

Can dispersal mode predict corridor effects on plant parasites?

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Abstract. Habitat corridors, a common management strategy for increasing connectivity in fragmented landscapes, have experimentally validated positive influences on species movement and diversity. However, long-standing concerns that corridors could negatively impact native species by spreading antagonists, such as disease, remain largely untested. Using a large-scale, replicated experiment, we evaluated whether corridors increase the incidence of plant parasites. We found that corridor impacts varied with parasite dispersal mode. Connectivity provided by corridors increased incidence of biotically dispersed parasites (galls on *Solidago odora*) but not of abiotically dispersed parasites (foliar fungi on *S. odora* and three *Lespedeza* spp.). Both biotically and abiotically dispersed parasites responded to edge effects, but the direction of responses varied across species. Although our results require additional tests for generality to other species and landscapes, they suggest that, when establishing conservation corridors, managers should focus on mitigating two potential negative effects: the indirect effects of narrow corridors in creating edges and direct effects of corridors in enhancing connectivity of biotically dispersed parasites.

Key words: Cercospora; Colletotrichum; dispersal; gall-inducing insects; habitat fragmentation; landscape corridors; *Lespedeza* spp.; movement ecology; pine plantation; plant disease; *Solidago odora*; Uromyces.

INTRODUCTION

Habitat corridors are commonly proposed in conservation to counteract the negative effects of habitat fragmentation by facilitating plant and animal movement between isolated habitat patches and by increasing population persistence (Hilty et al. 2006). Empirical studies on both small and large scales indicate that corridors slow rates of species loss (e.g., Gonzalez et al. 1998), and increase movement of diverse taxa that vary in size and dispersal mechanisms, including insects (Haddad et al. 2003), pollen, and seeds (Tewksbury et al. 2002). However, some predict that corridors may also negatively impact the same species they are meant to benefit by also facilitating movement of antagonists like competitors, predators, and diseases (Simberloff and Cox 1987). Working within a large corridor experiment, we test the effects of corridors on the incidence of plant antagonists: fungal pathogens and gall-inducing insects (hereafter “parasites”; Tooker et al. 2008).

Corridors affect two landscape-level processes that may influence parasites: habitat connectivity, and the amount of habitat edge. Habitat connectivity is especially important because it can determine the spread of parasitic organisms. Previous studies of connectivity effects on parasites focus on the distance between plants or habitats, and have found that as the degree of

isolation increases the probability of pathogen infection decreases (e.g., Thrall et al. 2003, Brooks et al. 2008). Here we consider the structural connectivity created by corridors, as opposed to isolation. Corridor structure also tends to increase the amount of edge because of its long and relatively narrow shape. Edges can influence the infection and survival of plant pathogens by altering local environmental conditions such as light intensity and humidity (Jarosz and Burdon 1988, Agrios 2005, Laine and Hanski 2006, Meentemeyer et al. 2008). Further, both connectivity and edge can influence the distribution of host plants (Damschen et al. 2008), thus potentially impacting the distributions of plant parasites (e.g., Burdon and Chilvers 1982, Mitchell et al. 2002). Our experimental design allows us to simultaneously test for effects of habitat edges and connectivity.

We tested the effects of corridors on the incidence of plant parasitism based on the trait that most closely connects parasites to movement across landscapes: their dispersal mode (Damschen et al. 2008). We predicted that corridors would increase the incidence of both biotically and abiotically dispersed parasites by increasing landscape connectivity, but that this effect would be more pronounced with biotic dispersal (Fig. 1 B and C). This prediction emerges from prior results demonstrating that corridors increase dispersal of organisms that can control their own movement (Haddad et al. 2003, Damschen et al. 2008, Gilbert-Norton et al. 2010). Corridor effects on movement of organisms dispersed by wind is weaker (Damschen et al. 2008), and may not be

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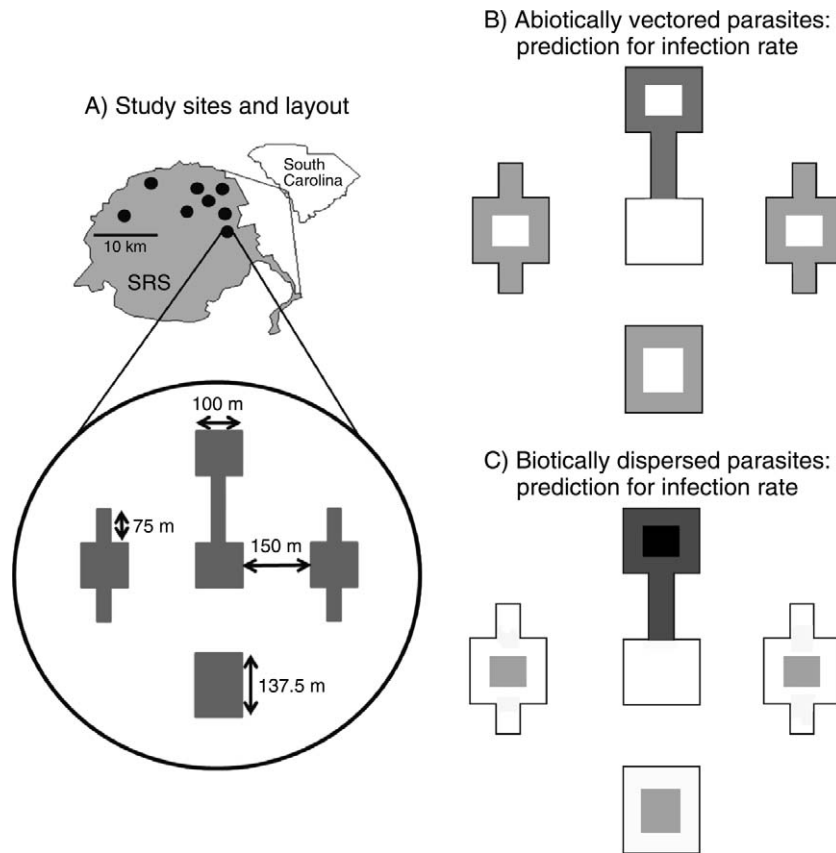


FIG. 1. Experimental layout at the study sites in the Savannah River Site (SRS), a National Environmental Research Park near New Ellenton, South Carolina, USA. (A) Each of the eight blocks is composed of five habitat patches with the center patch connected to one surrounding patch by a landscape corridor. The unconnected patches are shaped for control for the increased habitat area and edge caused by the corridor addition. (B, C) Our conceptual framework for predictions of parasite incidence is based on Damschen et al. (2008). Darker shading indicates areas in the landscape where we predict higher parasite incidence. We predicted that (B) connectivity and edge habitat would increase the incidence of abiotically dispersed parasites, and (C) connectivity would increase and edge habitat would decrease the incidence of biotically dispersed parasites.

expected because wind may disperse parasites over large scales (Plantegenest et al. 2007), and because wind direction is not primarily determined by landscape pattern (i.e., not aligned with corridors). We also predicted that incidence of biotically and abiotically dispersed parasites would be influenced by habitat edge. More specifically, in our open-habitat patches surrounded by pine forest we expected higher incidence of abiotically dispersed fungal parasites near edges due to lower temperature and higher humidity, and higher incidence of biotically dispersed insect galls far from edges due to higher solar load, which favors insect activity (e.g., Louda et al. 1987, Jarosz and Burdon 1988, Meentemeyer et al. 2008).

We tested this framework in the largest experimental test of structural connectivity effects via corridors using naturally occurring foliar fungi and insect-induced galls. Our study differs from prior studies of connectivity on parasites in that we work at scales relevant to conservation to provide the first experimental test of how structural corridors affect natural plant parasite

incidence. Our results support a dispersal-based framework for assessing corridor effects on parasites; concerns about connectivity enhancing the spread of parasitic species should focus on biotically dispersed parasites.

METHODS

Site description

We conducted our study at the Savannah River Site, a National Environmental Research Park near New Ellenton, South Carolina, USA, in a large-scale replicated corridor experiment. The experiment, established in 2000, is composed of eight ~ 50 -ha experimental blocks, each consisting of five ~ 1.4 -ha forest openings (habitat patches), created by harvesting a densely planted longleaf (*Pinus palustris*) and loblolly (*P. taeda*) pine plantation, which now forms the matrix (Fig. 1A). Patch vegetation established naturally after clearing, and consists of an herbaceous and shrubby ground layer, while the pine plantation matrix has a dense layer of pine litter with few of the herbaceous species from patches. Experimental blocks are ~ 1 – 10 km apart, and

thus vegetation is likely genetically unrelated. Patch arrangement within blocks consists of a central 100×100 m patch and four surrounding patches 150 m away. The central patch and one peripheral patch are connected by a 25-m-wide corridor. The other three peripheral patches are unconnected and are of two types: rectangular or winged. Rectangular patches consist of the same 100×100 m area as the central patch plus the area of a corridor added on to make a larger patch. Winged patches have two 75-m dead-end "corridors," each half the area of the corridor, added to either side of a 100×100 m area (Fig. 1). This design tests for (1) effects of patch shape by holding connectivity constant (comparison of winged and rectangular patches), and (2) effects of connectivity by holding patch shape, or edge-to-interior area ratios, constant (comparison of connected and winged patches).

Species descriptions: hosts and parasites

We surveyed for incidence of three species of abiotically dispersed foliar fungi and five species of insect-induced galls. All parasite species and their respective host individuals naturally colonized patches after creation of the experiment. Of the foliar fungi, one species was found on *Solidago odora* and two were found simultaneously on three common species of *Lespedeza*. All biotically dispersed, gall-inducing insects were found to oviposit on *S. odora*. Gall-inducing insects and foliar fungi infect plants by invading plant cells with either insect larvae or fungal hyphae (Gagne 1989, Agrios 2005), and both can decrease plant fitness by parasitizing host plant tissue (Jarosz and Davelos 1995, Legee 2006).

Solidago odora (Asteraceae) is a perennial clonal forb native to the southeastern United States (Weakley 2010). As a genus, *Solidago* is commonly infected by both foliar fungi and gall-inducing insects (Farr et al. 1989, Root and Cappuccino 1992). *Lespedeza hirta*, *L. stuevei*, and *L. virginica* (Fabaceae) are perennial clonal legumes native to the southeastern United States (Weakley 2010). *Lespedeza* species are commonly infected by a variety of foliar pathogens (Farr et al. 1989) that cause easily distinguishable lesions on the leaf surface.

Foliar lesions were identified at the North Carolina State University Department of Plant Pathology in consultation with Dr. D. Shew. We classified fungal pathogen spores from these lesions to genus and confirmed known presence of disease on our species using Farr et al. (1989). Although these diseases had not previously been identified in South Carolina, they have been confirmed on plants in surrounding states.

Foliar leaf spots of *S. odora* were identified as anthracnose caused by pathogens in the genus *Colletotrichum* (Farr et al. 1989). Spores of this genus are abiotically dispersed by splashing and windblown rain (Sinclair 1982). We quantified three main types of foliar lesions on *Lespedeza*. Two were foliar fungal pathogens from the genera *Uromyces* and *Cercospora*. Spores of

these genera disperse primarily by wind, but *Cercospora* can also be dispersed by water (Sinclair 1982). A third and less common type of lesion was caused by insect damage to the leaf tissue. On *L. hirta*, we found *Cercospora* damage to be the most common type of lesion (60.7% of all leaves with lesions showed this type), followed by *Uromyces* lesions (28.9%), and insect damage (24.5%). On *L. stuevei*, we found *Uromyces* lesions to be the most common type of lesion (64.5%), followed by *Cercospora* lesions (30.3%), and insect damage (10.6%).

Gall-inducing insects on *S. odora* were identified as two types of stem galls induced by tephritid flies and moths, and three types of apical meristem galls induced by midge flies. Midge gallers were the most common parasite, making up 92% of the infections, followed by moth galls (5%) and tephritid fly galls (3%). Because of low sample size, gall-inducing insects were pooled for analysis.

Data collection

For all species we collected data in one patch of each type (connected, winged, and rectangular) per block. When duplicate patch types occurred within a block, we randomly selected one patch of each type per block to sample. We collected data for *S. odora* in six blocks and for *Lespedeza* species in eight blocks. To determine the effects of edge on parasite incidence, we selected plants along edge transects within 12.5 m of the patch edge and interior transects within the center 25×25 m of each patch (>37.5 m from the edge) for *Lespedeza* and the center 50×50 m (>25 m from the edge) for *S. odora* (Fig. 1A). We conducted *S. odora* surveys in September and October of 2008 and *Lespedeza* surveys between June and August of 2007 and in August of 2008. These surveys corresponded with periods at or near maximum annual prevalence of each parasite.

Abiotically dispersed foliar fungi.—Since both *S. odora* and *Lespedeza* spp. were multistemmed, we defined individuals as all ramets arising from a single point. Ramets arising from points >20 cm apart were considered different individuals. On randomly chosen individuals, we selected one ramet either at random (*S. odora*) or by selection of the tallest ramet (*Lespedeza* spp.). On each selected ramet we surveyed all leaves for presence/absence of foliar lesions. In each patch, we sampled up to 20 *S. odora* individuals per distance and 8 *Lespedeza* individuals of each species per distance.

Biotically dispersed gall-inducing insects.—We surveyed insect galls on the same *S. odora* plants as for foliar lesions. Due to lower occurrence of galls, we included up to 40 additional individuals per patch at each distance from the edge. Once an individual plant was selected, we surveyed all ramets and counted the total of each of five types of galls per individual.

Density surveys.—To control for the potential effects of host density during our tests of corridor effects on parasite incidence, we quantified density of host plants during parasite surveys. We surveyed density of

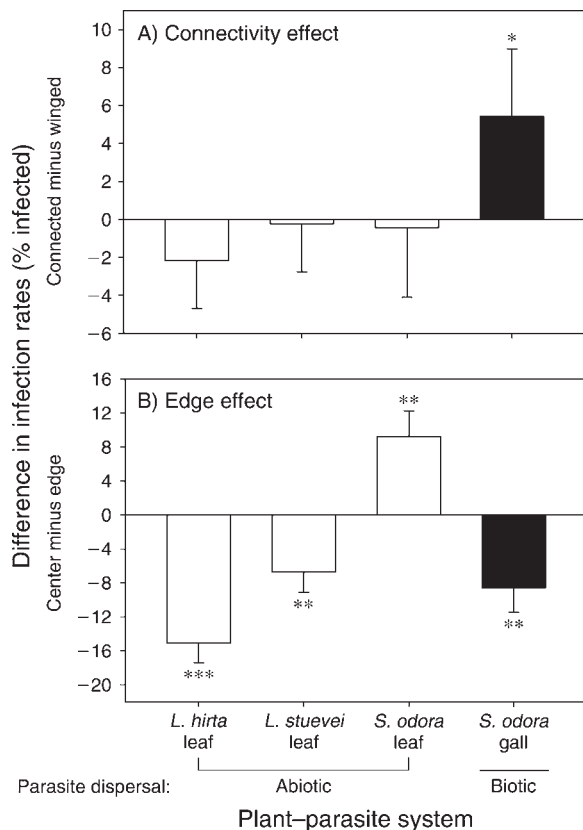


FIG. 2. Effects of experimental (A) connectivity and (B) edges on abiotically and biotically dispersed plant parasites. Parasite systems were wind-dispersed *Uromyces* and *Cercospora* fungus on *Lespedeza hirta*, wind-dispersed *Uromyces* and *Cercospora* fungus on *L. stuevei*, splash-dispersed *Colletotrichum* fungus on *Solidago odora*, and insect-dispersed galls on *S. odora*. Open bars indicate abiotically dispersed parasites; black bars represent biotically dispersed parasites. Data (means and SE) are the differences in infection rates between patches.

* $P < 0.05$; ** $P \leq 0.01$; *** $P < 0.0001$.

Lespedeza during surveys for lesions and density of *S. odora* in August of 2009. For *Lespedeza* we quantified density by counting the number of ramets from each individual surveyed as well as all congener ramets within 2 m of each focal ramet. For *S. odora* we counted the total number of plants and stems in two randomly selected 12.5×12.5 m plots at the centers and edges of all patches surveyed the previous year.

Statistical analysis

We tested for effects of corridors on plant-parasite incidence using mixed models in SAS (9.1.3: PROC MIXED; SAS Institute 2003). Models included patch type (connected, rectangular, winged), edge distance (edge, interior), and their interaction as fixed effects, experimental block as a random effect, and density of congeners as a covariate. Prior to analyses, we pooled data from *Lespedeza stuevei* and *L. virginica* (henceforth *L. stuevei*), as these two species naturally hybridize and

could not be clearly differentiated in the field (Hanson and Cope 1955). We tested the incidence of parasites for each plant-parasite system in separate models (*L. hirta*-leaf fungus, *L. stuevei*-leaf fungus, *S. odora*-leaf fungus, *S. odora*-stem gall). Response variables were, for leaf fungal systems, the percentage of leaves per stem showing lesions, and for the stem gall system, the percentage of stems per clone with galls. For each plant-parasite system prior to analyses, we averaged values for each response variable to arrive at one value per distance in each patch. Gall data were natural-log-transformed to normalize the residuals; other variables were normally distributed. We used linear contrasts to explicitly test for effects of connectivity (connected vs. winged patches), patch shape (winged vs. rectangle patches), and edge distance (edge vs. interior).

RESULTS

Connectivity increased incidence of biotically dispersed, but not abiotically dispersed parasites. Corridors increased the incidence of biotically dispersed galls on *Solidago odora* plants by 30% relative to incidence in winged patches, based on raw means (Fig. 2; $t = 2.1$, $P = 0.05$). Thus, it was by increasing connectivity, not altering patch shape ($t = 1.7$, $P = 0.09$), that corridors increased incidence of biotically dispersed parasites. Incidence of abiotically dispersed parasites were similar in all patch types and not influenced by connectivity (Fig. 2; maximum $t = 0.9$, $P = 0.4$) or patch shape (maximum $t = 1.0$, $P = 0.3$).

Pronounced edge effects were seen across all parasite types, but the direction of these effects differed with parasite identity. In both *Lespedeza* systems, abiotically dispersed leaf fungal-pathogen incidence was greater along patch edges (Fig. 2). Effects for both were of similar magnitudes, with parasite incidence 64% and 57% higher in plants close to patch edges when compared to plants farther from patch edges for *L. hirta* ($t = 6.5$, $P < 0.0001$) and *L. stuevei* ($t = 2.8$, $P = 0.007$), respectively. For *S. odora*, incidence of abiotically dispersed leaf fungal pathogens was 13% higher in plants farther from patch edges ($t = 2.8$, $P = 0.01$), whereas incidence of biotically dispersed gall was 51% higher in plants closer to patch edges ($t = 3.1$, $P = 0.005$) (Fig. 2). See Appendix A for results of full statistical models.

DISCUSSION

We found that the effects of corridors on parasite incidence varied across parasite species, and that parasite responses could be predicted by their dispersal mode. Consistent with our prediction, the incidence of biotically dispersed galls on *Solidago odora* was higher in connected patches; however, contrary to our predictions, abiotically dispersed foliar fungi showed no response to connectivity. Because gall incidence was 30% higher in connected patches relative to winged patches, the connectivity effect seen in galls was due to the connections created by corridors, and not the modifica-

tion of patch shape. The connectivity effect we observed for galls suggests gall-inducing insects use corridors as movement pathways, leading to higher densities of oviposition in connected patches. Although we did not track insect movement in our experiment, studies of other insects within our experimental landscapes found that corridors increase movement of butterflies and other generalist pollinating insects (e.g., Tewksbury et al. 2002), and other flies (Fried et al. 2005).

Contrary to our predictions, gall incidence was higher at patch edges, with the exception of connected patches where incidence at the center and edge were similar (Appendix B). These patterns might be explained by changes in microclimate at the edge combined with increased movement of gall-inducing insects to connected patches. Patch edges have more shade than centers due to shadows cast by the ~20-m-tall trees surrounding patches. More frequent gall-inducing insect oviposition along patch edges may have been caused by higher levels of water and shade available to plants, corroborating other findings. Psyllid leaf-gall density was 55–65% higher on shade leaves than sun leaves in Redbay (*Persea borbontia*) (Legee 2006), while tephritid gall-inducing flies were less common in water-stressed environments (Sumerford et al. 2000). In connected patches, higher insect movement to connected patches could increase parasite densities and oviposition at less preferable locations away from patch edges.

All abiotically dispersed parasites showed strong edge effects, but no connectivity effects. These results are consistent with previous findings where, at large scales, microclimatic differences may overwhelm connectivity effects (Laine and Hanski 2006, Ellis et al. 2010). The direction of these edge effects varied across parasite species. In accordance with our predictions, incidence of both genera of abiotically dispersed foliar fungi (*Cercospora* and *Uromyces*) found on *Lespedeza* species infected a larger percentage of leaves at patch edges. Contrary to our predictions, the incidence of *Colletotrichum* infection on *S. odora* was higher at patch centers than edges. Two factors could explain the opposing edge effects for abiotically dispersed species. First, edges alter microclimatic conditions, including solar load, temperature, and leaf wetness, that affect development of fungal pathogens (Jarosz and Burdon 1988, Agrios 2005, Fagan et al. 1999, Tschardt et al. 2002). Second, for wind-dispersed pathogens, landscape features that alter wind patterns will affect their movement and deposition (Plantegenest et al. 2007). Edges in our experimental system consist of an abrupt transition between the ~0.5–2 m tall shrubby and herbaceous vegetation in our patches and ~20-m-tall pine plantation trees that form the matrix. Habitat edges increase wind turbulence (Detto et al. 2008), which could create differential patterns of spore deposition to patch centers (*Colletotrichum*) or edges (*Cercospora* and *Uromyces*).

Further experiments are needed to test the mechanisms supporting our observed relationship between

dispersal mode and landscape connectivity (Johnson and Haddad 2011), and to test the generality of our results in other species and landscapes. For example, other parasite transmission systems such as pollinator-transmitted fungi (Thrall and Antonovics 1995) could be considered. Yet, we provide support for the usefulness of dispersal mode as a generalizable trait on which to assess the impact of landscape connectivity via corridors. These generalizations may be especially important in the context of plant parasites, whose occurrence may be dependent on a suite of environmental variables and host characteristics, the specific effects of which on individual parasite species are often unknown. It should also be noted that the impacts of parasite spread on host-population viability still need evaluation, and this information is invaluable for determining effects of parasites on host fitness.

We have shown that the impact of fragmentation and corridors on plant parasites can be predicted in part by the mode of parasite dispersal. Our findings demonstrate that corridors may facilitate the spread of some parasites by altering the movement of insect vectors, whereas habitat edges have more pervasive impacts, influencing both insect- and wind-vectored parasites. For over 20 years, ecologists have been concerned that corridors may act counter to conservation goals by spreading parasites (Simberloff and Cox 1987). Our results provide further support that corridors are most likely to have strong, negative effects when they increase the amount of edge habitat in the landscape (Orrock et al. 2003, Weldon and Haddad 2005). These results and our dispersal-based predictive framework show that landscape connectivity may have negative effects only for parasites spread by animals, suggesting that management and mitigation can be directed toward that one group of parasites where they are of concern.

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APPENDIX A

A table presenting results of full statistical models from tests of corridor effects of plant parasite abundance (*Ecological Archives* E092-130-A1).

APPENDIX B

A figure showing the connectivity and edge effects on parasite infection of all four parasite types (*Ecological Archives* E092-130-A2).