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Increasing woody cover facilitates competitive exclusion of a savanna specialist

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ABSTRACT

Anthropogenically modified systems tend to have homogenous wildlife communities. While this process is well documented, the mechanisms driving the convergence of species in human-modified systems are unclear. There are at least two compelling ecological explanations for the loss of specialized species in these settings; changes to the distribution and quality of resources (i.e. environmental conditions) and changes to competitive interactions. Without a better understanding of the mechanisms behind biotic homogenization, it is difficult to take appropriate conservation and management actions to maintain diverse communities.

We investigated the roles of environmental conditions and competition in driving biotic homogenization in one of the world's most imperiled ecosystems; the longleaf pine (*Pinus palustris*) savanna of the American Southeast. Specifically, we investigated how generalist gray squirrels (*Sciurus carolinensis*) are replacing the more specialized fox squirrels (*S. niger*) in shrub and hardwood encroached Southeastern savannas. To test how changes to habitat and competition affect the specialist fox squirrel, we undertook a landscape scale manipulation. We experimentally manipulated competition by removing gray squirrels from closed-canopy patches embedded in longleaf pine savanna.

Fox squirrels showed a strong response to gray squirrel removal, increasing their activity by 300% in the interior of closed-canopy patches. Fox squirrels in control patches did not use the interior of closed-canopy patches.

Our experimental results support the hypothesis that biotic homogenization occurs when human-induced changes to the environment alter competitive interactions.

1. Introduction

Humans are reshaping landscapes and animal communities across the globe (Vitousek et al., 1997; Dirzo et al., 2014; Lewis and Maslin, 2015). Specifically, biotic homogenization, the replacement of unique assemblages of species by a common suite of “cosmopolitan” species is a growing threat to the planet's biodiversity (McKinney and Lockwood, 1999). Homogenization is occurring in urban, freshwater, woodland, old growth, and savanna ecosystems (McKinney and Lockwood, 1999; Sirami and Monadjem, 2012; Buisson et al., 2013; McCleery et al., 2018). While this pattern of human-driven global change is well documented, the mechanisms that shape this process are often overlooked or unclear

(Lambin et al., 2003; Olden and Poff, 2003; Fischer and Lindenmayer, 2007). There are multiple ecological explanations for how species replace one another, including changes to the quality and availability of resources and changes to competitive interactions (Connell, 1961; Connell, 1983). Primarily, authors cite habitat degradation and shifts in resource availability as driving the decline of specialist species (Means, 2007; Ibarra and Martin, 2015). Additionally, human activities may alter the environment in a manner that allows a limited suite of generalists to out-compete more specialized species (Clavel et al., 2010; Ciuti et al., 2012).

One system that has experienced rapid physical change and species homogenization is the savanna biome. Human driven changes to grassy

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biomes appear to favor generalist species and lead to biotic homogenization on multiple scales (Brudvig and Asbjornsen, 2009; Li and Waller, 2015; Sirami and Monadjem, 2012; Vander Yacht et al., 2017; McCleery et al., 2018). The increase of woody cover due to changes in farming, grazing, and fire frequency alters vertebrate species composition as savannas become forests (Blaum et al., 2007; Bond and Parr, 2010; Stanton et al., 2018). Invading woody species decrease available light, alter available surface water, change soil chemistry, and reduce food availability for some species (Archer et al., 2001; Eldridge et al., 2011; Archer et al., 2017). However, increasing shrub cover and canopy closure can also change how species perceive predation risk and other species interactions (Blaum et al., 2007; Wheeler and Hik, 2014; Sovie et al., 2019). Savanna biomes, like those of the Southeastern Coastal Plain, are among the ecosystems most altered by human behavior (Parr et al., 2014). In the Southeastern United States, the remaining fragments of longleaf pine savanna are undergoing structural change due to human driven changes in fire frequency. Without frequent (3–5 year) burns, the longleaf pine ecosystem changes as hardwood trees close the canopy and shrub species invade the grassy understory (Gilliam and Platt, 1999). Without a mechanistic understanding of how hardwood encroachment leads to biotic homogenization in savannas it is difficult to take appropriate conservation action to maintain the unique ecology of these systems (Goodrich and Buskirk, 1995; Linnell and Strand, 2000; Means, 2007).

Elucidating the relative importance of environmental changes that decrease or degrade resources versus changes that alter competitive interactions, is important for biological conservation and management. However, there is a lack of experimental evidence isolating these factors (Hardin, 1960; Hubbell, 2005). Competing eastern fox (*Sciurus niger*) and gray (*S. carolinensis*) squirrels provide a model system to evaluate potential mechanisms leading to biotic homogenization. Squirrels can be bio-indicators of forest health, are ecologically important seed dispersers/predators, and provide a prey base for other species (Weigl et al., 1989; Steele et al., 2005; Greene and McCleery, 2017). Further, squirrels respond to their environment at meaningful scales for management and are relatively easy to observe and manipulate given their ubiquity and diurnal behavior (Steele and Koprowski, 2001; Sovie et al., 2019).

Gray squirrels are a highly adaptable species, inhabiting deciduous woods, pine uplands, anthropogenically modified, and urbanized areas (Steele and Koprowski, 2001; Parker and Nilon, 2008; Benson, 2013). Fox squirrels inhabit savannas, margins of deciduous forests, farmland and urbanized areas (Steele and Koprowski, 2001). In western North America, both species have expanded their range through human introductions (Benson, 2013; Claytor et al., 2015). A recent survey found gray squirrels followed by fox squirrels as the two most common species found on North American college and university campuses (Peplinski and Brown, 2020). Despite being widespread elsewhere in North America, fox squirrels exhibit specialized habitat needs in pine forests along the Atlantic coast of the United States, and in longleaf pine forests of the southeastern United States (Loeb and Moncrief, 1993). All three subspecies of conservation concern – Delmarva fox squirrel (*S. n. cinereus*), big cypress or mangrove fox squirrel (*S. n. avicennia*), and Sherman's fox squirrel (*S. n. shermani*) – occur in pine or cypress (*Taxodium* spp.) savannas. Relative to gray squirrels, fox squirrels favor open canopy forests that mimic historic savannas (Greene and McCleery, 2017) resulting in a more restricted distribution, particularly as savannas are lost to human development or become closed-canopy forests (Steele and Koprowski, 2001).

Historically, the coastal plains of the Southeast offered extensive savannas including longleaf pine. Closed-canopy forest stands were common but patchily distributed (Hiers et al., 2014), allowing for both squirrel species to persist on the landscape. Urbanization, fire suppression and hardwood encroachment have closed the canopies of the forests that fox squirrels typically inhabit (Kantola and Humphrey, 1990). Eastern gray squirrels have proliferated in these closed-canopy forests

(Allen, 1982; Brown and Batzli, 1984). However, it is unclear if closed canopies no longer contain resources fox squirrels select for or simply create a competitive advantage for gray squirrels.

Are closed-canopy forests part of, or absent from, the fox squirrel's fundamental niche? We hypothesized that closed-canopy forests offer fox squirrels sufficient forage and refuge (Conner and Godbois, 2003; Perkins et al., 2008) and negative interactions with gray squirrels have restricted the realized niche of fox squirrels to more open habitats (Sexton, 1990; Vander Merwe et al., 2005). To test for the relative importance of resources, versus competition, in fox squirrel activity, we experimentally removed gray squirrels in areas where they co-occur with fox squirrels. If competition is the driving force behind fox squirrel activity, fox squirrels should colonize closed forest patches devoid of gray squirrels. Alternatively, if environmental resources determine fox squirrel activity then removal of gray squirrels should not be followed by fox squirrel incursion or colonization (Fig. 1).

2. Methods

2.1. Study species

Fox and gray squirrels share a broad distribution throughout the eastern United States and feed on mast crops, fungi, buds and lichens (Korschgen, 1981; Edwards et al., 1989; Edwards et al., 1998; Steele and Koprowski, 2001). Fox and gray squirrels appear to utilize a variety of strategies to minimize competition including spatial and temporal partitioning (Conner et al., 1999; Sovie et al., 2019). Eastern fox squirrels are large (500–1000 g) and generally found in areas with open or broken canopy (Steele and Koprowski, 2001). Fox squirrels often move and forage on the ground (Weigl et al., 1989) and their size may be an adaptation to open forests (Moore, 1957). In contrast, Eastern gray squirrels (400–600 g) are a small squirrel found in areas with continuous canopy cover (Shepherd and Swihart, 1995; Nupp and Swihart, 2000; Zollner, 2000; Steele and Koprowski, 2001). Gray squirrels are more vulnerable to avian predators than fox squirrels and avoid foraging in open areas (Dill and Houtman, 1987). Gray squirrels are also more gregarious than fox squirrels, tolerating overlap – especially with related individuals (Steele and Koprowski, 2001). Further, gray squirrels are superior foragers compared to fox squirrels (Brown and Batzli, 1985) and act more aggressively towards other squirrel species in their home range (Wauters and Gurnell, 1999).

2.2. Study area

We monitored gray and fox squirrel populations in and around closed-canopy patches at The Jones Center at Ichauway in Newton, GA (Fig. 2). The Jones Center at Ichauway is a 12,000 ha property managed for conservation and scientific research. At the time of our study, Ichauway was comprised of a range of ecological communities including longleaf (*Pinus palustris*), slash (*P. elliotii*), and loblolly pine (*P. taeda*) savannas as well as mixed pine hardwoods, riparian hardwood forests, wetlands, and shrub-scrub uplands. Over 7000 ha of the property was open canopy upland pine-grassland vegetation comprised of second-growth longleaf, managed with frequent prescribed fire and silviculture. Closed-canopy hardwood patches were less common on the property occurring in alluvial soils adjacent to riparian zones. The closed-canopy patches included a diverse array of oak species: bluejack (*Quercus incana*), red (*Q. falcate*), turkey (*Q. laevis*), post (*Q. stellate*), Southern live (*Q. virginiana*), and laurel (*Q. hemisphaerica*) (Jacqmain et al., 1999; Loudermilk et al., 2013).

2.3. Study design

From April 2017–January 2018, we conducted a case-controlled before-after removal experiment. First, we randomly selected twelve 1.3–4.0 ha closed-canopy patches in the northern most portion of the

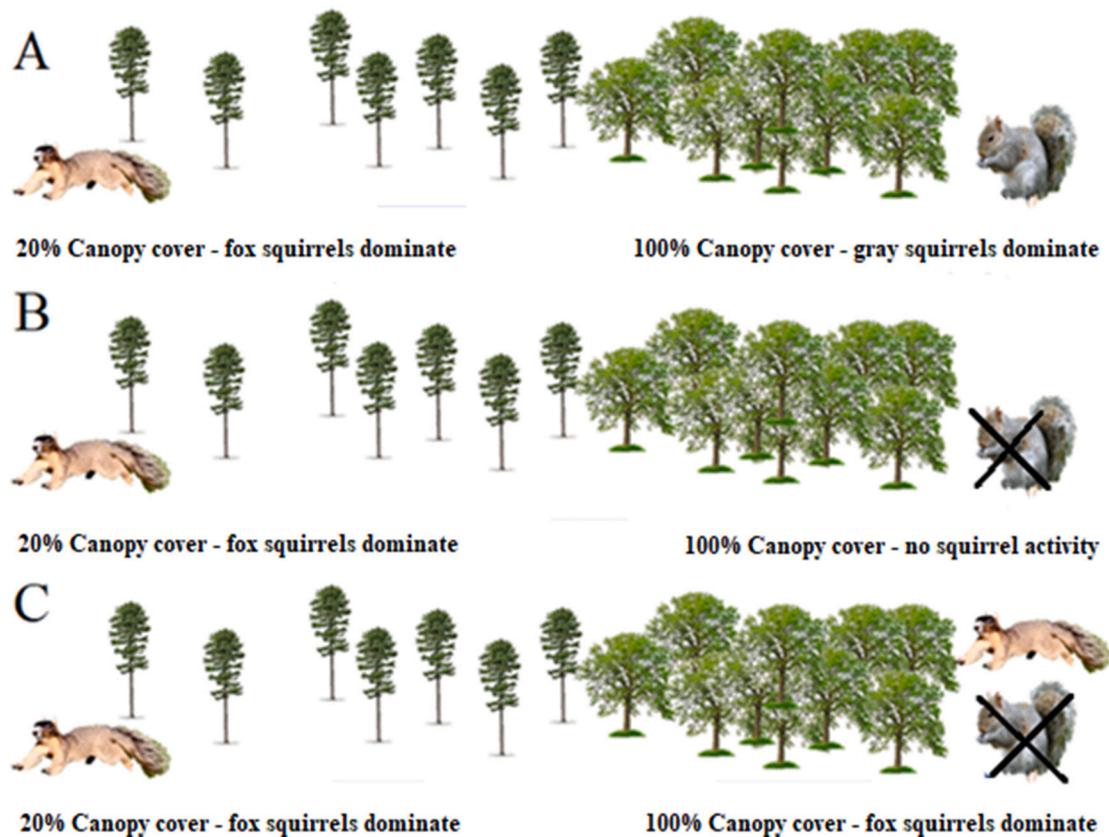


Fig. 1. Schematic of hypothesized fox squirrel responses to gray squirrel removal. A) Current system - gray squirrels are found in closed-canopy (~100%) oak patches and fox squirrels in open canopy (~20%) pine savanna. B) Hypothesized response of fox squirrels to gray squirrel removal if closed-canopy hardwoods are not part of their fundamental niche. C) Hypothesized response of fox squirrels to gray squirrel removal if closed-canopy hardwoods are part of their fundamental but not realized niche.

Jones Center property (Fig. 2). We monitored squirrel activity in (10 m into the patch) and around (10 m into the savanna) patches using trail cameras (Bushnell HD Trophy Cam, Overland Park, KS, USA) for two weeks (O'Connell et al., 2010). We installed each camera 50 cm above the ground and angled it towards a bait pile of pecans and cracked corn which we refreshed every four days (Greene et al., 2016). We programmed cameras to take three photos every time the camera was tripped using the camera's normal sensitivity setting with a latency of 3 min between bursts. During this survey (April 1–April 30), we prioritized detecting squirrels (i.e. setting cameras near trees) and did not randomly place cameras in the patches. We discarded patches that had only one species present or low overall activity (<5 observations of both species during the monitoring period), leaving us with seven experimental patches.

To increase trapping and monitoring efficiency, we assigned the seven experimental patches to three groups based on habitat type and size: Group 1 = two large oak patches (2–4 ha), Group 2 = three small oak patches (<2 ha), and Group 3 = two mixed oak and cypress patches (2–4 ha). We randomly selected one patch in each group to act as a control. We carried out treatments and monitored fox squirrel activity in patches within a group simultaneously.

2.4. Squirrel activity

Within each patch we monitored fox and gray squirrel activity for a minimum of fourteen days prior to and post treatment. To monitor squirrel activity, we established four camera trapping transects in each patch. We randomly selected four points along the patch edge to center a perpendicular transect of three cameras each 10 m apart. We placed a camera 10 m into the savanna (savanna), one at the transition from

savanna to closed-canopy patch (edge), and one 10 m into the closed-canopy patch (interior). To increase independence, we made sure transects were at least 25 m apart.

2.5. Seasonality

Seasonality may affect how fox squirrels use closed-canopy patches as the distribution of resources changes throughout the year. To test for this possibility, we compared fox squirrel activity in the savanna, edge, and interior of control patches across seasons. We utilized the seasonal definitions of Perkins and Conner (2004). We defined March through June as the “early growing season” when squirrels are foraging on new plant growth and tree buds. We defined July through October as the “longleaf pinecone” season when pine seeds become available and squirrels may move into the savannah to forage for cones (Weigl et al., 1989; Loeb and Moncrief, 1993). Finally, we defined November through February as the “hard mast season”, a period of oak mast availability when fox squirrels may be more likely to use closed-canopy patches.

2.6. Gray squirrel removal

We captured gray squirrels from treatment patches using wooden box traps, handmade to the specifications of Baumgartner (1940). Each treatment consisted of saturating the experimental patch with 20–25 box traps for a minimum of five days, and until we failed to capture any gray squirrels for three consecutive days. We focused our trapping effort in the interior of patches and 10 m into the savanna. After the initial intensive trapping session, we maintained a small trap line (5–10 traps) within each treatment patch to remove any re-colonizing gray squirrels. If we identified gray squirrels during camera surveys, we targeted those

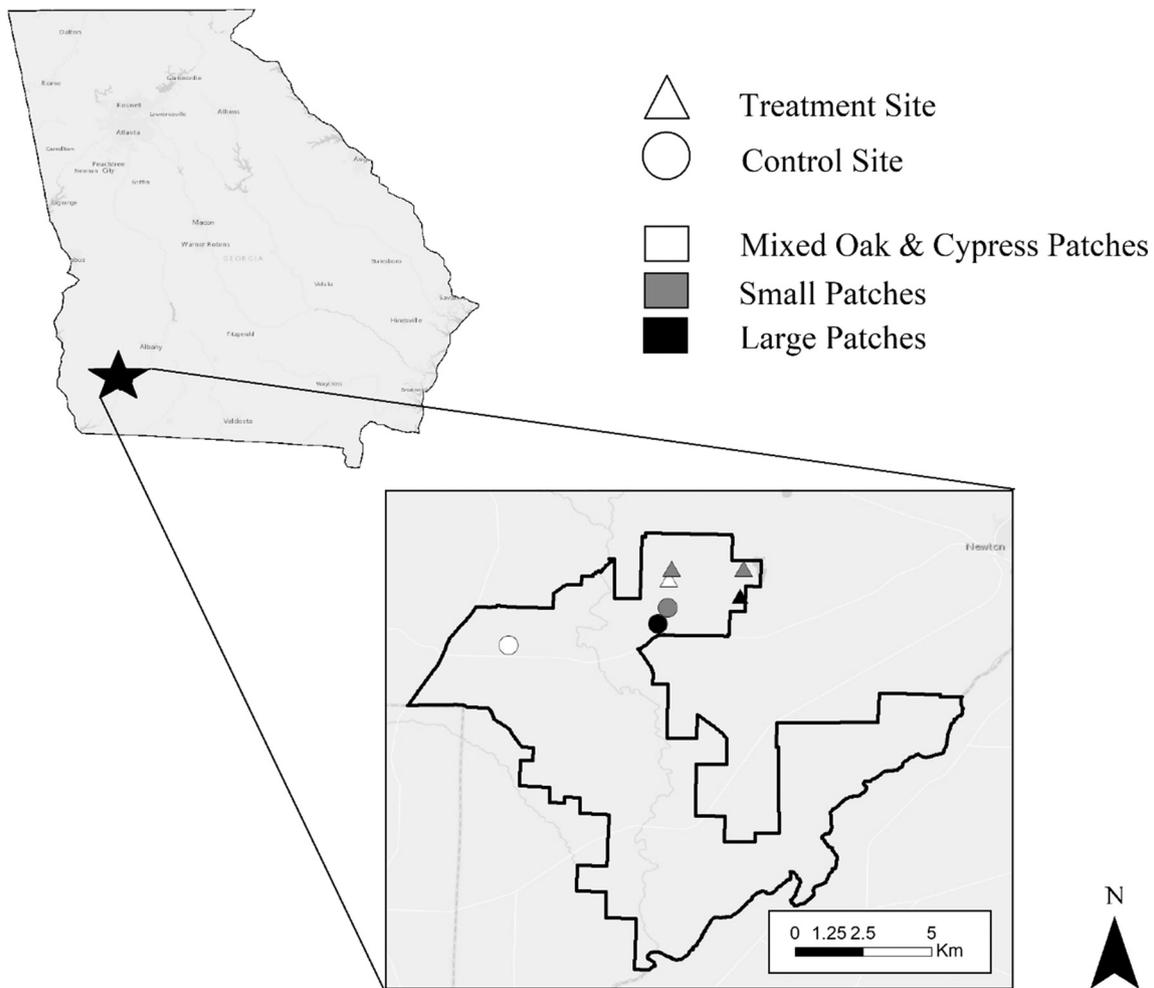


Fig. 2. Location of The Jones Center at Ichauway, Georgia, United States, and locations of closed-canopy study sites (inset).

individuals for removal. We placed traps at the base of trees and situated the trap such that it would be shaded by the tree at noon. We pre-baited traps for a week before opening, and rebaited weekly with pecans and cracked corn. To ensure that we did not bias our results by baiting the interior of experimental units we placed an equivalent amount of pecans and cracked corn at control sites. We opened traps at dawn and closed them just before dusk. We did not trap on days when temperatures dropped below 0 °C or rose above 37 °C. We immediately released all by-catch at the site of capture. We did not handle captured fox squirrels in order to reduce stress and/or fear of the patch. We released gray squirrels ≥ 10 km from the site of capture (Hungerford and Wilder, 1941) on the Jones Center property. Prior to release, we restrained gray squirrels using a handling cone (Koprowski, 2002) and took basic measurements including sex, age, reproductive status, mass (g), hind foot length (mm), and fitted each squirrel with a metal ear tag (#44 National Band and Tag Co). We followed the American Society of Mammologists guidelines (Sikes et al., 2016) for trapping and handling mammals. The University of Florida Institutional Animal Care and Use Committee (IACUC) approved our study (Protocol #: 201709855). We conducted trapping efforts within each group of patches simultaneously.

2.7. Timeline

Starting with Group 1 (large patches) on May 1, 2017, we monitored squirrel activity for three 5–10-day sessions and then experimentally removed gray squirrels starting June 12. We then conducted four 5–10-day post removal camera trapping sessions until October 15. We started

pre-removal monitoring of Group 2 (small patches) on July 4 for two 7–10-day sessions and began removing gray squirrels July 20th. We conducted three 7–10-day post removal camera trapping sessions until January 12. We started pre-removal monitoring of Group 3 (mixed oak and cypress) on September 10 for 14 days and began removing gray squirrels on September 26th. We conducted three 7–10-day post removal camera trapping sessions until December 9. We did not monitor fox squirrel activity during the intensive gray squirrel removal treatment and we returned to monitor activity a minimum of ten days post gray squirrel removal.

2.8. Data analysis

We conducted all statistical analyses in R version 3.3.3 (R Core Development Team, 2020). To determine if competition influences fox squirrel habitat use, we compared activity levels before and after the gray squirrel removal. We tabulated the number of independent squirrel observations, (photographs a minimum of 20 min apart; Greene et al., 2016) at each camera per 24-h period. For each camera, and 24-h period, we converted fox squirrel camera trap data into an activity index [(# obs) / 24-h period]. Daily repeated measures from the same camera may not be independent and can potentially bias statistical results (Bakdash and Marusich, 2017). Thus, we tested for non-independence between activity indices taken from the same camera using the ACF function. Also, due to the spatial distribution of camera traps, statistical tests between cameras in the same transect and patch may be biased due to autocorrelations in the data (Koenig, 1999). To test

for spatial autocorrelation, we fit a spline correlogram using the function `spline.correlog()` in package `ncf` and considered values <0.2 lacking autocorrelation (McMurry and Politis, 2010, Bjornstad, 2009). A spline correlogram estimates spatial dependence as a continuous function of distance. We found no indication of spatial autocorrelation between activity measures taken from a camera on different days or among cameras within transects. Thus, within a patch, we pooled cameras in the interior together, cameras at the edge together, and cameras in the savanna together.

To model how fox squirrel activity responded to gray squirrel removal, we fit a zero inflated negative binomial (ZIBIN) model using the `zeroinfl()` function in package `pscl` (Jackman, 2017). We used a ZIBIN because of the large number of zeros in our data (~30% of observations) (Cheung, 2002). Zero-inflated count models are two-component mixture models. There are two sources of zeros: zeros may come from a binomial process with each value having a probability P_0 that the value is zero. There is also a probability $(1-P_0)$ that a zero comes from a negative-binomial process where the observation may take any integer greater than or equal to zero (Yau et al., 2003). Our model included the additive and interactive effect of treatment (removal, control), camera location (savanna, edge, interior), and time (pre/post removal) to explain fox squirrel activity.

3. Results

We removed 55 gray squirrels from 12 June–30 November 2017. Prior to removal, the majority of gray squirrel observations occurred in the interior of patches (Sup 1). We removed 6–16 squirrels from each treatment site and successfully reduced gray squirrel activity by 75% (Sup 1). We did not capture or photograph any gray squirrels with ear tags or clipped ears, indicating squirrels did not return to patches of origin. However, gray squirrels did recolonize sites at a rate of approximate 1–2 squirrels a week; we targeted and removed these individuals.

We documented 168 independent fox squirrel observations during our monitoring. We did not detect seasonal changes in fox squirrel use of untreated closed-canopy patches (Sup 1). Our model indicated that treatment and location along the savanna to closed-canopy gradient affected fox squirrel activity (Table 2). Fox squirrels increased their activity at the edge and interior of closed-canopy patches when gray squirrels were removed (Fig. 3). The largest change in total activity occurred within the interior of closed-canopy patches, with fox squirrel activity increasing by 300% (Fig. 3, Table 1). After treatment, cameras

Table 1

Point estimates of fox squirrel (*Sciurus niger*) activity (observations/day) along a savanna to closed-canopy gradient before and after experimental gray squirrel (*Sciurus carolinensis*) removal in control and removal sites at the Jones Center at Ichauway in Newton, GA.

	Estimate	Upper	Lower
Savanna _{pre-control}	0.024	0.012	0.036
Savanna _{post-control}	0.027	0.015	0.048
Savanna _{pre-removal}	0.095	0.07	0.13
Savanna _{post-removal}	0.061	0.04	0.07
Edge _{pre-control}	0.006	0.001	0.01
Edge _{post-control}	0.008	0	0.013
Edge _{pre-removal}	0.028	0.019	0.038
Edge _{post-removal}	0.04	0.029	0.046
Oak _{pre-control}	0.002	0	0.003
Oak _{post-control}	0.0001	0	0.0001
Oak _{pre-removal}	0.008	0.004	0.015
Oak _{post-removal}	0.025	0.016	0.32

in the savanna experienced a 65% decline in fox squirrel activity, however the CI's around the point estimates overlapped, suggesting only a weak relationship (Table 1). Post treatment, cameras at the edge experienced a 43% increase in activity, however the CI's around the point estimates overlapped, again suggesting a weak relationship. In control closed-canopy patches fox squirrel activity did not change (Table 1).

Table 2

Model results for fox squirrel activity (observations/day) in control and gray squirrel removal sites, pre- and post-removal along a longleaf pine to oak hammock gradient at the Jones Center at Ichauway, Newton, GA.

Variable	Estimate	Std. error	z value	Pr(> z)
Intercept ^a	4.5421	1.3141	3.456	0.0005
Removal	-6.3175	1.3344	-4.734	0.0000
Pre	-4.8466	2.5255	-1.919	0.0549
Location	-4.6719	0.7853	-5.949	0.0000
Removal:Pre	7.6521	2.7577	2.775	0.0000
Removal:Location	4.5792	0.9036	5.068	0.1198
Pre:Location	3.1099	1.9992	1.556	0.0621
Removal:Pre:Location	-4.0447	2.1683	-1.865	0.5822

^a Reference is control site, after removal, in the longleaf pine.

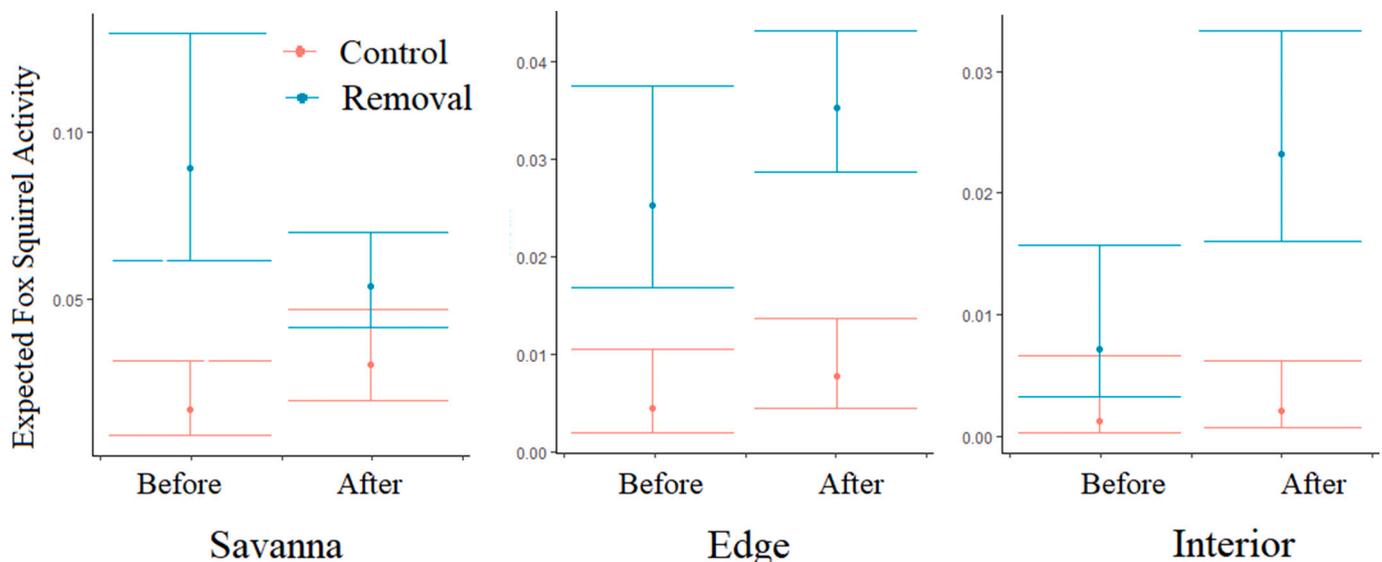


Fig. 3. Point estimates of fox squirrel (*Sciurus niger*) activity (observations/day) along a savanna to closed-canopy gradient before and after experimental gray squirrel (*S. carolinensis*) removal in control and gray squirrel removal sites at the Jones Center at Ichauway in Newton, GA.

4. Discussion

When we removed gray squirrels, fox squirrels rapidly colonized previously avoided closed-canopy patches. This suggests that closed-canopy patches are within the fundamental but not the realized niche of fox squirrels when they coexist with gray squirrels. Closed-canopy patches likely represent acceptable vegetation structure for fox squirrels but competition from gray squirrels limits their use of these areas. Our results support the hypothesis that human driven environmental changes that alter competitive interactions are important drivers of biotic homogenization, particularly when one habitat type undergoes major reduction in extent relative to other habitat types.

While oaks may provide resources for fox squirrels over much of their range, hardwood encroachment appears to change the competitive balance between fox and gray squirrels. Our results support the results of correlative studies that show fox squirrels will readily utilize areas of closed-canopy in the absence of gray squirrels (Sovie et al., 2020). Oak encroachment into pine savannas may represent an increase in available forage for fox squirrels because acorns are more energetically profitable than pine cones (Steele and Koprowski, 2001). Fox squirrel occupancy generally increases with increased oak density yet declines when oaks form a closed-canopy (Perkins et al., 2008; Boone et al., 2017; Greene and McCleery, 2017). Indeed, fox squirrels appear to be highly responsive to changes in the landscape as long as the tree canopy remains open (i.e. agricultural fields & golf courses; Derge and Yahner, 2000, Ditgen et al., 2007, Greene and McCleery, 2017).

Increasing canopy cover possibly alters competition between fox and gray squirrels by reducing the hunting efficiency of predators (Bechard, 1982; Preston, 1990; Potash et al., 2019). Predation is an important mechanism in promoting co-existence between competing species and differences in habitat selection and body size may result from trade-offs between predation risk and foraging efficiency (Caswell, 1978; Kotler, 1984; Sovie et al., 2020). While gray squirrels will readily utilize resources found in the open pine savannas and commonly eat longleaf pine seeds and nest in pines (Spritzer, 2002; Steele et al., 2005), they do not exclude fox squirrels from these areas (Sovie et al., 2020). Gray squirrel lack of competitive dominance in open savannas is likely because they require more time to handle the larger pine cones and they are more vulnerable to predation than the larger bodied fox squirrel (Steele and Koprowski, 2001; Sovie et al., 2019). However, as the structure of the Southeastern savannas change, the gray squirrels' competitive advantage in foraging efficiency will allow them to replace fox squirrels in the relative safety of closed-canopy forests.

The critical role of predation risk in limiting the dominance of gray squirrel has been documented in several other systems. In metropolitan Chicago, gray squirrels are replacing fox squirrels across the city yet, fox squirrels remain in neighborhoods with an elevated risk of predation from cats and dogs (Vander Merwe et al., 2005). Outside of their native range, gray squirrels also negatively affect native Western gray squirrels (*S. griseus*) and European red squirrels (*S. vulgaris*) (Palmer et al., 2007). One notable example of the importance of predation mediating the competitive advantage of gray squirrels occurred in Scotland, where predation from rebounding populations of native pine martens suppresses gray squirrels, allowing red squirrel populations to rebound (Sheehy et al., 2018; Twining et al., 2020).

In our system, the proximate force of homogenization is fire suppression, followed by the success and dominance of native generalists that outcompete other species (Clavel et al., 2010). Longleaf specialists [barking tree frogs (*Hyla gratiosa*), Bachman's sparrow (*Peucaea aestivalis*), red-cockaded woodpecker (*Leuconotopicus borealis*)] are often replaced by generalists [green tree frogs (*Hyla cinerea*), song sparrow (*Melospiza melodia*), southern flying squirrels (*Glaucomys volans*)] when fire is suppressed (Darracq et al., 2016). These "native invasions" are likely to be seen in other systems that had been relatively stable over time but are now experiencing direct and indirect human modification. Such systems include freshwater streams (Buisson et al., 2013), old

growth forests (Kelly et al., 2003), and savannas (Sirami and Monadjem, 2012; McCleery et al., 2018). For example, changes in forest structure in the Great Plains appears to facilitate range expansion by the generalist barred owl (*Strix varia*) at the expense of the Northern spotted owl (*S. occidentalis caurina*) (Long and Wolfe, 2018).

Our experiment may be limited by the inherent difficulty of manipulating wild populations of animals. Despite our best efforts to select sites similar in habitat type and size and the random assignment of treatments, our control sites had lower initial fox squirrel activity than our treatment sites. This may have been a function of greater gray squirrel activity on some control sites (Sup 1). However, within the interior of the close-canopy patches, where we saw the largest response to gray squirrel removal, control and treatment sites did not differ in before-treatment fox squirrel activity. Further, our manipulations occurred over a relatively short period of time (2–3 months) and it is unclear if fox squirrels would continue to utilize the interior of closed-canopy patches over longer periods of time. Regardless, it remains noteworthy on the treatment plots that overall fox squirrel activity was highest in the savanna and lowest in the closed-canopy habitats prior to removal and switched to lowest in the savanna and highest along the edge following gray squirrel removal.

Here we provide empirical evidence that changing species interactions are an important mechanism driving biotic homogenization. Understanding the link between landscape change, species interactions and community composition is critical to conserving biodiversity on multiple scales. With careful attention to species interactions, human altered landscapes may not necessarily result in homogeneous communities made up of a few "winners" and many "losers." Habitat restoration and development planning with an understanding of species interactions are long term solutions to reverse the trend of biotic homogenization (Gámez-Virués et al., 2015). In addition to habitat preservation, managers may also harness the power of species interactions as a complementary means for preventing extirpations (Goodrich and Buskirk, 1995).

CRediT authorship contribution statement

AS, LMC, JB, and RM conceived the ideas and designed methodology; AS collected and analyzed the data; AS and RM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.108971>.

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