

Habitat corridors alter relative trophic position of fire ants

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Abstract. Habitat fragmentation disrupts species movement, leading to local extinctions and altered community structure. Habitat corridors, which connect isolated patches of habitat and facilitate movement between patches, provide a potential solution to these negative impacts. However, most studies to date have examined the movement of species alone without considering emergent effects on the community (e.g., altered trophic structure). We use large-scale, experimental landscapes and nitrogen stable isotopes ratios (δ^{15} N) of a common generalist consumer (the fire ant, *Solenopsis invicta*) to determine how corridors affect trophic structure. Thus, because the fire ant is a species whose trophic position is flexible and whose diet typically reflects local prey availability, we assume that shifts in fire ants' trophic position between connected and isolated patches are likely to reflect shifts in patch trophic structure. We found that colonies in isolated patches had lower means and ranges of $\delta^{15}N$ than colonies in otherwise similar connected patches, suggesting that corridors may increase fire ants' trophic position and breadth, respectively. Previous work in our landscapes documented higher species richness of plants in connected than unconnected patches. Patch means of ant $\delta^{15}N$ were positively correlated with plant richness, suggesting that increased plant richness may influence the observed responses in fire ant δ^{15} N. Together these results suggest that fragmentation may reduce trophic position and narrow trophic breadth of dietary generalists such as the fire ant. These shifts likely reflect an alteration of food webs in isolated patches. Our results suggest that corridors may be effective in preventing or reducing such alterations.

Key words: connectivity; corridor; fire ant; fragmentation; patch shape; plant diversity; *Solenopsis invicta*; stable isotope analysis; trophic structure.

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INTRODUCTION

The alteration of area, shape, and isolation of habitat patches can drive changes in species composition, biotic processes, and trophic structure (Kruess and Tscharntke 1994, Gilbert et al. 1998, Fahrig 2003, Collinge 2009). Such changes are increasingly common as natural landscapes become subdivided by anthropogenic processes. Corridors are a commonly implemented management strategy to mitigate the negative effects of fragmentation because they facilitate movement of organisms between otherwise isolated patches (Hilty et al. 2006). Indeed, many studies have demonstrated that corridors generally increase rates of inter-patch movement (Sutcliffe and Thomas 1996, Gonzalez et al. 1998, Tewksbury et al. 2002, Haddad and Tewksbury 2005, Gilbert-Norton et al. 2010, but see Hilty et al. 2006 and Haddad et al. 2011*a*). These increases in

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movement are linked to increased species richness (Gilbert et al. 1998, Damschen et al. 2006, Damschen et al. 2008) and greater persistence of predators in connected habitat patches (Gilbert et al. 1998). However, the impact of corridors on community and trophic structure is still not well understood.

Determining how changes in landscape characteristics affect trophic structure is important, given the central role of trophic dynamics in ecosystem stability and function (McCann 2000, Estes et al. 2011). Fragmentation may alter trophic structure via several mechanisms. Theory predicts a positive relationship between the number of trophic levels and habitat area (Schoener 1989, Holt 1993, Pimm 2002), a pattern supported by non-experimental, empirical studies (Vander Zanden et al. 1999, Komonen et al. 2000, Post et al. 2000, Layman et al. 2007a, Takimoto et al. 2008, McHugh et al. 2010). Although such studies provide insight on potential effects of habitat loss, confounding factors make it difficult to pinpoint the underlying mechanisms. Studies that experimentally manipulate fragmentation and connectivity to test how they affect organisms of different trophic levels are rare (Gilbert et al. 1998, Holyoak 2000, Davies et al. 2001).

A particular challenge in fragmentation and corridor studies is to separate connectivity effects from edge effects. The challenge arises because corridors essentially always increase the edge-toarea ratio of associated patches, and edges are well known to alter species abundance, distribution, interspecific interactions, and ecosystem processes (Harrison and Bruna 1999, Davies et al. 2001, Laurance et al. 2002, Ries et al. 2004). This confounding of connectivity and edge effects raises the question, "To what extent could differences in trophic structure between habitat patches with and without corridors be due to connectivity versus differences in patch shape (i.e., edge-to-area ratio)?" An equally difficult challenge is quantification of the trophic structure of a food web. A potential solution is provided by stable isotopes; recent work suggests that stable isotope ratios of generalist consumers reflect fragmentation effects on trophic structure (see below, Layman et al. 2007*a*).

In a large-scale experiment, we quantified corridor and patch shape effects on trophic

structure. We did so by quantifying indirect measures of trophic position and dietary breadth for a generalist consumer, the fire ant (Solenopsis *invicta* Buren). We used stable isotopes, the ratio of ${}^{15}N/{}^{14}N$ (hereafter $\delta^{15}N$), to estimate the relative trophic position of fire ants between patch types (Bearhop et al. 2004, Newsome et al. 2007). In particular, we use mean $\delta^{15}N$ of colonies in a patch to estimate fire ant trophic position (higher δ^{15} N indicates higher trophic position) and range (maximum minus minimum values of δ^{15} N within a patch) to estimate of range of trophic positions (hereafter trophic breadth). Fire ants are ideal study organisms for answering our questions about whether corridors alter trophic structure because they are trophic generalists (Tschinkel 2006). As such, the $\delta^{15}N$ of a fire ant colony likely reflects the average trophic position of nearby prey items and $\delta^{15}N$ of a population of colonies in a habitat patch can be interpreted to reflect the trophic structure of that patch (Layman et al. 2007*a*).

We address three questions. (1) Do corridors increase trophic position and trophic breadth of fire ant colonies? Because corridors increase the movement of organisms (Gilbert-Norton et al. 2010), help sustain species richness (Gilbert et al. 1998, Damschen et al. 2006), and allow greater persistence of predators in connected habitat patches (Gilbert et al. 1998), we predicted that fire ant colonies in unconnected patches would have a lower mean trophic position and narrower trophic breadth than those from patches connected by a corridor but otherwise similar in shape (i.e., edge-to-area ratio). Because our experimental design also allows us to test for patch shape effects while controlling for connectivity, we also asked: (2) Does patch shape affect trophic position and trophic breadth of fire ants? To address possible mechanisms underlying connectivity effects, we ask: (3) Does plant species richness positively correlate with the mean $\delta^{15}N$ of fire ants across patches? Plant species richness is enhanced by connectivity (Damschen et al. 2006) and can increase abundance of predatory arthropods (Haddad et al. 2009). If corridors indeed increase the trophic position of fire ants (question 1), a positive relationship between plant species richness and δ^{15} N of fire ants would suggest that plant species richness is likely affecting the trophic structure of consumers (i.e., the prey of fire ants) and ultimately influencing the higher trophic position of fire ants in connected patches.

Methods

Study site

We conducted this study at the Savannah River Site, South Carolina (33.20° N, 81.40° W) in ten randomized and replicated blocks designed to test effects of corridors on ecological processes. Patches were created by clearing mature pine plantation forest and are now managed for restoration to longleaf pine savanna, a speciesrich, endangered habitat (Van Lear et al. 2005, Jose et al. 2006). Restoration practices include prescribed fire, planting of longleaf pine (*Pinus palustris*) seedlings, and mechanical removal of hardwood trees. As a result, the ground-layer vegetation in patches is diverse and productive relative to the understory of the pine forest matrix.

Each block consists of five patches. In the center of each block is a 1 ha "center" patch, and four peripheral patches. Peripheral patches are 150 m from the center patch and are of three "connected", "rectangular", types: and "winged". Connected patches are connected to the center patch by a 150 m long, 25 m wide corridor of the same habitat (Fig. 1A). Rectangular and winged patches lack a corridor connecting to the center patch and are thus isolated or unconnected. They are equal in area to the connected patch, 1.375 ha (1 ha plus the area of the corridor, 0.375 ha). The equivalent area of the corridor is added to the winged patches as two lateral 75 m long, 25 m wide "wings" and to the rectangular patches as additional area on the far side of the patch. Connected and winged patches have similar edge-to-area ratios (491 m/ha and 509 m/ha, respectively) which are substantially higher than the edge-to-area ratio of rectangular patches (345 m/ha). This design allows us to test for corridor effects independent of patch shape effects by comparing response variables from connected patches to those from winged patches, which are unconnected but nearly identical in edge-to-area ratio. Similarly, we can test for patch shape effects independent of corridor effects by comparing response variables from winged patches to those from rectangular patches, which

differ greatly in edge-to-area ratio but are identical with respect to connectivity (i.e., they are both unconnected). Each block contains either a second winged or a second rectangular patch (Fig. 1B). We averaged response variables from duplicate patch types within each block.

Study organism, sampling, and stable isotope analysis

Fire ants are opportunistic, omnivorous feeders that consume a wide variety of invertebrate prey, scavenged vertebrates, small seeds, plant exudates, and homopteran honeydew. Their diet typically reflects immediately available food sources rather than strong dietary preferences (Tschinkel 2006). Depending on resources available, they can be highly carnivorous (Tillberg et al. 2007) or omnivorous (Lofgren et al. 1975).

Stable isotopes are frequently used to characterize food webs and estimate trophic position of consumers (Layman et al. 2007b, Newsome et al. 2007, Schmidt et al. 2007). δ^{15} N is particularly useful because nitrogen from the tissue of consumers is enriched in ¹⁵N relative to that of prey, which means that $\delta^{15}N$ is positively correlated with a consumer's trophic position (Gannes et al. 1998, Post 2002). $\delta^{15}N$ values of consumers are often calibrated against $\delta^{15}N$ baseline values of plants. We did not make baseline adjustments. However, a recent study suggests that at spatial scales comparable to our within-block comparisons, unadjusted $\delta^{15}N$ of consumers result in reliable comparisons of relative trophic position (Woodcock et al. 2012).

The enrichment in $\delta^{15}N$ for one consumer trophic level transfer (including insects) is generally 3–4‰ (Mooney and Tillberg 2005, Tillberg et al. 2006). In their native range, fire ant nests are highly variable in δ^{15} N ratios. This variance reflects an estimated span of two trophic levels (Tillberg et al. 2006). Here we use the patch mean δ^{15} N, which estimates the average trophic position of fire ant colonies in a given patch, and patch range (maximum minus minimum) of δ^{15} N, which estimates the breath of trophic positions of fire ant colonies in a given patch. Both mean and range of $\delta^{15}N$ have been used previously to characterize trophic structure in fragmented landscapes (Layman et al. 2007a) and mean $\delta^{15}N$ has been used to infer trophic position and prey availability in ants (Bluthgen

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Fig. 1. (A) Photograph of one of ten experimental landscapes taken from a center patch looking down the corridor to the connected patch. (B) Sampling design within an experimental landscape. Dotted lines depict a 3×3 grid centered in each patch, where *S. invicta* workers were collected in each of the 33.3 m² cells.

et al. 2003, Palmer 2003, Tillberg et al. 2007, Gibb and Cunningham 2011).

In each peripheral patch (connected, rectangular, and winged) we collected fire ants using a stratified design. We divided each patch into a 3 \times 3 sampling grid (*N* = 9 cells, each 33.3 m \times 33.3 m; Fig. 1B). We attempted to collect fire ants from one nest per cell within the grid in all patches.

100 m

When we did not find nests within a cell, we collected whenever possible from the nearest fire ant nest in an adjacent cell with the same amount of edge habitat. From each nest, we collected approximately 200 workers and stored them at -17°C. Of these, we haphazardly selected 30-50 individuals for stable isotope analysis. To obtain an estimate from a relatively long time window of nitrogen assimilation and unbiased by the last meal ingested, we analyzed only heads and thoraxes (Tillberg et al. 2006). Samples from a given nest were thoroughly mixed, weighed to the nearest $\pm 1 \mu g$, and analyzed for $\delta^{15}N$ at the University of Georgia Savannah River Ecology Laboratory using continuous flow isotope ratio a mass spectrometer (Finnigan Delta ^{plus}XL; Finnigan-MAT, San Jose, CA). We report stable isotope ratios in per-mil units (‰) in the standard delta (δ) notation. We tested for normality of response variables in each patch type using a Shapiro-Wilk test. Response variables did not require transformation. Data on plant species richness were collected via visual censuses over the entire area of all patches in eight blocks (Damschen et al. 2006).

To determine whether trophic position was increased by corridors (question 1) we tested a directional hypothesis using paired, one-tailed ttests on the mean and range of δ^{15} N from winged vs. connected patches. To determine whether trophic position was affected by patch type (question 2) we tested a non-directional hypothesis using paired, two-tailed t-tests on the mean and range of δ^{15} N from winged vs. rectangular patches. One block was omitted from the range of δ^{15} N analysis because one patch type within that block was inadequately sampled. To examine the relationship between plant species richness and trophic position of fire ants (question 3), we used a linear regression of plant species richness and mean $\delta^{15}N$ of fire ants from the same patch. All analyses were conducted using R (R Development Core Team 2009).

Results

We collected fire ants from 322 nests, with a mean of 8.05 (\pm 2.17 SD) nests per patch. δ^{15} N from these nests varied substantially, ranging from -1.03% to 4.13‰. Mean δ^{15} N values were $\sim 10\%$ higher in connected than in unconnected

patches of similar shape (δ^{15} N = 1.86 and 1.69 in connected and winged patches, respectively; *t* = 2.10; *P* = 0.03), supporting our prediction (Fig. 2). Likewise, the range of δ^{15} N was ~33% greater in connected than unconnected patches of similar shape (ranges = 1.70 and 1.28 in connected and winged patches, respectively; *t* = 1.95; *P* = 0.04; Fig. 2), as predicted.

Patch shape did not affect the trophic signature of fire ant colonies. In particular, mean and range of δ^{15} N did not differ between winged and rectangular patches, which differ greatly in edge-to-area ratio but are identical in size and connectivity (t = 1.13; P = 0.29 for mean; t = 0.72; P = 0.50 for range; Fig. 2).

The relationship between plant species richness and δ^{15} N of fire ant colonies was highly dependent on patch type (Fig. 3). In connected and rectangular patches the relationship was strong and positive ($r^2 = 0.60$ and 0.52, respectively; P's < 0.05), whereas in winged patches there was no apparent relationship ($r^2 = 0, P > 0.94$).

Discussion

Our results suggest that patch connectivity (but not patch shape) has an effect on relative trophic position and breadth of a generalist consumer. As predicted, fire ant nests in connected patches had lower mean and range of δ^{15} N than those in similarly shaped, unconnected patches. While the mechanism driving this pattern is uncertain, the positive correlation between patch plant species richness and mean fire ant δ^{15} N in most patch types suggests that plant diversity may play a role, since plant species richness is higher in connected than unconnected patches (Damschen et al. 2006).

Due to the wide range of resources consumed by fire ants, the dietary shifts we observed may reflect local trophic structure of the habitat patches in our study system (see Layman et al. 2007*a*). Assuming that fire ants' diets reflect local food sources, the lower δ^{15} N in isolated (winged) patches could signify an overall decrease in availability of animal prey, a decrease in trophic position of those prey or both. Likewise, the lower δ^{15} N range in isolated patches suggests that fire ants in those patches occupy a narrower range of trophic positions than those in connect-



Fig. 2. (A) Corridor effects on mean δ^{15} N (t = 2.10; P = 0.03), (B) patch shape effects on mean δ^{15} N (differences not significant; NS), (C) corridor effects on range of δ^{15} N (t = 1.95; P = 0.04) (D) patch shape effects on range of δ^{15} N (NS). For A-C, n = 10. For D, n = 9. Bars represent mean ± 1 SE.



Fig. 3. The relationship between species richness of plants and mean $\delta^{15}N$ of fire ants for each patch type (connected, rectangular, and winged).

ed patches. While we are unable to discern whether corridors increased the abundance or trophic position of prey, our results nevertheless suggest that isolation negatively impacts prey and that corridors mitigate such disruptions. Further work of this kind using focal organisms of other trophic levels could disentangle how trophic structure is might be impacted by isolation.

An impact of fragmentation on the contraction of trophic structure would be consistent with other studies. Layman et al. (2007*a*) concluded

that fragmentation collapsed trophic structure of a tidal creek food web. That collapse was evident in intraspecific comparisons of isotopic ratios from generalist consumers (gray snapper (Lutjanus griseus Linneaus)) in fragmented and intact tidal creeks. Small-scale experimental studies have also found that fragmentation affects trophic structure. In a microbial food web, for example, fragmentation reduced the density of a top predator (Holyoak 2000). In another experimental study, Gilbert et al. (1998) found that fewer predator species persisted in moss patches that were isolated than in patches that were connected by corridors. Our findings are congruent and extend these results to a much larger spatial scale.

Although our results suggest that corridors may affect trophic position of fire ants via differences in plant species richness, we note that the strong positive relationship between plant species richness and mean δ^{15} N of fire ants occurred in just two of three patch types, connected and rectangular. We have no explanation for the absence of the relationship in winged patches, but it suggests that increased prevalence of edges may disrupt the relationship between the plant richness and trophic position of fire ants and certainly calls for additional research. The pattern in connected and rectangular patches, however, coincides with studies documenting positive relationships between plant diversity and consumer abundance and diversity (Siemann et al. 1998, Haddad et al. 2009). Furthermore, experiments by Haddad et al. (2009 and 2011b) found that plant species richness is positively related with species richness of consumers and with abundance of arthropod predators.

In conclusion, we teased apart potential effects of patch shape and connectivity on the isotopic signature and likely trophic position of a generalist consumer, and found that connectivity effects have the most influence. These results have relevance in the context of land management and conservation because they suggest that habitat corridors can help maintain food web structure in fragmented landscapes.

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