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Corridors promote fire via connectivity and edge effects

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Abstract. Landscape corridors, strips of habitat that connect otherwise isolated habitat patches, are commonly employed during management of fragmented landscapes. To date, most reported effects of corridors have been positive; however, there are long-standing concerns that corridors may have unintended consequences. Here, we address concerns over whether corridors promote propagation of disturbances such as fire. We collected data during prescribed fires in the world's largest and best replicated corridor experiment (Savannah River Site, South Carolina, USA), six ~50-ha landscapes of open (shrubby/herbaceous) habitat within a pine plantation matrix, to test several mechanisms for how corridors might influence fire. Corridors altered patterns of fire temperature through a direct connectivity effect and an indirect edge effect. The connectivity effect was independent of fuel levels and was consistent with a hypothesized wind-driven "bellows effect." Edges, a consequence of corridor implementation, elevated leaf litter (fuel) input from matrix pine trees, which in turn increased fire temperatures. We found no evidence for corridors or edges impacting patterns of fire spread: plots across all landscape positions burned with similar probability. Impacts of edges and connectivity on fire temperature led to changes in vegetation: hotter-burning plots supported higher bunch grass cover during the field season after burning, suggesting implications for woody/herbaceous species coexistence. To our knowledge, this represents the first experimental evidence that corridors can modify landscape-scale patterns of fire intensity. Corridor impacts on fire should be carefully considered during landscape management, both in the context of how corridors connect or break distributions of fuels and the desired role of fire as a disturbance, which may range from a management tool to an agent to be suppressed. In our focal ecosystem, longleaf pine woodland, corridors might provide a previously unrecognized benefit during prescribed burning activities, by promoting fire intensity, which may assist in promoting plant biodiversity.

Key words: connectivity; corridor; disturbance; ecosystem management; edge effect; habitat fragmentation; landscape ecology; longleaf pine woodland; prescribed fire; structural equation modeling.

Introduction

Habitat loss and fragmentation are leading causes of biodiversity decline (Wilcove et al. 1998). Species in fragmented landscapes are threatened by reduced patch area, increased patch isolation, and the increased prevalence of edge effects caused by adjacent matrix habitat (Ries et al. 2004, Collinge 2009). Landscape corridors are a popular management tool in fragmented landscapes and seek to mitigate isolation effects by increasing rates of movement between otherwise isolated patches (Crooks and Sanjayan 2006). To date, reported corridor effects have been largely positive and include increased rates of inter-patch movement (Haddad et al. 2003, Gilbert-Norton et al. 2010), enhanced plant–animal interactions, such as pollination and seed dispersal (Tewksbury et al. 2002, Levey et al. 2005, Van Geert et al. 2010), reduced extinction rates (Gonzalez et al. 1998), and increased biodiversity (Damschen et al. 2006).

Corridors, however, may not be without their dangers. First, corridors are long, narrow, landscape features and corridor implementation may introduce substantial edge habitat to a landscape. Second, by providing a connection, corridors could promote the spread or incidence of deleterious agents, such as predators, diseases, or disturbances, which could harm the species targeted by corridor conservation (Simberloff and Cox 1987). In spite of these concerns being nearly a quarter-century old, they have been only modestly addressed (e.g., Hess 1994, Orrock et al. 2003, Orrock and Damschen 2005, Weldon 2006, Sullivan et al. 2011). Here, we explore one such concern that, to our knowledge, has never been rigorously assessed: whether corridors promote propagation of fire.

Understanding how corridors influence fire is critical, given fire's role as a ubiquitous worldwide disturbance

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(Bowman et al. 2009) and the wide disparity in the consequences of burning, ranging from highly positive to strongly negative. In systems where fire is used as a management tool, corridors may help achieve management goals, like promoting native biodiversity (e.g., Hiers et al. 2007, Mitchell et al. 2009). Conversely, in other systems, fire is less desirable. Fire regimes have been modified by humans through, for example, introduction of exotic grasses (D'Antonio and Vitousek 1992) and habitat fragmentation (Laurance 2004), resulting in increased fire frequency or intensity, which may have negative impacts on native biodiversity. Furthermore, even unaltered fire regimes may be dangerous to human well-being. This may be particularly true in systems where fire activity is dictated by weather and, thus, less responsive to management and suppression activities (Moritz et al. 2004). A mechanistic understanding of how corridors impact fire behavior would help with fire management, regardless of whether the goal is prescription or suppression, and would aid in interfacing landscape ecology and ecosystem processes, such as disturbance (Turner 2005, 2010).

Implementation of corridors in fragmented landscapes could alter fire through mechanisms related to connectivity or edges. Effects of connectivity may be straightforward, resulting from the connection of flammable target patches with flammable corridors, within nonflammable matrix habitat. For example, grassland corridors might connect grassland patches in a tilled field matrix, allowing fire to spread from one patch to another. Other connectivity effects might be less intuitive. Forest edges exhibit modified wind conditions, elevated wind speed, and turbulence in clearings, relative to interior forest (Laurance 2004, Ries et al. 2004, Detto et al. 2008), and these effects can increase with the amount of edge in a patch (Laurance 2004). In systems with a forested matrix, open corridors might exhibit particularly pronounced effects on wind due to the high amounts of edge associated with their creation. Several lines of evidence suggest that these effects could be apparent in systems with relatively narrow corridors: (1) tree-scale canopy gaps in forests can increase wind (turbulence) sufficient to influence seed dispersal by wind (Bohrer et al. 2008), (2) wind flowing above canopy can rapidly adjust at forest edges, resulting in near-ground wind velocities along forest edges that are similar to those in clearings far from edges (Detto et al. 2008), and (3) corridors can increase wind-related phenomena, such as movement of wind-dispersed seeds (Damschen et al. 2008). Given well-established positive relationships between wind speed and rates of fire spread and burn temperature (e.g., Beer 1991, Pyne et al. 1996), corridors could thus modify fire dynamics through influence on wind, either by providing or breaking connectivity of wind or by modifying wind dynamics along forest edges. Interestingly, the role of corridors for spreading fires has been a topic of interest both within the structural (i.e., buildings) and wildland fire literature, with evidence for hallways (e.g., McGuire 1968, Quintiere 1975) and riparian corridors (e.g., Dwire and Kauffman 2003, Pettit and Naiman 2007) promoting fire spread by similar mechanisms to those described above.

Corridors could also influence fire through the creation of edges and ensuing modification of fuels (Laurance 2004). Such a situation could arise in systems with flammable patches and matrix, but where flammability differed among the two habitat types, e.g., a more flammable matrix could supply fuels to an adjoining patch or corridor. This could result in corridors promoting or discouraging fire, depending on the flammability of patch (and corridor) vs. matrix habitat. Alternately, as a result of modified microclimate conditions (Ries et al. 2004), edges could impact fuel moisture levels without changing fuel loading levels. Depending on whether the result was drier or wetter fuels, edges could thus increase or decrease fire temperature or the likelihood that locations near edges burn, relative to patch centers.

Using the world's largest and best-replicated corridor experiment, we evaluate the effects of corridors on fire. We monitored fire temperatures during prescribed understory burns across six replicated, experimentally fragmented landscapes. Importantly, our experimental design controls for the potentially confounding effects of patch area and shape, allowing for evaluation of competing mechanisms underlying corridor function (see *Methods*), and the scale of our experimental landscapes is large enough to produce connectivity effects that are comparable to "natural corridors," those present in actual, managed landscapes (Gilbert-Norton et al. 2010). We then assessed mechanisms for how corridors impact fire through effects of connectivity and edges using structural equation modeling and the consequences of these fire patterns for plant communities. Specifically, we addressed the following hypotheses:

1) Corridors elevate fire temperatures or patterns of spread, assessed as the likelihood that a location will burn during prescribed fires, through an emergent connectivity effect. We hypothesize that this emergent effect might occur in our system and other systems where patches and corridors are clearings within a forested matrix, as a result of wind channelization, acceleration of wind speed down corridors that we term a "bellows effect," which could increase fire temperatures or spread. In our study system, near-ground ($\sim$5 m height) wind speeds average $\sim$20–125% greater in corridors than wind speeds simultaneously observed in unconnected rectangular patches (E. I. Damschen and D. Baker, *unpublished data*), suggesting the likelihood of bellows effects. Elevated fire temperatures or spread, but similar or reduced fuel levels, in or near corridors relative to patch centers and along patch edges, would provide support for this hypothesis.

2) Corridors alter fire temperatures or spread through edge effects that modify fuel levels. Elevated fuel levels

and fire temperatures or spread along patch edges, relative to patch centers, would provide support for this hypothesis.

3) Corridors alter fire temperatures or spread through edge effects independent of fuel levels, due to the influence of factors such as wind or fuel moisture. Elevated fire temperatures or spread, but similar fuel levels along patch edges relative to patch centers, would provide support for this hypothesis.

4) Patterns of fire temperature or spread are unrelated to connectivity or edges, but rather are a product of variation in fuel loading, which in turn is driven by soil moisture availability: a primary driver of productivity in our system (Kirkman et al. 2001). Similar fire temperatures or spread along edges, in and near corridors, and in patch centers, coupled with a correlation between soil moisture availability, fuel loading, and fire temperature or spread, would provide support for this hypothesis.

5) Patterns of fire temperature observed in our experiment will have implications for plant communities by impacting the relative abundances of woody plants and bunch grasses. Specifically, we predict that woody species abundance would decline and bunch grass abundance would increase in hotter burning plots, whereas woody species would increase and bunch grasses would decline in cooler burning plots (Thaxton and Platt 2006, Hiers et al. 2007, Myers and Harms 2009).

Methods

Study site

We conducted this study within six experimentally fragmented landscapes in the uplands of the Savannah River Site (SRS) near Aiken, South Carolina, USA. SRS is located in the southeastern U.S. coastal plain, with gently rolling to flat uplands primarily supporting sandy Paleudult soils (80–90% sand; Kolka et al. 2005) and *Pinus palustris* Mill. (longleaf pine) and *Pinus taeda* L. (loblolly pine) plantations (Blake 2005). The experimental landscapes, located on level uplands, were created in winter 1999–2000 by harvesting trees from mature (>50 years old) pine plantations, creating open habitat patches within a pine plantation matrix. The habitat patches have since become dominated by shrubs and grasses and are managed with prescribed fire to promote longleaf pine woodland, the historically dominant ecosystem at our sites and throughout the uplands of SRS (White 2005).

Each of the six experimental landscapes was 50 ha in area and represented a single statistical block. Each block contained one central 100 $\times$ 100 m patch surrounded by four peripheral patches 150 m from the central patch (Fig. 1). One of the peripheral patches was 100 $\times$ 100 m and connected to the central patch by a 25 $\times$ 150 m corridor, which was also composed of open habitat. The other peripheral patches were isolated from the central patch by 150 m of matrix habitat and were either rectangular (100 $\times$ 137.5 m) or winged (100 $\times$ 100 m with two 25 $\times$ 75 m projections on opposite sides). Each block contained one duplicate rectangular or winged patch. Three of the experimental landscapes contained one winged and two rectangular patches, with the winged patch opposite the connected patch and wings and corridor at 90° angles (as in Fig. 1), whereas the other three landscapes contained two winged and one rectangular patch, with the rectangular patch opposite the connected patch and wings and corridor aligned. For this study, we used one of each patch type (connected, rectangular, winged), randomly selecting one of the duplicate patches, in each block. This study design allowed us to distinguish between how corridors alter fire through creating a connection (comparison of connected and winged patches) as opposed to changes associated with the creation of edge (comparison of rectangular and winged patches, which contain ~50% more edge).

Wildfires have been suppressed at SRS since its creation in the early 1950s and although prescribed fire has been widely implemented at SRS during the past decade (Shea and Bayle 2005), little if any burning occurred within the locations comprising our six experimental landscapes between 1950 and 1999. The six landscapes have received low-intensity prescribed surface fires in 2004, 2007, and 2009 (this study). The 2007 and 2009 burns were conducted during the dormant season, whereas the 2004 burns were conducted during the growing season. Individual landscapes were burned as parts of larger burn units (i.e., all patches within a landscape were burned together, along with the surrounding matrix) and different landscapes were burned on separate days. The six burns in this study occurred between late January and late March 2009, on days supporting a variety of environmental conditions (Table 1). Half of the sites were ignited by hand and half aerially (Table 1). For hand ignitions, multiple fire fighters ignited surface fuels with drip torches while walking burn unit peripheries. From these ignitions, fires burned into the internal portions of the landscapes, including the study patches and matrix. Ignitions were made without reference to experimental landscape orientation. Aerial ignition occurred via delayed aerial ignition devices (DAIDs) deployed via helicopter. DAIDs were deployed throughout the experimental landscapes, resulting in numerous ignition points in study patches and matrix. Reports from ignition crews suggest that a higher density of DAIDs were deployed into experimental patches than matrix; however, we do not have reason to suspect any bias among experimental patch types (i.e., connected patches did not receive more ignitions than unconnected patches).

Fire temperature and effects

To assess effects of corridors on fire temperature, patterns of spread, and ensuing effects of these patterns on vegetation, we established a set of 5 $\times$ 5 m sampling

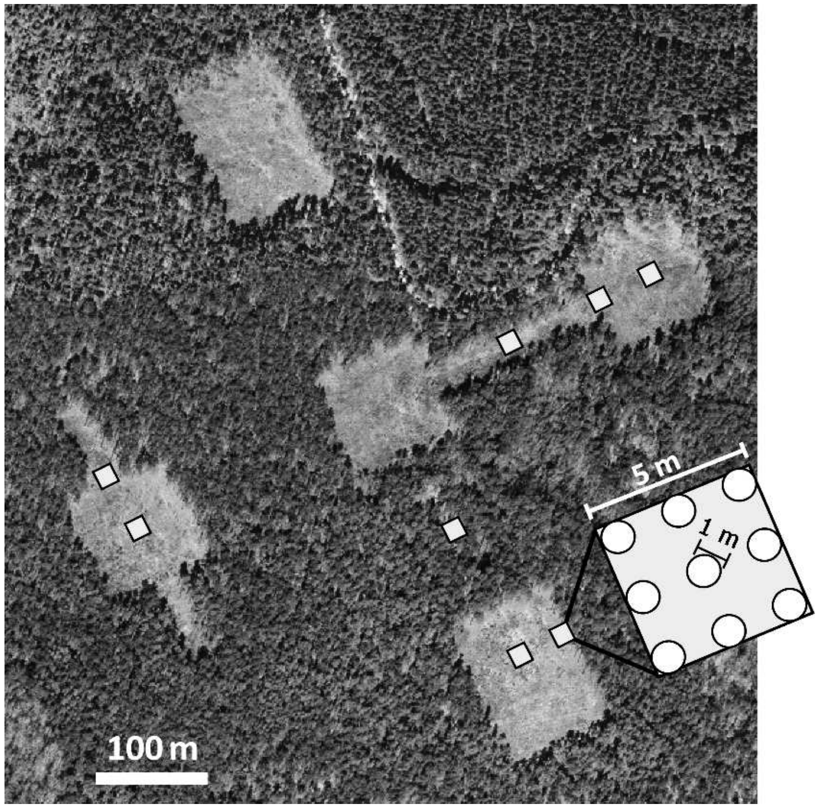

FIG. 1. Experimental and sampling design testing effects of fragmentation and corridors on fire dynamics (pictured is one of six experimental landscapes). Each landscape consisted of a central 1-ha patch and four ~1.4-ha peripheral patches, each of open (herbaceous and shrubby) habitat. One peripheral patch was connected by a corridor, while three were unconnected and isolated by matrix pine plantation forest. Sampling plots ($n = 8$ plots per landscape) were located in patch centers, the opening of the corridor in a connected patch, the opening of a "wing" in a winged patch, along an edge in a rectangular patch, in the corridor, and in the matrix. Within each plot, vegetation, fuels, and fire temperature were sampled in nine circular subplots (inset).

plots within each block (Fig. 1). We used eight total plots per block (Fig. 1). Connected center, rectangle center, and winged center plots were located in the center of each respective patch type. Corridor plots were located in the center of the corridor. We also positioned plots along patch edges, to evaluate the different types of edges in each patch type. Corridor opening plots were in the connected patch, at the opening of the corridor. Winged opening plots were in the winged patch, at the opening of a randomly selected wing. Rectangle edge plots were in the rectangular patch, located at the midpoint of a randomly selected long-axis edge, adjacent to the pine plantation matrix. Matrix plots were located halfway (75 m) between the central patch and a randomly selected unconnected peripheral patch (winged or rectangular). To account for small-scale heterogeneity in fire temperature (Wally et al. 2006, Mitchell et al. 2009), each plot contained nine circular

TABLE 1. Details of prescribed fires conducted in six experimentally fragmented landscapes at the Savannah River Site (South Carolina, USA).

					Wind		
Block	Burn date	Ignition method	High temp. (°C)	Low RH (%)	Mean speed (km/h)	Max. speed (km/h)	Direction
52	7 Feb 2009	aerial	21	25	6	19	WSW
53N	10 Mar 2009	aerial	28	42	5	14	SSW
53S	10 Feb 2009	aerial	23	41	5	26	SSW
54N	23 Mar 2009	hand	23	22	2	11	S
54S	31 Jan 2009	hand	13	26	8	19	W
57	26 Feb 2009	hand	20	49	6	19	SE

Notes: Weather data are daily means/highs/lows for Barnwell, South Carolina (USA), obtained from Weather Underground (www.wunderground.com). Abbreviations are: temp., temperature; RH, relative humidity, max., maximum; W, west; S, south; E, east.

subplots. The subplots were 1 m in diameter spaced 1 m apart on a 3×3 grid.

We used metal pyrometers to determine fire intensity at each subplot (Hobbs et al. 1984, Iverson et al. 2004, Wally et al. 2006). Pyrometers are ideal for landscape-scale fire-temperature monitoring, as they are easily produced, deployable over large spatial scales, and provide temperature readings that are highly correlated with data logger thermocouples (Iverson et al. 2004, Wally et al. 2006). We constructed pyrometers out of copper tags streaked with 15 Tempilaq Temperature Indicating Liquid paints (Tempil, South Plainfield, New Jersey, USA) ranging from 177°C to 538°C, in 28°C increments. To prevent difficulty in interpreting pyrometers due to charring, we secured a second copper tag over the paints. We deployed the pyrometers during the morning before each prescribed burn and collected them the following day. We placed one pyrometer in the center of each subplot, supported 5 cm above the soil surface by steel wire.

To understand the influence of fuel loading on fire intensity, we quantified fuels prior to prescribed fires using a two step process in January 2009. We first nondestructively sampled fuels for each subplot. We visually estimated bunch grass cover, measured litter depth at the center of the subplot, and counted downed woody material (DWM) in four diameter classes (0–0.64, 0.65–2.54, 2.55–7.62 and >7.62 cm) along a transect bisecting each subplot. We used Brown's calculations (Brown 1974) to convert DWM counts into biomass estimates. We then converted these nondestructive measurements to biomass for our system, using linear regression models and data from 35 destructively sampled plots, of equal area to our subplots, but located outside of our study plots. Following destructive sampling, we dried (at 60°C for 48 hours) and weighed biomass from each destructive plot, sorted by litter, bunch grass, and DWM. We predicted biomass, based on regression models, for bunch grass, litter, and DWM from these 35 destructively sampled plots. Model fits for individual components were strong (bunch grass $r^2 = 0.76$; litter $r^2 = 0.80$; DWM $r^2 = 0.64$).

To understand effects of fire on vegetation, we counted live woody stems and visually estimated bunch grass cover, which is one of the most common and abundant species groups at our study sites (E. I. Damschen and L. A. Brudvig, *unpublished data*) for each subplot prior to and after prescribed fire (January and June 2009).

Analyses

We assessed the effects of corridors on fire using a three-phase analytical approach. We first explored univariate correlations between our measured variables using linear regression. Second, we used ANOVA to evaluate differences in measured variables across the eight landscape positions. Finally, we created a structural equation model (SEM; Grace 2006) to explicitly test among the mechanisms underpinning our hypotheses: that corridors might influence fire directly through connectivity or edges or indirectly by modifying fuel loading through the creation of edge. SEM is an especially appropriate approach for our study due to its ability to test hypotheses involving direct and indirect pathways, allowing us to evaluate complex relationships among variables, whereby individual variables may simultaneously act as responses (e.g., edges influence fuel loading) and predictors of other variables (e.g., fuel loading influences fire temperature) (Grace 2006).

We first determined relationships between our measured variables with simple linear regression (PROC REG; SAS Institute 2008). To understand how fuels contributed to fire temperatures and inform the choice of fuel variable(s) in our SEM, we tested how fire temperature was influenced by litter, bunch grass, DWM, and total biomass. To understand fire effects on vegetation (hypothesis 5), we tested the difference in the number of woody stems and bunch grass cover prior to and after fire as a function of fire temperature. All regressions were performed using mean values per plot for all variables (48 total observations per regression), after first removing the 96 (of 432) unburned subplots (instances where pyrometers did not register a temperature reading). Prior to analysis, we square-root transformed litter to improve homoscedasticity.

We next tested for effects of landscape position with randomized complete block ANOVA. Coupled with our SEM analysis, these tests address hypotheses 1–3. We use a mixed model (PROC MIXED; SAS Institute 2008) with the six replicate landscapes as random block effects and the eight landscape positions as fixed effects (connected patch center, corridor opening, corridor, matrix, rectangular patch center, rectangular patch edge, winged patch center, wing opening). We tested the following response variables: fire temperature (after first removing unburned subplots), litter fuel loading (the strongest predictor of fire temperature; see *Results*), and the proportion of burned subplots per plot, to assess patterns of spread. We then used independent linear contrasts to test between landscape positions. All response variables were tested as means per plot. Prior to analysis, we square-root transformed litter biomass and arcsine square-root transformed the proportion of burned subplots to meet homoscedasticity assumptions of ANOVA.

Finally, to further address hypotheses 1–3 and to address hypothesis 4, we created an SEM in AMOS (Arbuckle 2009) to test for direct and indirect effects of connectivity and edges on fire temperature. We used this SEM to specifically test our main hypotheses: (1) corridors directly affect fire temperature by modifying wind, independent of fuel levels, (2) corridors indirectly affect fire temperature by increasing fuel loading through edge creation, (3) corridors directly affect fire temperature by creating edges, which modify fuels

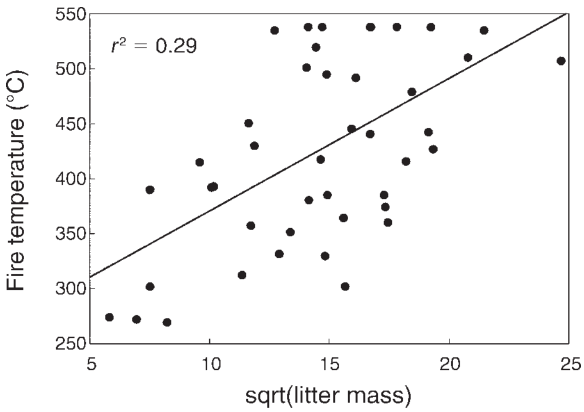

FIG. 2. Litter was positively correlated with fire temperature and was the strongest fuel type predictor of fire temperature across plots in experimentally fragmented landscapes. Downed woody material and bunch grass fuels were not significant predictors of fire temperature. Data points are plot-level means from six experimental landscapes ($n = 8$ plots per landscape). Litter mass was square-root (sqrt) transformed.

through microclimate conditions, independent of fuel levels, and (4) soil moisture availability indirectly affects fire temperature by increasing fuel accumulation (Kirkman et al. 2001), independently of corridors or edges. We did not test for a direct effect of connectivity on fuel loading, as we saw no theoretical basis for such a relationship. We parameterized the SEM with plot-level values for litter fuel loading (square-root transformed) and fire temperature, from plots in corridor openings (high connectivity; low edge), rectangle edges (low connectivity; high edge), and wing openings (low connectivity; low edge), and patch-level soil moisture holding capacity data (Damschen et al. 2006). We chose to use these three plot types in this model because their levels of connectivity (i.e., adjacency to a corridor) and edge (i.e., adjacency to a forested edge) are clearly definable, relative to one and other, allowing for unambiguous tests of edge and connectivity.

RESULTS

Fuel–fire relationships

Fire temperature was most strongly and positively predicted by litter fuel loading ($r^2 = 0.29$, $P = 0.0002$; Fig. 2). Fire temperature was positively, but less strongly, correlated with total biomass ($r^2 = 0.22$, $P = 0.001$), but was not correlated with DWD ($r^2 = 0.0004$, $P = 0.90$) or bunch grass fuel loading ($r^2 = 0.01$, $P = 0.59$). This result, that litter forms the predominant fuel source in our system, is consistent with past findings from longleaf pine woodlands (Mitchell et al. 2009).

Fire–vegetation relationships

Fire temperature was positively correlated with plot level changes in bunch grass cover ($r^2 = 0.15$, $P = 0.01$; Fig. 3). Hot-burning plots contained similar cover by bunch grass prior to and following burning, whereas cool-burning plots tended to decline in bunch grass cover the season following burning, relative to pre-burn levels, a pattern suggesting that productivity is limited by detritus accumulation in instances where litter combustion was incomplete (Knapp and Seastedt 1986). Conversely, there was no relationship between fire temperature and the change in the number of woody stems ($r^2 = 0.001$, $P = 0.87$).

Effects of landscape position

Landscape (i.e., plot) position modified fire temperature ($F_{7,29.8} = 2.92$, $P = 0.02$) and litter fuel loading ($F_{7,35} = 5.1$, $P = 0.0005$) through both connectivity and edge effects (Fig. 4).

Corridors increased fire temperatures by providing connectivity to plots adjacent to their openings. Plots at corridor openings burned on average 75°C hotter than plots in the openings of wings ($t = 2.3$, $P = 0.03$): a direct result of connectivity, as these two plot types did not differ in the amount of litter fuel loading ($t = 0.5$, $P = 0.61$). This connectivity effect appeared short lived, however, as plots in corridor openings burned 82°C hotter than plots 50 m away in connected patch centers ($t = 2.0$, $P = 0.05$), with no evidence for a difference in litter fuel loading between these plot types ($t = 0.5$, $P = 0.64$). Conversely, and providing further support for a connectivity-driven fire effect, plots in wing openings and winged patch centers did not differ in fire temperature ($t = 0.9$, $P = 0.40$) or litter fuel loading ($t = 0.9$, $P = 0.40$).

Plots in the pine plantation matrix supported the highest fire temperatures (Fig. 4a) and the greatest amounts of litter fuels (Fig. 4b). Matrix plots burned 88–120°C hotter than plots in wing openings or patch centers, regardless of patch type (all $t > 2.4$, $P < 0.02$), apparently due to 186–207 g more litter fuel in matrix subplots (all $t > 3.5$, $P < 0.001$). Conversely, fire temperatures did not differ between matrix plots and

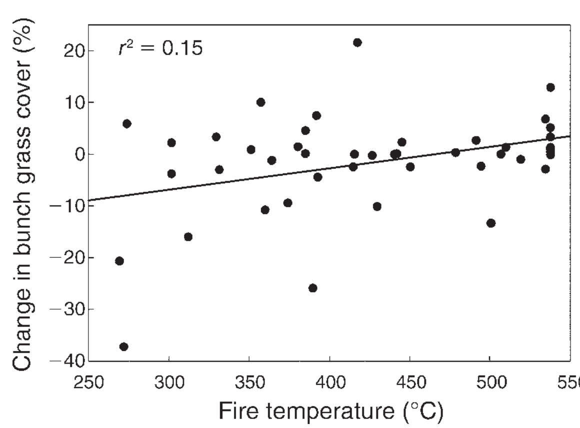

FIG. 3. Prescribed-fire-induced change in bunch grass cover was positively correlated with fire temperature. Data points are plot-level means from six experimental landscapes ($n = 8$ plots per landscape).

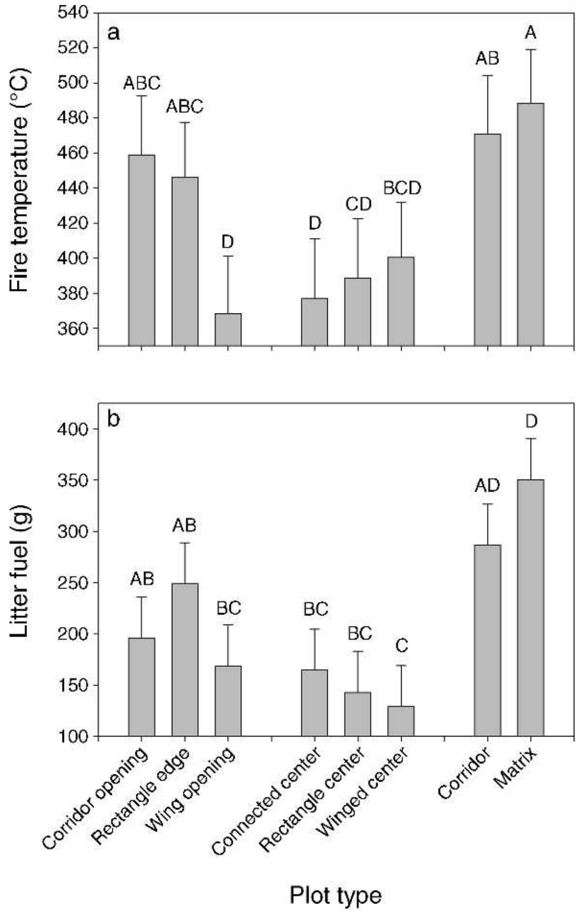

FIG. 4. (a) Fire temperatures and (b) litter fuel loading across plot types in six experimentally fragmented landscapes. Values are means + SE. Temperatures were elevated via a connectivity effect (comparison of plots in corridor openings, relative to plots in patch centers or in wing openings) and an edge effect (comparison of plots at rectangle edge relative to plots in patch centers). Matrix pine plantation trees elevated litter levels, resulting in the highest fuel loading in the matrix, rectangle edge (adjacent to the matrix), and in corridors, where plots were proximal to two edges. Within each panel, significant ($P < 0.05$) differences between plot locations are indicated by different letters above bars.

plots in corridor openings ($t = 0.8$, $P = 0.45$) or along rectangle edges ($t = 1.2$, $P = 0.25$). Plots in corridor openings supported on average 155 g less litter fuel per subplot, relative to matrix plots ($t = 2.8$, $P = 0.008$), demonstrating that two different mechanisms (connectivity vs. fuel loading) led to comparable fire temperatures. Similar fire temperatures between matrix and rectangle edge plots may be due in part to the influence of edge through elevated litter inputs. Litter fuel loads in rectangle edge plots were lower than levels in matrix plots (102 g; $t = 2.2$, $P = 0.04$), but on average 106 g greater than plots in rectangle centers. However, we found only marginal support for this translating to higher fire temperatures along rectangle edges vs. centers ($t = 1.5$, $P = 0.15$).

Although a substantial proportion of subplots in our study did not ignite (96/432), the probability of subplot ignition was unrelated to landscape position. Across plot types in this study, there was no difference in the proportion of burned vs. unburned subplots ($F_{7,29.8} = 1.3$, $P = 0.28$). This suggests that fire spread patterns were similar throughout our experimental landscapes.

Structural equation model

The SEM accounted for 51% of the variation in fire temperature (cumulative $r^2 = 0.51$) and fit the data well ($\chi^2 = 0.15$, df = 2, $P = 0.93$; model fit is considered good with $P > 0.05$; Grace 2006). Connectivity ($P = 0.04$) and litter ($P = 0.003$) had direct positive effects on fire temperature, while soil moisture availability ($P = 0.08$) and edges ($P = 0.13$) showed trends for indirect effects on fire temperature, by positively influencing the amount of litter fuel (Fig. 5). We did not find support for a direct effect of edges on fire temperature (standardized regression weight = 0.24; $P = 0.25$).

DISCUSSION

We show how corridors can promote fire through two different pathways. In our experiment, corridors elevated local fire temperatures during prescribed burns by increasing inter-patch connectivity and through within-patch edge effects. Corridors did not, however, impact

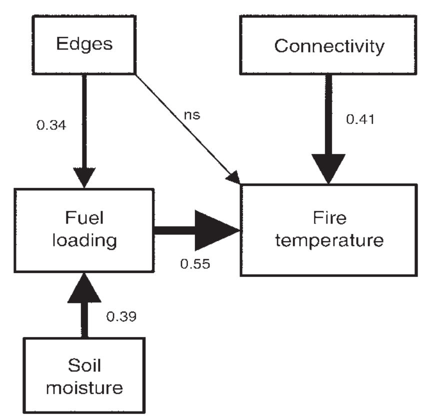

FIG. 5. Structural equation model (SEM) predicting fire temperature during prescribed burns in fragmented landscapes. Fire temperature was directly increased by connectivity and litter fuel loading and indirectly increased by soil moisture-holding capacity and habitat edges, through effects on litter fuel loading. Arrows indicate hypothesized direct and indirect relationships between connectivity, edges, and soil moisture-holding capacity on fire temperature; arrow widths are scaled to the strength of the respective path coefficients. The SEM was parameterized with plot-level values for litter fuel loading (square-root transformed) and fire temperature from plots in corridor openings (high connectivity; low edge), rectangle edges (low connectivity; high edge), and wing openings (low connectivity; low edge). Numbers next to arrows are standardized regression coefficients for significant effects (connectivity, litter fuel loading) and marginally significant effects (soil moisture holding capacity, edges); "ns" stands for not significant. Cumulative model $r^2 = 0.51$.

landscape-scale patterns of fire spread; subplots burned with comparable probability across all study locations in our landscapes. To our knowledge, this represents the first rigorous test of the long-standing concern that landscape corridors might facilitate fire (Simberloff and Cox 1987).

The influence of connectivity on fire is consistent with our hypothesized bellows effect: elevated fire temperatures resulting from increased wind speed due to wind channelization down open corridors. This effect was independent of fuel levels and we did not observe a similar effect along patch edges, where only a single edge exists. Thus, this was not a simple effect of edges on wind, but an emergent connectivity effect produced by corridors. In fact, we found no evidence for a direct effect of edges on fire temperature in our SEM, suggesting that neither wind along singular edges nor microclimatic edge effects, which may influence fuel moisture levels, were drivers of fire temperatures in our system. We did, however, observe an edge effect on fire temperature that was due to elevated fuel levels resulting from litter deposition by overstory pine trees along edges.

The full implications of our findings depend in part on the desired role of fire during landscape management (Baker 1992). Prescribed understory fire is central to the management and restoration of longleaf pine woodlands (Jose et al. 2006, Mitchell et al. 2009) and, thus, the elevation of fire temperature by corridors may be considered advantageous in our system. Frequent understory fire maintains understory plant diversity in longleaf pine woodlands by promoting coexistence of herbaceous plants and otherwise dominant shrubs (Thaxton and Platt 2006, Hiers et al. 2007, Myers and Harms 2009). We found partial support for this hypothesis. By promoting hot fires, corridors modestly increased the cover of bunch grasses (Fig. 3); however, we found no effects of fire temperature on woody species. This may have been a result of the strong resprouting ability of shrubs following fire (Drewa et al. 2002), particularly at our sites, which have a long history of fire suppression (<50 years) and relatively recent initiation of fire management. Regardless, this suggests that corridors may aid in promoting plant species coexistence though the promotion of bunchgrasses following fire.

As a ubiquitous worldwide disturbance, fire plays an important role in promoting species coexistence, through the production of spatially and temporally variable levels of disturbance (Platt and Connell 2003, Thaxton and Platt 2006, Bowman et al. 2009). Here, we show three pathways that lead to spatial variation in fire intensity: habitat edges and fuel levels, soil moisture and fuel levels, and landscape connectivity (Fig. 5). Spatial variation in litter was clearly important for patterns of fire temperature in our experiment: this was the strongest effect in our SEM. However, the factors that led to fuel levels, edges (path coefficient $= 0.34 \times 0.55 = 0.19$) and soil moisture (path coefficient $= 0.39 \times 0.55 = 0.21$), had substantially weaker influences on fire temperatures than did connectivity (path coefficient $=$ 0.41) (Grace 2006). This was because effects of habitat edges and soil moisture on fire temperature were indirect. Edges led to increased litter deposition by matrix pine trees into open habitat patches, which in turn resulted in increased fire temperature, whereas soil moisture holding capacity was positively correlated with litter fuel levels, which resulted in increased fire temperatures. Our use of SEM allowed for these direct and indirect paths to be disentangled. Increased attention should be given to the multiple direct and indirect roles of landscape features, like corridors and edges, for processes of interest, like fire.

Research at the interface of landscape ecology and ecosystem processes, including disturbance, remains a key challenge (Turner 2005, 2010). This holds true for corridor research, as a subset of landscape ecology, where most work has focused on understanding impacts on organisms (Crooks and Sanjayan 2006). We show the influence of landscape management through corridors on a key ecosystem process and disturbance, fire; however, this work raises new questions and underscores the need to understand how corridors impact ecosystem processes. Among these is understanding the mechanistic role of corridors and connectivity on wind, which may impact a suite of relevant ecological processes, from seed dispersal (Damschen et al. 2008) to the vectoring of disease (Burdon et al. 1989) to fire, as we suspect in this study. Further, while we found no evidence for a microclimatic influence of habitat edges on fire, it remains likely that corridors influence ecosystem processes through edge creation (Ries et al. 2004).

In our experiment, fire temperature was a function of fuel loading and, we suspect, wind conditions: two factors that, while components of all fire regimes, also vary across ecosystems. Thus, system-specific influences of corridors on fire dynamics likely exist and it is worthwhile to ask: how general might our findings be? In our experiment, patches and corridors are created by clearing pine plantation forest, as these clearings better represent longleaf pine woodlands, which have only scattered overstory trees, than does the pine plantation matrix (Jose et al. 2006). Indeed, clearing has resulted in elevated plant biodiversity levels in patches, relative to the matrix (Brudvig et al. 2009). As a starting point for understanding generality, we consider how our results might have differed, had our landscapes been the inverse, containing forested patches/corridors and cleared openings as the matrix. We believe that this would have had little influence on some of our findings, but potentially large impacts on others. Edge effects and soil moisture would still indirectly impact fire temperature and general patterns of spread should remain similar, though patches would have burned hotter and the matrix cooler (Fig. 4). Of interest, however, is how such an inverse landscape might modify our connectivity results. We suspect that the role of wind-bellowed fire might be most pronounced in systems with open corridors, such as our system, other grassland, savanna, or shrubland systems with forested matrices, or systems where utility right-of-ways are utilized as corridors. However, there is evidence that suggests the potential for wind-driven fire to be promoted by riparian forest corridors contained within forested landscapes (Dwire and Kauffman 2003, Pettit and Naiman 2007). Largely anecdotal, more work is needed to confirm and then establish mechanisms for these observations (e.g., whether they are due to direct or indirect connectivity or edge effects).

Additional important avenues for future research include investigation of how our findings might scale up to larger landscapes, where corridors might be longer and wider than in our experiment. Presumably, very wide corridors would not produce a bellows effect, owing to a minimal level of wind constriction; however, what this width is and how the bellows effect scales with width remain unknown. Additional work might apply our findings to systems where the matrix does not burn and fire is confined to patches and corridors. Our study is the first test of how corridors impact fire dynamics and represents an important starting point; however, more work is clearly needed before we achieve a comprehensive understanding of how corridors impact fire and other disturbances.

As is the case with all potential unintended conservation outcomes, the possible advantages and disadvantages of corridors must be calculated and then weighed against each other. In our experimental system, the net outcome of corridors on one important metric, plant biodiversity, has been strongly positive (Damschen et al. 2006), suggesting that if corridor dangers do exist, they have been outweighed by benefits, such as increased rates of inter-patch movement, seed dispersal, and pollination (Tewksbury et al. 2002, Haddad et al. 2003, Levey et al. 2005). We might now add the effects of corridors on fire to this list, owing to the influence of corridors on fire intensity and ensuing promotion of herbaceous vegetation over shrubs. We do recognize, however, that promoting intense fire is not desirable in all situations. These include systems that are not fire dependent or where corridors connect flammable habitats in urban/suburban settings, thereby posing a danger to people or structures in the human-occupied matrix areas. Thus, the promotion of fire by corridors should remain a concern for the subset of ecosystems where burning is not a desirable management outcome (Simberloff and Cox 1987).

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