Corridors affect plants, animals, and their interactions in fragmented landscapes

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Among the most popular strategies for maintaining populations of both plants and animals in fragmented landscapes is to connect isolated patches with thin strips of habitat, called corridors. Corridors are thought to increase the exchange of individuals between habitat patches, promoting genetic exchange and reducing population fluctuations. Empirical studies addressing the effects of corridors have either been small in scale or have ignored confounding effects of increased habitat area created by the presence of a corridor. These methodological difficulties, coupled with a paucity of studies examining the effects of corridors on plants and plant–animal interactions, have sparked debate over the purported value of corridors in conservation planning. We report results of a large-scale experiment that directly address this debate. In eight large-scale experimental landscapes that control for patch area and test alternative mechanisms of corridor function, we demonstrate that corridors not only increase the exchange of animals between patches, but also facilitate two key plant–animal interactions: pollination and seed dispersal. Our results show that the beneficial effects of corridors extend beyond the area they add, and suggest that increased plant and animal movement through corridors will have positive impacts on plant populations and community interactions in fragmented landscapes.

Corridors are thought to facilitate movement between connected patches of habitat, thus increasing gene flow, promoting reestablishment of locally extinct populations, and increasing species diversity within otherwise isolated areas (1–4). But the utility of corridors in conservation and management has generated extensive controversy because the case for corridors has been built more on intuition than on empirical evidence (5–7). Although recent studies suggest that corridors increase movement rates between patches for a broad range of animal species (2, 8–12), other studies show no such response (13–16). In large part, controversy has arisen because most studies have been limited in two ways. First, most corridor studies have had a narrow taxonomic focus on one to several species of animals. Such focus precludes generalizations and overlooks the fact that animals are only one component of biological communities. If corridors facilitate animal movement, they should also have strong indirect effects on plant populations due to increased movement of pollen and seeds by animals (17–20). These indirect effects are critically understudied (21), and there have been no studies linking the effects of corridors across these plant–animal interactions. Maintenance of these interactions is a growing concern, as efforts to preserve biodiversity move beyond their traditional focus on individual species (22–25). Second, most previous corridor studies have neglected the inherent difficulty of teasing apart effects due to corridor-facilitated movement from effects due to changes in patch size and shape that accompany the addition of a corridor (15). In particular, linking two patches of habitat with a corridor increases the area of those patches. If corridors function by increasing patch area, the population dynamics within a patch connected by a corridor should be identical to the dynamics of a patch that is increased in area by the size of the corridor (15, 26, 27). In this situation, management schemes solely oriented toward corridors would be misdirected.

A further complication is that corridors affect patch shape in ways that may alter their function in unexpected ways. For example, they may act as "drift-fences," intercepting individuals moving through matrix habitat and diverting them into connected patches (15). This function has not been separated from the traditional corridor effect (i.e., the facilitation of movement between connected patches). From a conservation perspective, these problems are not trivial. Should policies focus on increasing the area of reserves, regardless of connectivity, or does the addition of a corridor provide benefits to plants and animals above and beyond those afforded by increased area alone?

Here we present results from an experiment designed to explicitly test corridor effects on animals and plant–animal interactions at a landscape scale, while experimentally controlling for changes in patch size and shape.

Methods

Creating Experimental Landscapes. In the winter of 1999–2000, we selected eight 50-hectare landscapes on the 1,240 km² Savannah River Site, a National Environmental Research Park in South Carolina. All landscapes were composed of mature (40- to 50-year-old) forest, dominated by loblolly pine (*Pinus taeda*) and longleaf pine (*Pinus palustris*). Within each landscape, five early-successional habitat patches were created by cutting and removing all trees, then burning the cleared areas. We compared movement rates of animals and animal-dispersed pollen and seeds from a 1-ha central patch, created at the center of each landscape, to four surrounding peripheral patches, created at the same time, each 150 m from this central patch (Fig. 1). A 25-m-wide corridor connected the central patch to one of the peripheral patches (hereafter called the "connected" patch). All other peripheral patches ("unconnected" patches) were equal in size to the area of the connected patch plus the area of the corridor (1.375 ha), thus controlling for effects of increased patch area in the connected patches. In unconnected patches, the corridor's area was added either as 75-m "wings" projecting from the sides of patches ("winged" patches) or as additional habitat added to the back of patches ("rectangular" patches; Fig. 1). This design allowed us to explicitly test two mechanisms of corridor function. First, by comparing rates of movement from the central patch into connected patches vs. movement into unconnected patches, we tested the hypothesis that corridors function as conduits for movement. Second, by comparing movement into winged patches vs. movement into rectangular patches, we tested the hypothesis that corridors act as drift fences. The orientation of the connected patch within each experimental landscape was

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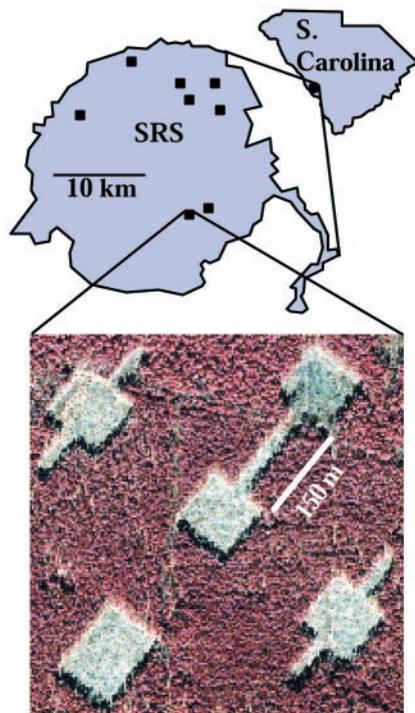
Fig. 1. Map of experimental landscape locations and aerial photograph of one landscape, showing patch configuration. Each of the eight landscapes (squares) consists of five early-successional patches surrounded by mature coniferous forest (see *Methods*). In each landscape, the central patch (1 ha) is connected to one peripheral patch by a 25 × 150-m corridor. The other three peripheral patches in each landscape are equal in distance from the central patch, and equal in area to the connected patch plus the area of the corridor (1.375 ha). In each landscape, one unconnected patch is winged, one is rectangular, and the third is either winged (four landscapes) or rectangular (four landscapes).

randomly determined, and all habitat within 150 m of all patches was closed-canopy forest. We tested these hypotheses of corridor function by studying movements of butterflies, pollen, and bird-dispersed seeds.

Butterfly Movement. To examine the effects of corridors on individual butterflies, we tracked the movements of two species, the Common Buckeye (*Junonia coenia*) and the Variegated Fritillary (*Euptoieta claudia*), both common in early-successional habitats and rare in mature forest habitats on the Savannah River Site (11, 15). We marked naturally occurring butterflies in the central patches and recaptured marked individuals in the peripheral patches (Fig. 1). Butterfly movements were detected by surveying all patches in all experimental landscapes 5 days per week for 9 wk in spring, 2001. Observers walked 12.5-m-wide transects at a speed of 25 m/min, covering all areas in each patch equally. All captured butterflies were marked, and the locations of initial captures and subsequent recaptures were recorded. Surveys were conducted no earlier than 0930 and no later than 1630. Each day we randomized patch visitation order. We used general linear models (28) to examine the effects of connectivity and shape on the proportion of individuals marked in the central patch that were recaptured in peripheral patches. We marked 292 Common Buckeyes (29 recaptured in peripheral patches) and 145 Variegated Fritillaries (39 recaptured in peripheral patches). We considered the patch as the independent unit, and, thus, all analyses used experimental landscape and connection (connected peripheral patches vs. unconnected peripheral patches) as main effects, with patch shape (rectangular or

winged, $n = 12$ of each) nested within connection. *P* values are one-tailed, matching our hypotheses.

Pollen Movement and Fruit Set. To measure the effects of corridors on pollen movement, we used a deciduous holly, *Ilex verticillata*. *I. verticillata* has a generalist pollination syndrome, and flowers are visited by a wide variety of insects. We tracked pollen movement by planting three mature female *I. verticillata* in each peripheral patch and a total of eight male *I. verticillata*, four each of two different cultivars, in each central patch. *I. verticillata* blooms later in the season than naturally occurring hollies at our site, and the cultivars (Apollo and Southern Gentleman) have incomplete overlap in flowering time, which allowed us to limit pollen to that available in the source patch and to extend the time over which pollen was available to female hollies in the peripheral patches. We counted all flowers on two randomly selected branches on each female holly, and then returned throughout the summer to record fruit set as a direct measure of pollen movement from the source patch to the connected patches.

All branches used to assess fruit set within an experimental landscape were in bloom at the same time, and pollen was continuously available from blooming males in the central patch during this time. Because resource limitation and qualitative differences in pollination may cause a change in the duration of fruit retention (22), we repeatedly sampled fruit production during the season, measuring fruit set as the proportion of flowers on each branch that set fruit. Fruit abscission did not show any interaction with patch type ($P > 0.6$); thus, all analyses are based on our final count of fruit set in mid-August, 2001. We averaged fruit set across branches within each plant, and then across plants in each patch, so that we could use the same analysis that we used to test for corridor effects on butterflies. We recognize that this is a conservative approach, and thus we also used a repeated measures multiple ANOVA (MANOVA) design to block by patch, treating each plant as a within-subject effect of the patch. Results of the two analyses did not differ substantially. A late frost caused nearly complete bud drop in three experimental landscapes where hollies were transplanted before the last frost; thus, we restricted our analysis to the other five experimental landscapes, where hollies were planted later and were unaffected by frost.

Seed Movement. To examine effects of corridors on seed dispersal by birds, we used two species of large fruiting shrub, yaupon holly (*Ilex vomitoria*; Aquifoliaceae), consumed by Eastern Bluebirds (*Sialia sialis*) and other thrushes (Turdinae), and wax myrtle (*Myrica cerifera*; Myricaceae), consumed primarily by Yellow-rumped Warblers (*Dendroica coronata*), Pine Warblers (*Dendroica pinus*), Ruby-crowned Kinglets (*Regulus calendula*), and Eastern Bluebirds.

We placed fruit-bearing cuttings and transplanted live trees into the central patch of each landscape. We collected fecal samples from seed traps under 16 artificial perches placed in each peripheral patch ($n = 512$, total). Perches were 3-m poly(vinyl chloride) (PVC) poles, equally spaced in a grid such that all poles were ≥12.5 m from the edge of the patch and 25 m from all other poles. Each pole had a basket trap attached just beneath its top (29) and a horizontal dowel 1.2 m from the ground over a seed trap (27 × 51 cm) covered with 1-cm grid hardware cloth to prevent seed removal by granivores. All fecal samples were collected from seed traps weekly from 1 December through 15 February, 2000–2001.

We wired 2- to 3-m-tall cuttings of *I. vomitoria*, each with 1,500–5,000 fruits, to four rebar stations in the central patch of each landscape. Cuttings were positioned to look like actual trees and were replaced with fresh cuttings every 2 wk from 1 January through 15 February, 2001. *I. vomitoria* naturally occurs in dense, infrequent patches, and we were thus able to remove all females

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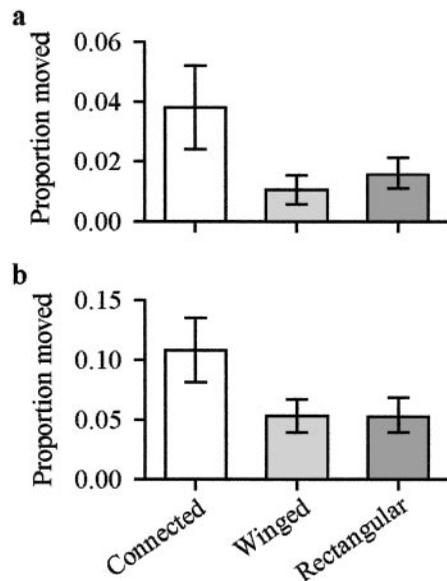
Fig. 2. Movement rates of butterfly species between connected and isolated patches. *J. coenia* (*a*) and *E. claudia* (*b*) both moved between connected patches more often than between isolated patches (*J. coenia*: $F_{1,22} = 12.0$, $P = 0.001$; *E. claudia*: $F_{1,22} = 5.3$, $P = 0.016$). There was no indication of a drift-fence effect (comparing winged to rectangular patches, both $P > 0.7$). Data in both panels are means $\pm$ 1 SE for proportion of individuals marked in the central patch and recaptured in connected, winged, and rectangular peripheral patches.

near our sites, giving us confidence that all seeds found in seed traps came exclusively from the cuttings in the central patch.

Unlike *I. vomitoria*, *M. cerifera* is abundant, and removal of naturally occurring individuals from the surrounding habitat was unfeasible. To track the movement of *M. cerifera* seeds, we planted three mature (>2 m) female *M. cerifera* bushes in each central patch, and supplemented this fruit source with four to eight cuttings wired into bushes. We then sprayed a solution of Wilt-Pruf (Wilt-Pruf Products, Essex, CT) and fluorescent powder onto all *M. cerifera* fruits in the central patches. Birds ingested the powder with the fruit and passed it with the seeds into our traps (29). Fresh cuttings were added to the central patches each week to provide a constant source of marked fruits throughout the field season. The presence of fluorescent powder in fecal samples was determined by examination under a Nikon Optiphot 2 epifluorescent microscope with an FITC filter block and $\times 20$ objective lens. We examined a total of 3,805 fecal samples collected from the 32 peripheral patches. We tested for the effect of corridors on seed dispersal by using the same model as that used to test for effects on butterfly movement.

Results and Discussion

Movement from the center patch to peripheral patches connected by corridors was higher than movement to unconnected patches for all taxa studied (Figs. 2 and 3). The Common Buckeye was three to four times more likely to move from center patches to connected patches than to unconnected patches (Fig. 2*a*), and the Variegated Fritillary was twice as likely to move down corridors than through forest when moving from the center patch (Fig. 2*b*). Neither butterfly was more likely to move to winged patches than to rectangular patches. The corridors thus facilitated the movement of both butterfly species between connected patches, even after controlling for patch size and shape, but did not function as drift fences.

Pollen movement mirrored the movement of the butterflies studied. A significantly higher proportion of flowers produced
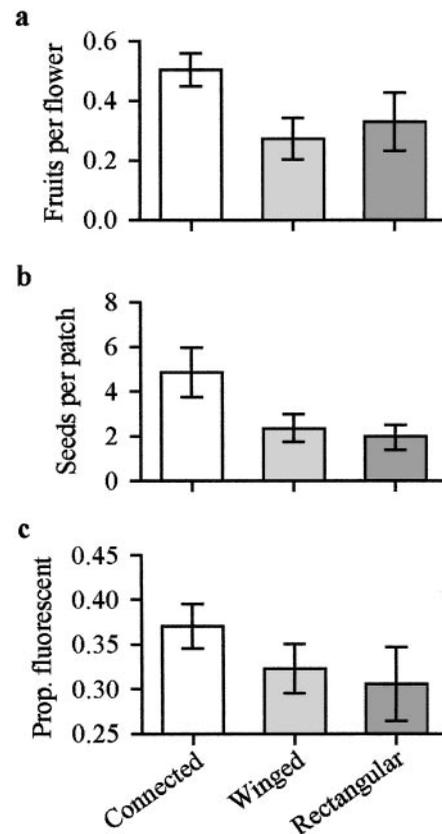
Fig. 3. Effects of corridors on fruit set and seed dispersal. (*a*) *I. verticillata* had a greater proportion of flowers setting fruit in connected patches ($F_{1,13} = 6.8$, $P = 0.022$); (*b*) *I. vomitoria* seeds consumed in the central patch were more likely to be found in connected patches ($F_{1,22} = 10.6$, $P = 0.002$); and (*c*) a greater proportion of fecal samples in connected patches contained fluorescent powder sprayed on *M. cerifera* in the central patch ($F_{1,22} = 4.9$, $P = 0.018$). No differences were detected between winged and rectangular patches in fruit set ($P = 0.316$), or seed dispersal (*Ilex*, $P = 0.12$; *Myrica*, $P = 0.489$).

fruit in the connected patches than in the unconnected patches (Fig. 3*a*), with fruit set increases averaging 69% in connected patches compared with unconnected patches. Because the only pollen available was in the central patches, and all hollies within each experimental landscape were planted at the same time and watered equally, differences in fruit set are directly attributable to differences in pollen movement from the central patch. Holly flowers in our patches were visited by flies, wasps, bees, and butterflies, including both the Common Buckeye and the Variegated Fritillary. Our results confirm that corridors are used preferentially by at least some of these insects, presumably resulting in higher fruit set in connected patches. Hollies in winged patches did not have higher fruit set than those in rectangular patches (Fig. 3*a*), reinforcing our finding that corridors do not act as drift-fences for insects crossing the forested matrix.

I. vomitoria seeds were more than twice as likely to be found in connected patches than in isolated patches (Fig. 3*b*), and a significantly greater proportion of fecal samples collected in connected patches contained fluorescent powder compared with fecal samples from unconnected patches (an increase of 18%, Fig. 3*c*). Fluorescent powder was sprayed only on *M. cerifera* fruits in the center patches of each landscape. These results show a clear effect of corridors on seed movement by birds. Winged and rectangular patches did not differ in the number of *I.*

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vomitoria seeds and had similar portions of fluorescently marked samples, indicating no drift-fence effect for either species.

These results provide a large-scale, experimental demonstration that habitat corridors facilitate movement of disparate taxa between otherwise isolated habitat patches, even after controlling for area effects. We found no evidence that corridors function as drift fences. Our results also link corridor effects across plant–animal interactions, because fruit set (a function of pollen movement) and seed dispersal were higher in connected than unconnected patches. Increased fruit set and seed movement between connected patches have additive effects on gene flow and population dynamics. Given that plants producing more fruit are likely to attract more frugivores (30), plants in connected patches are likely to contribute more to gene flow both within and between patches due to increases in pollen movement, fruit removal, and seed movement down corridors.

The ability of plant populations to persist, expand, and colonize habitat in fragmented landscapes is determined in large part by pollination and seed dispersal (22, 24, 31). Our results provide evidence that corridors can have substantial effects on these processes, and thereby help overcome the depressed reproduction frequently reported for isolated plant populations (17, 19–20). Because the increases in fruit set and seed movement we observed in connected patches occurred across diverse sets of pollinators and seed dispersers, these effects may be relatively wide-spread.

Debate over the efficacy of corridors typically focuses on systems in which forest patches are surrounded by disturbed, early-successional, or human-dominated landscapes. Our design, in which early-successional patches are surrounded by mature forest, presents a different view, but the responses to corridors we observed may be analogous to more traditional fragmentation studies because all share a defining feature of fragmented landscapes: patches of suitable habitat surrounded by a matrix of unsuitable habitat (1–3, 8–9). In addition, we use a broad range of taxa with diverse life histories, and we examined both the movement of individual animals (butterflies) and the collective movement of pollen and seeds by a wide range of animals. In all cases, we found strong effects of corridors. These results clearly suggest a role for corridors in connecting populations of both plants and insects. However, extension of these results to even larger scales and landscapes must proceed with caution. We advocate the use of a large-scale experimental approach in conjunction with studies in unmanipulated landscapes, so that the potential biases of "natural experiments" can be tested.

Limited funds often force a decision between land purchases that enlarge existing reserves and those that restore or maintain connectivity within a landscape. Such decisions are complicated because it may be more expensive to create corridors than to expand existing protected areas. Most of all, these decisions are complicated by lack of data. Our study demonstrates that corridors provide benefits above and beyond the associated increase in habitat area, facilitating interpatch movement and maintaining key mutualisms between plants and animals. We predict that the effect of corridors will have greater demographic and genetic consequences for populations at larger scales, where movement among isolated patches becomes rare or nonexistent.

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