regimes because cut *R. hirta* flowers quickly withered after trials and because we did not allow *L.*

camara to set seed (it is potentially invasive). Nonetheless, it is well established that other insect-pollinated plants in small, isolated populations have lower reproductive success than conspecifics in large, non-isolated populations (Rathcke and Jules 1993, Aizen and Feinsinger 1994, Steffan-Dewenter and Tschardtke 2002). Exceptions occur (Cunningham 2000b, Costin et al. 2001, Donaldson et al. 2001), but this demographic difference is surprisingly robust. It holds for species in fragments of forest and of grassland (Menges 1991, Prober et al. 1998, Morgan 1999, Cunningham 2000a, Tomimatsu and Ohara 2001, Van Rossum et al. 2002) and for self-compatible and self-incompatible species (Groom 1998, Morgan 1999, Steffan-Dewenter and Tschardtke 1999, Wolf and Harrison 2000). In some cases, individuals in small or isolated populations exhibit complete reproductive failure (Groom 1998, Donaldson et al. 2001).

Low per capita reproductive rates of plants in small populations can be generated by mechanisms related to pollination. First, the quantity of pollen delivered to flowers is often reduced in fragmented populations (Steffan-Dewenter and Tschardtke 2002). Hand-pollination experiments in small populations typically reveal pollination limitation (reviewed in Keller and Waller 2002), targeting attention on how habitat fragmentation affects pollinator behavior (Schulke and Waser 2001, Goverde et al. 2002). Many pollinators are poor dispersers relative to the distance between isolated populations of flowering plants, and many apparently are not attracted to small floral displays (Ågren 1996, Groom 1998). Indeed, recent field experiments have causally linked low population size and high isolation with low pollinator visitation, low pollinator diversity, and low plant reproductive success (Groom 1998, Steffan-Dewenter and Tschardtke 1999, Schulke and Waser 2001).

A second pollination-related mechanism that can reduce reproductive success in small populations is a reduction in the quality of pollen, typically caused by a decrease in pollen transfer among populations. Inbreeding and reduced genetic variation result, but the extent to which they impact plant reproduction remains unclear; inbreeding is not cleanly linked to inbreeding depression in plants (reviewed in Byers and Waller 1999, Keller and Waller 2002).

Implications for conservation.—The ability of plant populations to persist in shrinking habitats and to colonize new habitats largely depends on the movements of mutualistic pollinators and seed dispersers. Habitat fragmentation may have major impacts on plant demography through disruption of such mutualisms (Rathcke and Jules 1993, Hamilton 1999, Cordeiro and Howe 2001, Spira 2001). With respect to pollination, it is sobering that most angiosperms (more than 90% by some estimates) are animal pollinated (Kearns et al. 1998) and that the majority of those examined already

show evidence of pollen limitation or inbreeding depression (Kearns et al. 1998, Keller and Waller 2002).

Corridors may alleviate negative impacts of habitat fragmentation for animal-pollinated plants. Specifically, the quality and quantity of pollen delivered to flowers in connected patches may be higher than in unconnected patches because connectivity increases pollinator density, diversity, and interpatch movement (Haddad 1999, Haddad and Baum 1999, Steffan-Dewenter 2003). Our results also demonstrate that corridors have beneficial impacts on pollination independent of those associated with the additional area that corridors typically provide. From a management perspective, this suggests that establishment of corridors will provide dual benefits of increased area and increased interpatch movement. We emphasize, however, that our study examined only one plant–animal interaction, a mutualism. If corridors also increase herbivory and seed predation (Orrock et al. 2003), their net effect on plant demography may be negative. More generally, the role of corridors in conservation should remain tempered by their inability to mitigate habitat loss (Rosenberg et al. 1998, Harrison and Bruna 1999).

ACKNOWLEDGMENTS

J. Blake, E. Olson, and other members of the U.S. Forest Service at the Savannah River Institute were instrumental in the construction of the experimental landscapes. We thank M. Wasserman, L. Adams, C. Bailey, A. Brinton, C. Brooks, J. Orrock, and J. Tewksbury for assistance in the field. D. Imm provided greenhouse space and valuable advice. R. Igo Jr., P. Sampson, U. Santra and L. Winner provided assistance with statistical analyses. The manuscript was improved by comments from C. Bailey, J. Brockmann, B. Bolker, M. Groom, K. Kitajima, F. Prado, D. Rosenberg, U. Valdez, and an anonymous reviewer. Funding was provided by the National Science Foundation, the Department of Energy-Savannah River Operations (Forest Service Interagency Agreements DEB-9815834, DE-IA09-76SR00056 and DE-IA09-00SR22188), and by the Society for Integrative and Comparative Biology.

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APPENDIX

A color version of Plate 1 is available in ESA's Electronic Data Archive: *Ecological Archives* E086-023-A1.