# Connectivity increases trophic subsidies in fragmented landscapes

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LETTER

# Connectivity increases trophic subsidies in fragmented landscapes

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**Abstract**

Landscape corridors mitigate the negative effects of habitat fragmentation by increasing dispersal. Corridors also increase biodiversity in connected habitat fragments, suggestive of metacommunity dynamics. What is unknown in this case is the mechanisms through which metacommunity dynamics act. Working in a large-scale fragmentation experiment, we tested the effect of corridors on the movement of prey species and subsequent effects on predator nutrition (which we call trophic subsidies). We enriched plants of central patches with $^{15}$N, then measured $\delta^{15}$N in green lynx spiders, the most abundant insect predator, in patches that were either connected to or isolated from the enriched patch. We found that corridors increased prey movement, as they increased spider $\delta^{15}$N by 40% in connected patches. Corridors also improved spider body condition, increasing nitrogen relative to carbon. We suggest a novel mechanism, trophic subsidies, through which corridors may increase the stability or size of populations in connected landscapes.

**Keywords**

Connectivity, corridors, habitat fragmentation, metacommunities, predators, spiders, trophic subsidies.

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## INTRODUCTION

Spatial subsidies are generated by the movement of nutrients, energy, and prey across neighbouring habitats, neighbouring ecosystems, or more distant areas of the same habitat (Loreau *et al*. 2003; Polis *et al*. 2004). They have mostly been documented in the form of cross-boundary subsidies from adjacent and contrasting habitats, like open ocean to intertidal areas and rivers to riparian banks (Polis & Hurd 1996; Nakano & Murakami 2001; Baxter *et al*. 2004). Trophic subsidies, the focus of this study, are those caused by prey movement to areas occupied by predators (Polis *et al*. 1997), or predator movement to areas occupied by prey (Wilcove 1985). Trophic subsidies can alter the persistence (Marczak *et al*. 2011), structure (Baxter *et al*. 2004; Rand *et al*. 2006), and stability (Huxel & McCann 1998) of food webs.

Fragmentation, degradation and destruction of habitats may cause predators to be especially vulnerable to the loss of subsidies (Layman *et al*. 2007; Pereira *et al*. 2010; Rands *et al*. 2010; Haddad *et al*. 2015). Because resource requirements increase with trophic level (Kruess & Tscharntke 1994; Holt *et al*. 1999), predators are especially sensitive to changes in the quality and quantity of available food sources in their environment. Martinson and Fagan (2014) performed a meta-analysis of arthropod predator–prey interactions and found that habitat fragmentation reduced predator resource consumption to 86% of the consumption rate measured in continuous landscapes. Habitat fragmentation and degradation can alter predators' resources primarily in three ways: (1) by reducing prey populations (Janzen 1983; Bender *et al*. 1998; Collins *et al*. 2009; although, see Prugh *et al*. 2008), (2) by reducing prey dispersal between isolated habitats (Zanette *et al*. 2009; Ripple *et al*. 2014), and (3) by reducing nutritional value of prey (Villafuerte *et al*. 1997; Naug 2009), which has been shown to limit predator growth, survival and reproduction (Mayntz & Toft 2001; Denno & Fagan 2003). Due to their sensitivity to prey availability, predators are often the first taxa to disappear from fragmented landscapes (Ripple *et al*. 2014). However, in some cases fragmentation may positively affect subsidies. For example, increased amount of edge habitat can increase subsidies by increasing movement of prey or predators across habitat boundaries (Murcia 1995; Ries *et al*. 2004).

Although there have been numerous studies of subsidies within fragmented landscapes across habitat edges (Wilcove 1985; Murcia 1995; Cadenasso *et al*. 2004), there are few studies that have tested effects of isolation on trophic subsidies (Hines *et al*. 2005). Isolation reduces successful dispersal of prey and predators, thus reducing resource availability for predators (Andrén 1994; Crooks *et al*. 2011). Therefore, landscape connectivity alone should act to subsidise predator resources and then increase predator fitness in fragmented landscapes (Ulanowicz *et al*. 2014; Ripple *et al*. 2014; but see Orrock *et al*. 2008). Food web subsidies can decouple predator fitness from local productivity, and thus connectivity can allow predators to survive even in low-productivity patches. Polis & Hurd (1996) found that food web subsidies from highly productive marine food webs were able to sustain consumers from low-productivity island food webs. Baxter *et al*. (2004) found that the density of tetragnathid spiders declined

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rapidly when stream subsidies via aquatic insects were experimentally removed. Similar mechanisms could operate between connected patches in fragmented landscapes. In this study, we test the effects of landscape connectivity, including landscape corridors created or maintained in conservation, on inter-patch subsidies.

In landscape conservation and management, the population size and persistence of predators may depend on spatial subsidies via landscape corridors (Taylor *et al.* 1993; Hilty *et al.* 2006; Resasco *et al.* 2017). By increasing prey abundances or immigration, corridors may increase resource availability, and thus increase predator population size and stabilise food web interactions (Briggs & Hoopes 2004; Huxel *et al.* 2004; Leibold *et al.* 2004). We have shown previously that corridors increase species richness in ways that are consistent with metacommunity dynamics (Damschen *et al.* 2006), but we do not know the mechanism driving the response. Because tracking species interactions through a landscape is logistically challenging, empirical studies of effects of landscape connectivity on predator–prey metacommunities have largely been conducted in microcosm experiments (LeCraw *et al.* 2014).

Working within a large-scale fragmentation experiment, we use a stable isotope of nitrogen to test effects of landscape connectivity on prey movement, predator consumption and nutrition. Our study of subsidies is supported by previous findings within our experiment: for example, we have found that habitat fragmentation mediates the spatial dynamics of other heterotrophic interactions, such as plants and pathogens (Sullivan *et al.* 2011), seeds and seed predators (Orrock & Damschen 2005) and plants and pollinators (Tewksbury *et al.* 2002; Townsend & Levey 2005). Within this system, spiders are optimal organisms to test effects of corridors on trophic subsidies because they are abundant predators at our experimental scale, and they prey on consumers that we have studied extensively (Haddad *et al.* 2011; Orrock *et al.* 2011; Nyffeler & Birkhofer 2017). Furthermore, spider abundance and body condition have been shown to be responsive to changes in prey availability (Kreiter & Wise 2001; Schmidt *et al.* 2013). Using stable isotope marking in this novel system, we test whether corridors (1) increase consumption of prey that originated in a connected patch and, in consequence, (2) increase predator body condition.

## METHODS

We performed this study within the SRS Corridor Experiment, an experimental landscape created in 2000 and located at the Savannah River Site (SRS), a National Environmental Research Park in Aiken and Barnwell Counties, South Carolina, USA (33.20 N, 81.40 W), Fig. 1a). In 2000, we worked within pine (*Pinus taeda* and *P. palustris*) plantation to create eight replicate landscapes (hereafter, 'blocks') by removing mature trees to create longleaf pine woodland habitat (Fig. 1b). Each block consists of a central patch (1 ha in size) of woodland, surrounded by four equidistant peripheral patches of identical habitat (Fig. 1c). One peripheral patch is connected to the central patch by a 150 m long × 25 m wide corridor (Tewksbury *et al.* 2002). The three unconnected patches are identical in area to that of the central patch plus the corridor (1.375 ha), but differ in shape to control for edge effects created by corridor presence. The similarity of edge-to-area ratio between high-edge patches and connected patches allow us to test for connectivity while controlling for patch shape effects. Unconnected, low-edge patches were unsuitable to test our hypotheses due to the higher edge-to-area ratio of connected and high-edge patches and were therefore excluded from our analysis. All blocks are separated by at least 1.5 km to minimise the probability of dispersal between them. Within patches, we restored habitats to native longleaf pine woodland by planting a low density of longleaf pine trees (*P. palustris*) and by burning with low-intensity prescribed fire on a return interval of 2–3 years, mimicking estimated historical frequencies (Frost 1998).

### Study species

We tested the effects of fragmentation and the role of corridors in providing trophic subsidies for the green lynx spider, *Peucetia viridans*, a large cursorial oxyopid spider that is abundant in our longleaf pine woodland habitat. *P. viridans* is an ambush predator that sits and waits on inflorescences. As a generalist predator, *P. viridans* has been documented preying on more than 30 species of pollinators (Hymenoptera and Diptera), aphids and moths (Whitcomb *et al.* 1966). *P. viridans* is generally semelparous (one egg sac per female), but can be iteroparous (multiple egg sacs) with increased food resources or loss of an egg sac (Fink 1986). Adult females guard egg sacs for 6–8 weeks until the clutch balloons as second instars (Fink 1986). Juveniles require eight molts through spring and summer. Individuals become reproductively mature in July and August, and create egg sacs in September and October.

### Arthropod sampling

We hand-collected *P. viridans* in August of 2011 and October of 2013 from the centre patch, connected patch and one high-edge peripheral patch in each block. These served as pre- and post-treatment samples for the $^{15}$N tracer study. To generate estimates of abundance, we performed four collections within 6 weeks of 2013 to meet assumptions of a closed population between surveys (Pollock 1982). In each survey, we searched for *P. viridans* in the central 75 m × 75 m area of each patch (Fig. 1c). We started surveys by walking along the periphery of this square (300 m), searching approximately 3 m on both sides of the route. We then moved 10 m towards the interior of the square and repeated the process until the entire 75 m × 75 m area had been searched. After collection, we immediately stored all individuals at −20°C.

Although we did not sample prey for this study, we were able to use data from a companion study (e.g. it was not implemented as part of our study of trophic subsidies) in which we measured the abundance of a primary prey group for *P. viridans*, wood-nesting wasps and bees (Randall 1982). To do this, we used a passive trapping method called trap-nesting, in which empty nesting resources (trapnests) were left in the field for a growing season to allow occupation by cavity-nesting hymenoptera (e.g. Schuepp *et al.* 2011). Trapnests

**Figure 1** The SRS Corridor Experiment is located (a) in western South Carolina at the (b) Savannah River Site. The eight blocks of the Corridor experiment are not to scale. (c) Each experimental landscape has five patches of a similar configuration, in which the centre patch was sprayed (area enclosed by dashed lines).

were each composed of a 10.16 cm diameter corrugated pipe packed with ~50, 20.32 cm-long hollow bamboo reeds, and were mounted on poles at chest height at the centre (37.5 m from the edge) of each habitat patch within a block (Fig. S1). We deployed two trapnests per patch in April 2013 and collected them in January 2014. We counted the total number of nests created per patch as a relative measure of reproductive individuals present within the patches over the growing season.

### $^{15}$N tracer

To test whether corridors increase the movement of prey, we added stable isotopes to central patches and traced the enriched signal through the food web in peripheral connected and unconnected patches. We have shown that $^{15}$N enrichment can be detected in spiders after enriching nearby flowering plants, likely because of the enrichment moving through the food web by consumption of plant material by pollinators, then the consumption of pollinators by spiders (Brown 2015). The only way the $^{15}$N signal can leave the plant is through seed dispersal (Carlo *et al.* 2009; Herrmann *et al.* 2016) or consumption, and even then, recapturing the signal is difficult because the movement is diffuse across a landscape. Spiders solve this problem as they integrate the signal through consumption of many individual prey. Beginning in May of 2013, we added $^{15}$N-urea to flowering plants in all eight central patches. We then analysed the $\delta^{15}$N of *P. viridans* in peripheral patches before and after $^{15}$N addition.

Following a protocol developed for tracking seed dispersal (Herrmann *et al.* 2016), we enriched flowers of plants most commonly visited by *P. viridans* (*Solidago* spp., *Eupatorium* spp.) in our landscapes. We selected these plants to increase the likelihood of marking pollinators that *P. viridans* actively hunts. In the central patch of each block, we enriched an 80 m × 80 m area surrounding the centre of the patch. Plants were sprayed with a solution of 0.125 g $L^{-1}$ $^{15}$N-urea (98.9 atom%; Sigma-Aldrich, St. Louis, MO, USA), water and one drop of Tween20 (Sigma-Aldrich, St. Louis, MO, USA) that reduced surface tension and improved contact to plant tissue (Carlo *et al.* 2009). We sprayed inflorescences using a handheld pump sprayer with a fine mist nozzle. Each plant received enough solution (~13 mL) to saturate all petals. To limit airborne drift, we sprayed plants on days with no wind or prior precipitation, completed spray treatments prior to 10:00 AM and sprayed at a downward-facing angle. We applied the spray treatments four times during the summer, ending in July.

We tested for the presence of $^{15}$N in *P. viridans* samples in 2011 and 2013 (before and after application of $^{15}$N) by drying them to constant mass, separately homogenising individuals with a Wig-L-Bug grinder (Dentsply, Elgin, IL, USA), weighing them to approximately 1 mg and wrapping them in tin capsules (5 mm × 9 mm, CE Elantech, Lakewood, NJ, USA) for mass spectrometry. All samples were analysed for $^{15}$N atom% using an elemental analyser (Costech ECS 4010 CHNSO Analyzer, Coatech Analytical Technologies, CA, USA) connected to a Thermo Scientific ConFlo IV Universal interface (Thermo Fisher Scientific, MA, USA), which served as an inlet to the flow isotope ratio mass spectrometer (Thermo Delta V Advantage; Thermo Fisher). Analyses were performed at the Laboratory for Isotopes and Metals in the Environment at Pennsylvania State University (State College, PA, USA). All stable isotope values are reported in the δ notation, $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$, where R is $^{15}N/^{14}N$. A net increase in $\delta^{15}$N would indicate the relative contribution of immigrant prey to *P. viridans* diet or the movement of *P. viridans* from the central patch to peripheral patches.

### Body condition

To test the effects of habitat fragmentation on body condition, we measured body size, dry mass, lipid content and carbon nitrogen ratio of *P. viridans*. We measured body size as cephalothorax width (Jakob *et al.* 1996) to the nearest 0.01 mm using a DinoCapture 2.0 digital microscope (Version 1.3.8, Dino Lite Microscopes; Naarden, The Netherlands). We measured the dry mass of spiders to the nearest 0.01 mg after drying samples for at least 48 h at 40°C. We estimated body condition using the Residual Index, a metric found to most accurately control for variation across body size in spiders (Jakob *et al.* 1996). We first regressed log-transformed body mass against log-transformed body size: ln(body mass)~ln(body size). The estimate for condition was the residual distances of individual points from the regression line. The points above the regression line indicated good condition (positive values), while the ones below the regression line indicated poor condition (negative values).

To test the effects of corridors on carbon-to-nitrogen (C : N) ratio, we measured the total carbon and total nitrogen of *P. viridans*. Carbon and nitrogen are key elements that can indicate resource allocation and shifts in their proportions has consequences for ecosystem functioning (Denno & Fagan 2003; Hawlena *et al.* 2012). Denno and Fagan (2003) found that predators are nitrogen limited, therefore decreased C : N ratio relates to better body condition. We weighed 1 mg of dry, homogenised *P. viridans* samples and analysed their elements using a mass spectrometer (Thermo Delta V Advantage; Thermo Fisher). Analyses were performed at the Laboratory for Isotopes and Metals in the Environment at Pennsylvania State University (State College, PA, USA).

To test corridor effects on lipid content, we measured lipid content gravimetrically using chloroform extraction (Wilder *et al.* 2010). Lipids are directly extracted from prey through metabolic pathways and are therefore a more accurate measure of consumption than allometry, another commonly used metric for body condition in spiders (Raubenheimer *et al.* 2007). Allometry represents investment to growth, leaving the investments in maintenance and reproduction unknown (Stearns 1989). Lipids, however, represent the amount of resources available for allocation (Post & Parkinson 2001). Lipids are a key nutrient used to build energy reserves to survive periods of food limitation and to invest in reproduction (Jensen *et al.* 2010; Wilder 2011).

After drying individuals but before processing for $^{15}$N extraction, we soaked each sample in 2 mL of chloroform for 24 h and repeated the extraction again with fresh chloroform. We then dried and reweighed samples to calculate the proportional difference in mass before and after lipids had been extracted using the following equation: $1 - (M_{AFTER}/M_{BEFORE}) \times 100$. We used logarithmic transformation on the percent lipid content to fit a normal distribution.

### Statistical analyses

To test the effects of corridors on consumption of immigrating prey, we calculated mean $\delta^{15}$N per patch of spiders collected before the spray treatment and spiders collected after the spray treatment. There is natural variation in the amount of $\delta^{15}$N caused by variation in diets of herbivores and consumers. To control for this, we compared the difference of $\delta^{15}$N *P. viridans* collected in 2013 to *P. viridans* collected in 2011. We then analysed the change in $\delta^{15}$N by patch type (connected and high-edge) with a generalised linear mixed-effects model, including block as a random effect. We found that the number of spiders per patch varied greatly, and to reduce heteroscedasticity, we weighted each patch mean $\delta^{15}$N so that patches with small numbers of spiders per patch did not disproportionally skew results. Patch weights were computed as one divided by the number of *P. viridans* found in each patch (Zar 1996).

To determine the effects of connectivity on *P. viridans* abundance and body condition, we used linear mixed-effects models, with block as a random effect and patch type (central, connected, and high-edge) as a fixed effect (package lme4, Bates *et al.* 2015). As our experimental unit is the patch, we analysed each metric per patch. Body size and $^{15}$N content have been shown to be positively correlated (France *et al.* 1998), thus we compared body size and $^{15}$N content per patch in spiders collected in 2013.

To test the effect of patch type on hymenopteran prey abundance, we used generalised linear mixed-effects models with negative binomial distribution (package glmmADMB, Skaug *et al.* 2015, Accessed 4 Jan, 2018) and number of nests produced in the trapnests as the response variable. We included block identity as a random effect and patch type (central, connected and high-edge patches) as a fixed effect. $\chi^2$ value and significance were estimated using the package afex (Singmann *et al.* 2015). We then conducted Tukey–Kramer contrasts (package lsmeans, Lenth 2016) to determine the effect of each patch type in our model. All analyses were performed in R (R Core Team, 2013).

## RESULTS

### $^{15}$N tracer

We analysed 342 female *P. viridans* collected from 15 connected and high-edge patches, including 137 females in 2011 before $\delta^{15}$N addition and 205 spiders in 2013 after $^{15}$N addition. *P. viridans* $\delta^{15}$N concentration was affected by patch type ($F_{1,13} = 10.82$; $P < 0.01$; Fig. 2) as, relative to pre-application levels, corridors increased *P. viridans* $\delta^{15}$N by 40%.

### Abundance

We collected a total of 258 green lynx spiders from 26 centre, connected and high-edge patches. The number found per patch ranged from 0 to 51, with an average of 11.09 per patch (SE = 2.03). There was no effect of connectivity on *P. viridans* abundance ($F_{2,24} = 0.95$, $P = 0.40$).

The most common prey items collected in the bamboo trapnests included mud wasps, ichneumonid wasps and leaf-cutter bees. Hymenopterans constructed 163 nests totally across all habitat patches. Patch type (centre, connected and high edge) did not have a significant effect on hymenopteran abundance

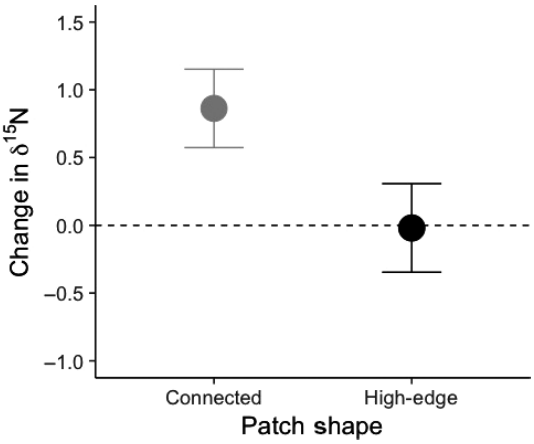

**Figure 2** The change in $\delta^{15}$N between 2011 and 2013 by patch type. Spiders in connected patches had significantly higher $\delta^{15}$N than those in unconnected, high-edge patches.

($\chi^2 = 2.87$, $P = 0.24$), and Tukey–Kramer contrasts did not reveal significant differences between patch types.

### Body condition

Patch type had no significant effect on *P. viridans* body size ($F_{2,19} = 1.38$, $P = 0.28$; Fig 3a). There was no correlation between body size and $^{15}$N content ($t_{20} = 1.71$, $P = 0.09$). Patch type had no significant effect on mass ($F_{2,20} < 0.01$, $P = 0.99$), or the body size residual index ($F_{2,19} = 0.08$, $P = 0.92$) of *P. viridans*. Patch type had a significant effect on C : N ratio $F_{2,22} = 4.0$; $P = 0.03$) where *P. viridans* in connected patches had a lower C : N carbon-to-nitrogen ratio than spiders in high-edge patches ($t_{14} = -2.69$: $P = 0.04$; Fig. 3b), but were not significantly different from those in centre patches ($t_{14} = -2.14$; $P$ = -0.11). Patch type also had a significant effect on lipid content ($F_{2,20} = 10.29$, $P < 0.001$), as *P. viridans* in centre patches had significantly higher lipid content than in high-edge patches ($t_{19} = 4.36$, $P < 0.001$; Fig 3c) and connected patches ($t_{19} = 3.33$, $P < 0.01$). Lipid content did not statistically differ between high-edge patches and connected patches ($t_{19} = 1.17$, $P = 0.48$).

## DISCUSSION

We show that corridors increase $^{15}$N movement between patches and thus increase trophic subsidies. We believe that $^{15}$N enrichment is caused by prey movement that subsidise *P. viridans* diet because: (1) we have previously shown that corridors increase movement of pollinators and other insects (Haddad *et al.* 2011), groups that are important prey sources for *P. viridans* (Turner 1979; Nyffeler et al. 1987); and 2) spiders disperse primarily after emerging, before they have consumed pollinators (Arango *et al.* 2000). Taken together, these factors support our conclusion that corridors increase trophic subsidies.

One effect of connectivity on spiders likely mediated by trophic subsidies is increases in a measure of body condition. The carbon-to-nitrogen ratio of *P. viridans* was lower in connected patches than high-edge, isolated peripheral patches, indicating higher levels of nitrogen, a limiting nutrient (Denno & Fagan 2003), due to higher prey quantity and/or quality (Mayntz *et al.* 2003; Toft *et al.* 2010). Lower carbon-to-nitrogen ratio was likely caused by corridors increasing prey quality (Cruz-Rivera & Hay 2000). In a study which used models to parse out the effects of prey quality from prey quantity on predator nutrient content, Sterner (1997) found that food quality can overcome limitations in food quantity. In our study, connectivity may increase prey quality by allowing foraging pollinators access to both greater amounts of floral resources, as well as a higher diversity of floral resources (Tewksbury *et al.* 2002). Connected patches have higher plant species richness than unconnected patches (Damschen *et al.* 2006), which could increase prey insect diversity and abundance (Haddad *et al.* 2009), and prey nutrition (Donkersley *et al.* 2017).

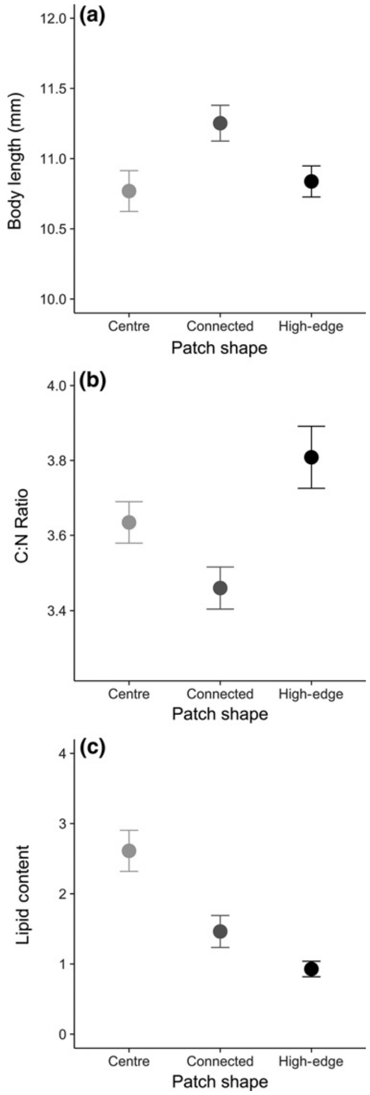

**Figure 3** The effect of connectivity on *P. viridans* body condition. (a) Body size did not differ significantly by patch shape. (b) Spiders in connected patches had significantly lower C : N ratios than those in unconnected, high-edge patches. (c) *P. viridans* in centre patches had significantly higher lipid content than those in both connected and unconnected, high-edge patches.

Higher prey movement to connected patches did not translate to increased abundance in the small set of prey species we measured nor in abundance of predators, as are traditional measures of trophic subsidies (Polis *et al.* 1997). Yet, we have previously shown that corridors increase abundances of some arthropods (i.e. Haddad & Baum 1999; Resasco *et al.* 2014), indicating that corridors may affect abundances of other prey. Future research of the prey communities' nutrition in fragmented systems is needed. Taken together, our results suggest that predators were obtaining most of their diet from the local prey population and were supplementing it with prey moving from the central patch. Our mass marking by stable isotopes is sensitive enough to permit an integrated assessment of prey movement.

Despite our findings of differences in movement and body condition, trophic subsidies in our system are likely not unidirectional (Nakano & Murakami 2001), and arthropod movement likely also occurs from the peripheral patches to the centre. Interestingly, *P. viridans* in centre patches had significantly higher lipid content than in either connected or high-edge, unconnected patches. One explanation for these differences may be that centre patches have the closest proximity to all four peripheral patches, and thus have the highest probability of receiving dispersing pollinators from any given patch (Braaker *et al.* 2014). As a result, spiders in centre patches may have different life-history responses to their respective habitats (Mayntz *et al.* 2003), leading to higher lipid content due to increased prey availability. Furthermore, pollinators dispersed into the centre patch are most likely to continue dispersing along the corridor (Tewksbury *et al.* 2002), thereby increasing prey influx into the connected patch.

We did not test whether the enrichment of $^{15}$N is caused by the movement of prey or the predators themselves, but we suspect that *P. viridans* in the peripheral patches acquired the signal through consumption of pollinators that consumed nectar and gathered pollen in the centre patches. While the consumption of pollen and nectar by *P. viridans* does occur (Taylor & Pfannenstiel 2008), it would not have affected our observed responses. Juvenile *P. viridans* could have consumed these plant materials in central patches, but they balloon in the winter, approximately 2 weeks after emerging from their egg sacs (Whitcomb *et al.* 1966). As we only analysed adults, these spiders would have ballooned at least 6 months prior to when our spray treatment in central patches began. This timing mismatch between the primary *P. viridans* dispersal and spray treatment leads us to conclude that enrichment in peripheral patches was caused by movement of arthropod prey from the sprayed area.

Our findings of spatial subsidies in food webs are relevant to basic ecology and applied conservation. Most knowledge of food web subsidies is in the context of cross-boundary subsidies of aquatic to terrestrial habitats or at habitat edges, where high variation in habitat productivity drives the movement of resource quantity or quality to impact consumer populations (Polis *et al.* 2004; Marcarelli *et al.* 2011). Furthermore, models of fragmentation effects on predator abundances are often built in the context where patch size is much smaller and patch isolation is much larger in relation to predators with large home ranges (Holt *et al.* 1999). In our study, we show that even in identical habitats, linking fragmented landscapes creates trophic subsidies that can shift predator body condition. Although we did not find an effect of subsidies on *P. viridans* abundance in our model system, the mechanisms we identified would be expected to produce stronger population responses in larger and more fragmented landscapes. There, supplemented diet and balanced nutrition can enable predators to be more robust to environmental or stochastic changes, thus increasing their likelihood of persistence (Bommarco 1998; Raubenheimer *et al.* 2009). In fragmented landscapes, predators can also change the dynamics of metapopulations and the persistence of prey through both consumptive and non-consumptive effects (Leibold *et al.* 2004; Orrock *et al.* 2008). Corridor effects on increasing prey movement and predator body condition has the potential to cascade through food webs and shape entire communities in fragmented landscapes (Schmitz *et al.* 1997; Estes *et al.* 2011).

Our connectivity treatment is meant to model landscape corridors that are used in conservation. The targets of large-scale conservation are often large predators with large home ranges living in small fragments with depleted resources (Crooks *et al.* 2011; Ripple *et al.* 2014). The results of our model system indicate that in these larger, real-world conservation scenarios, the beneficial effects of connectivity on trophic subsidies could possibly increase predator persistence. Conversely, if the conservation target is a prey species, our finding that corridors increase subsidies for predators indicate that the creation of corridors could be counterproductive under some circumstances (Simberloff *et al.* 1992; Hawlena and Schmitz 2010).

Our study shows that corridors increase prey movement and may improve patch quality for predatory spiders. It suggests that predators, which are sensitive to habitat fragmentation because of prey depletion, could benefit from increased movement of prey. Many studies have shown direct links between trophic subsidies and improved physiology and prey availability to benefit predators (Weaver *et al.* 1996; Gannes *et al.* 1998; Kreiter & Wise 2001; Schmidt *et al.* 2012). We show that the effects of corridors can extend to a broad meta-community, as corridors do not simply increase the movement of individuals, but connect food webs in fragmented landscapes. Corridors transform isolated patches into a single community linked by movement and consumption.

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## AUTHORSHIP

CH and NH designed the study, SG and JH conducted the prey abundance study, JH applied the stable isotopes tracer and CH collected the data. CH wrote the first draft of the manuscript, and all authors contributed to revisions.

## DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.27v6086

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## SUPPORTING INFORMATION

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