

Effects of habitat modification on cotton rat population dynamics and rodent community structure

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Abstract:

Concerns over climate change and finite fossil fuels have generated interest in biofuels. Switchgrass (*Panicum virgatum*), a biofuel feedstock, was planted in intensively managed loblolly pine (*Pinus taeda*) stands to investigate sustainability of this system for producing an alternative energy source. We hypothesized that changes in understory habitat conditions caused by intercropping switchgrass in pine stands would affect rodent population and community dynamics within three years. Therefore, we assessed effects of three treatments (control pine, switchgrass intercropped in pine, and switchgrass monocrop) on rodent population (abundance, survival, and recruitment) and community (diversity, richness, evenness, and community assemblages) measures. We conducted vegetation surveys and live-trapping during 2013–2015 summers in Kemper County, Mississippi, USA. We conducted 6 trapping sessions each summer (n = 14,112 trap nights per year) and captured 1,733 cotton rats (*Sigmodon hispidus*), 102 *Oryzomys palustris*, 31 *Mus musculus*, 28 *Reithrodontomys fulvescens*, 22 *Reithrodontomys humulis*, 20 *Peromyscus leucopus*, 9 *Microtus pinetorum*, 9 *Peromyscus gossypinus*, and 2 *Neotoma floridana*. We found greater cotton rat abundance and lower recruitment in monocrop versus control plots. Rodent diversity was lower in monocrop than control plots. Intercropped plots had intermediate levels of cotton rat abundance and recruitment, and rodent diversity. More dispersal may have occurred in monocrop plots because of high population abundance and limited habitat availability. Cotton rat survival and rodent community assemblage were similar among treatments but differed among years. Although rodents responded negatively to monocrop plots, our results suggested intercropped plots would be an appropriate management practice in pine plantations to produce biofuel feedstocks while maintaining rodent diversity.

Keywords: Intensive forestry | *Pinus taeda* | *Panicum virgatum* | Intercropping | Biofuel | *Sigmodon hispidus*

Article:

1. Introduction

Biofuel production has been increasing to reduce dependency on fossil fuels and lower greenhouse gas emissions (Cheng and Timilsina, 2011). For an alternative fuel to be feasible, it must be cost effective, provide a net energy gain, provide environmental benefits, and be producible without reducing food crops (Hill et al., 2006). Although first generation biofuels do not meet all of these criteria, there have been several technological advances to allow production of second generation biofuels (Cheng and Timilsina, 2011) from lignocellulosic materials such as grasses (Heaton et al., 2008), woody vegetation, and agricultural (Kim and Dale, 2004) and forestry residues. One promising second generation biofuel feedstock, switchgrass (*Panicum virgatum*), mainly has been studied in monocrop settings (Cassida et al., 2005, Fike et al., 2006, Wang et al., 2010). Switchgrass produced on a small farm-scale (3–9.5 ha fields, with an average 6.7 ha field) meets all of the criteria to be an alternative fuel (Schmer et al., 2008).

Planting switchgrass in a monocrop has production advantages and potential sustainability disadvantages. Processing a single species to biofuel is easier than a mixture of species during the conversion process (Bies, 2006). However, monocrops do not provide diverse wildlife habitat structure and when monocrops are harvested, they may not retain refugia for wildlife (Bies, 2006, Garratt et al., 2012). Intercropping, also referred to as alley cropping, is when two crops are planted in alternating rows (Garrett and Buck, 1997). Intercropping is an alternative to planting monocrops that has been promoted by agroforestry researchers to maintain biodiversity and provide other ecological benefits (Cutter and Garrett, 1993, Palm, 1995). Planting trees in agricultural settings potentially increases economic and environmental benefits, such as additional revenue streams to the landowner and wind protection that reduces soil erosion. Intercropping has been used to plant switchgrass on lands already encumbered for production of other crops, such as plantation forestry (Riffell et al., 2012). Planting switchgrass between loblolly pine (*Pinus taeda*) rows in plantations uses land where switchgrass is not competing with food crops and provides landowners with additional potential income (Milder et al., 2008). Wildlife also may find refugia in pine rows, particularly when switchgrass is harvested. Intercropping switchgrass in pine plantations may increase biodiversity compared to traditional pine plantations by providing both young, open pine and grassland habitat structure (Riffell et al., 2012).

In agricultural landscapes, switchgrass monocrops contained a lower diversity of grassland birds than areas planted with a mixture of cool-season grasses, likely because switchgrass is denser and more homogenous (McCoy et al., 2001). In a forestry setting, bird abundances initially declined when switchgrass was planted in an intercropping system, probably due to loss of snags from disturbance during site preparation and when planting switchgrass (Loman et al., 2014, Loman et al., 2013). The bird community changed in monocrop, intercrop, and control treatments between the year switchgrass was planted and the year after planting switchgrass (Loman et al., 2014), but by the third year after planting switchgrass, intercrop and control plots had similar avian community assemblages. However, there is a potential for further change as forest succession continues in the intercrop and control treatment plots (Loman et al., 2014). There is a need for research on effects of planting switchgrass on biodiversity, particularly in

intercropped stands (Riffell et al., 2012), because most studies that have examined effects of switchgrass on biodiversity have both compared switchgrass to row crops and native grasslands (Fletcher et al., 2010) and investigated effects on grassland birds and herpetofauna (Homyack et al., 2013, Loman et al., 2014) rather than mammals (but see Briones et al., 2013, Homyack et al., 2014, King et al., 2014, Marshall et al., 2012).

Microhabitat changes due to planting switchgrass are not well understood, but may affect animals that use understory vegetation. Rodents have key ecological roles as seed dispersers, regulators of invertebrate populations, and prey for several species (Panzacchi et al., 2010). Different rodent species prefer different habitat conditions, so vegetative heterogeneity throughout an area support a more diverse rodent community (Dueser and Shuggart, 1979, Mengak and Guynn, 2003). Abundance of white-footed mice (*Peromyscus leucopus*) has been negatively correlated with grass cover while cotton rat (*Sigmodon hispidus*) captures have been positively correlated with grass cover (Marshall et al., 2012, Mengak and Guynn, 2003). A previous study investigating functional role of white-footed mice in a switchgrass intercropped in a pine system in North Carolina, USA found that there were no differences in carbon or nitrogen isotope signatures between white-footed mice in switchgrass intercropped plots and pine plantation plots, suggesting no change in their functional role (Briones et al., 2013). In established switchgrass intercropped plots, rodent evenness and diversity were lower than in equal aged pine plantation plots (King et al., 2014). Intercropped plots also had greater cotton rat abundances than pine plantation plots, but survival and recruitment did not differ between intensively managed stands that were intercropped and those that were not (King et al., 2014).

To better understand possible effects of intercropping on rodent communities, we investigated microhabitat characteristics of switchgrass intercropped in newly planted pine plantations and associated responses of rodent populations and communities. We hypothesized that changes in understory structure caused by intercropping switchgrass in pine plantations would affect rodent population and community dynamics. We assessed effects of three treatments (control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]) on rodent population metrics (abundance, survival, and recruitment) and community structure (diversity, richness, evenness, and community assemblage). We predicted that cotton rats, a grassland specialist species, would have greater abundance, survival, and recruitment in monocrop plots and lower abundance, survival, and recruitment in control pine plots because of predicted resource availability. Further, we predicted monocrop plots would be dominated by populations of cotton rats and therefore would have the lowest rodent diversity, richness, and evenness, whereas intercrop plots would have greatest rodent diversity and richness. Lastly we predicted that community assemblages would differ among treatments. Specifically, we hypothesized that monocrop plots would be dominated by populations of cotton rats but intercrop and control plots would support more species.

2. Methods

2.1. Study area

‘Alamo’ variety switchgrass, a native biofuel feedstock, was intercropped in loblolly pine plantations in Kemper County, Mississippi, USA, on land owned and managed by Weyerhaeuser

Company on experimental plots established and maintained by Weyerhaeuser Company and Catchlight Energy LLC (CLE), a Chevron|Weyerhaeuser joint venture. Each stand received the same site preparation in September 2010 before pines and switchgrass were planted (Loman et al., 2013). One-year-old pine seedlings were planted during January-February 2010. Switchgrass was planted in August-September 2011 and May-June 2012 to ensure full establishment. Switchgrass (intercropped alleys and the entire monocrop plots) received fertilizer (Arborite) and herbicide [banded treatment of triclopyr (Garlon 4 Ultra®), metsulfuron methyl, and chlorsulfuron (Cimmaron Plus®)] in May-June 2014 and fertilizer (Arborite) in May 2015 to promote switchgrass productivity. We used 4 stands (as replicates or blocks) with 4 randomly assigned treatments plots (10 ha each) within each stand; two control plots, an intercrop plot, and a monocrop plot (Fig. 1). Two control plots were studied because of future plans to remove woody biomass between pine beds in one control plot per replicate. We averaged results from control plots within stands to reduce potential bias from increased sampling effort. Our study plots were the same as the pine control, intercropped switchgrass, and switchgrass monocrop plots described by Loman et al. (2014).

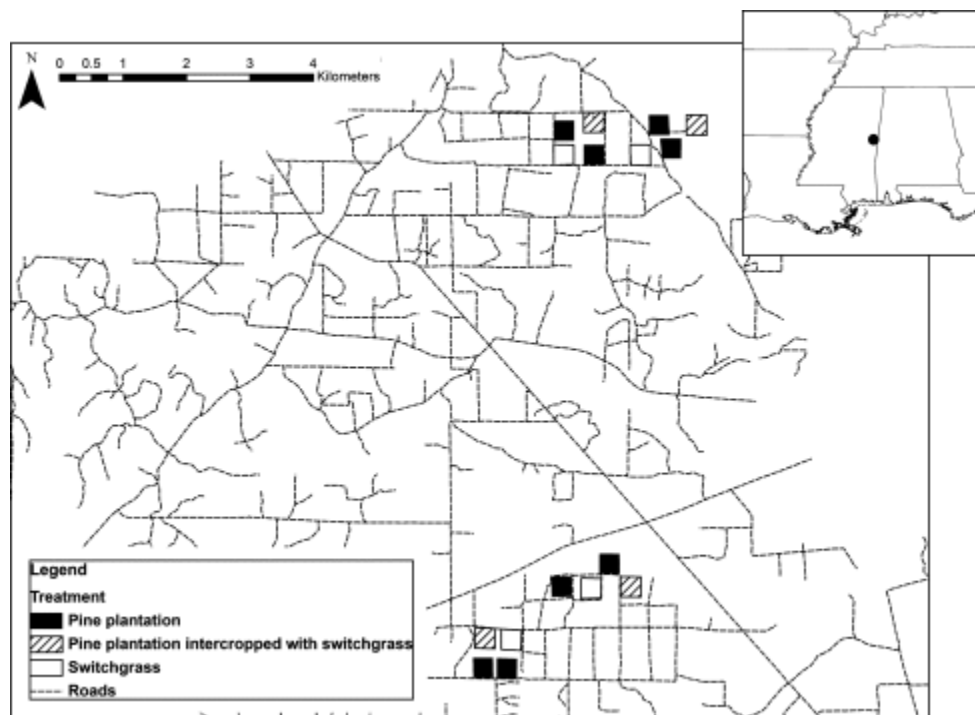


Fig. 1. Study site located in Kemper County, MS, USA (shown in locator map) on land owned and managed by Weyerhaeuser Company. There were 4 replicates, each containing four 10-ha treatment plots; two control loblolly plots (black squares), switchgrass intercropped in loblolly pine (hollow with lines squares), and switchgrass monocrop (hollow squares).

2.2. Vegetation

To measure microhabitat characteristics, we used 1.77-m² hoops centered over each trapping station (see Trapping below) in all plots during May each year. We visually estimated ground cover using the following percent cover classes (absent, 0–1, 1–5, 5–15, 15–25, 25–50, 50–75, 75–95, and 95–100%) for 9 cover types (pine, non-pine woody vegetation, grass, forb, moss, vine, bare ground, other debris [including pine needles and dead vegetation], and woody debris

[including downed trees, stumps, and branches]). We converted cover classes recorded at each trapping station to the midpoints of the ranges (e.g., for cover class 15–25 the midpoint value would be 20). We averaged microhabitat variable estimates at all trapping stations within a treatment plot.

We estimated vertical vegetation density using a cover board at the center of each hoop at all trapping stations (Nudds, 1977). We estimated cover of each section of the board while standing 14 m away at each of the 4 cardinal directions. The cover board had 6 sections and each section was 30 cm high by 18 cm wide. We averaged estimates across the 4 observations at each trapping station for each section separately. We then obtained treatment plot averages for each section. We analyzed near-ground (ground up to 90 cm) and aboveground (90 cm above ground to 180 cm aboveground) sections of the cover board separately to assess cover that may have different functions, particularly relating to ground and aerial predators. We had 2 observers for vegetation surveys each summer (one the lead author) to reduce potential observer bias.

2.3. Trapping

We established a 7 × 7-trapping grid (20 m between traps; 49 trap stations) at the center of each treatment plot that remained in the same location for all three years of our study. We used 42 Sherman 23-cm live traps (H.B. Sherman Traps Inc., 167 Tallahassee, Florida, USA) and 7 Longworth traps (Rogers Manufacturing Co., Peachland, British Columbia, Canada) or 18-cm non-folding Sherman traps per treatment plot (1 smaller trap was randomly placed per trap line) to prevent size bias when trapping (Anthony et al., 2005). We baited traps with crimped oats. We also applied a granular insecticide (Talstar PL, FMC Corporation, Philadelphia, Pennsylvania) around each trap at the beginning of each trapping session to prevent fire ants (*Solenopsis invicta*) from attacking captured rodents. We completed 6 trapping sessions of 3 consecutive nights on each treatment plot from May to August in 2013, 2014, and 2015. We trapped all treatments of a replicate simultaneously. The final trapping session in 2015 was only 2 consecutive nights because of a sudden increase in raccoon (*Procyon lotor*) disturbance to traps. We uniquely marked all captured animals with a numbered ear tag (Model 1005–1, National Band and Tag Company, Newport, Kentucky, USA). We also recorded species, sex, age-class (juvenile, subadult, adult), reproductive condition (scrotal, non-scrotal, perforate, pregnant, lactating, pregnant and lactating, post-lactating), and mass (g). We determined age-class using a combination of mass, pelage, and reproductive status. For cotton rats, we used similar age-classes as previous literature (DeBusk and Kennerly, 1975), but altered slightly to match our observations of pelage and reproductive status at our site: juveniles (<40 g), subadults (40–80 g), and adults (>80 g). We recorded hind foot, tail, and body lengths (mm) for all mice species to aid in identification. We conducted our work under annual scientific collection permits from the Mississippi Department of Wildlife, Fisheries, and Parks and UNCG IACUC 14-001.0. We followed the American Society of Mammalogists guidelines for use of wild mammals in research (Sikes and Gannon, 2011).

2.4. Population

We first completed a population analysis in Program MARK (White and Burnham, 1999) using a Robust design model. However this model produced unrealistic results, potentially because the

model did not converge, likely due to low capture and recapture rates in 2014 and 2015. Thus, we used minimum known alive (MNKA) numbers to estimate relative abundance of rodent populations and manually calculated recruitment and survival. Our MNKA numbers were obtained in a way analogous to the Robust design model in Program MARK (White and Burnham, 1999). We considered each trapping session as closed, but we considered time between each trapping session as open. Therefore, we obtained MNKA numbers from each trapping session separately. We then averaged MNKA numbers across trapping sessions to obtain a MNKA number for each year of trapping. We estimated recruitment as number of juveniles captured per adult reproductive female captured per treatment plot and averaged across plots (Long et al., 2015). We were not able to use our trapping data to estimate survival given low number of captures and recaptures, particularly in 2014 and 2015. Instead, we directly measured survival by following fate of 82 different resident, adult, female cotton rats (18 in 2013, 33 in 2014, and 31 in 2015) that were radiomarked (M1450 or M1520 Advanced Telemetry Systems [ATS], Isanti, MN, U.S.A.) as part of a separate study. Each year we radiomarked new individuals and we followed all radiomarked individuals for a single summer. We located all radiomarked individuals during daylight hours using homing techniques. We initially located each individual via homing 24 h after being radiomarked to allow the individual to acclimate to the radiotransmitter. We then located individuals via homing using a R4000 or R4500S receiver with a 3 element folding yagi (ATS) at least once a week until either the radiotransmitter was removed or the individual's fate was determined. When we were not locating individuals via homing during the day, we regularly conducted triangulation fixes, which provided information as to whether the individual was still alive or not. If we noticed any indication that an individual was no longer alive (i.e. the individual did not move during an entire night of triangulation fixes), we would use homing to visually locate the individual to determine status. We based all survival data on homing techniques.

2.5. Community

We calculated Shannon-Weiner diversity, Simpson's diversity, richness, and Pielou's evenness (Pielou, 1966) using MNKA for each plot in program R (R Core Team, 2014), package Vegan (Oksanen et al., 2013). Simpson's diversity is more dependent on dominant species than Shannon-Weiner diversity, but is recommended for small sample sizes, so we used both diversity indices (Smith and Grassle, 1977).

2.6. Statistical analyses

We used non-metric dimensional scaling (NMDS) to compare microhabitat variables within and among treatment plots. We used a two-way permutation multivariate analysis of variance (PerMANOVA) with interaction and stand as a blocking factor to test the null hypothesis that there were no differences in vegetation characteristics among treatments and years. We used a vector-fitting procedure with our vegetation data to find microhabitat characteristics significantly correlated with the ordination (Gallie and Drickamer, 2008, Letnic et al., 2004).

We used repeated measures, randomized block design analysis of variance (ANOVA) with an interaction to test the null hypothesis that there were no differences in treatment plot means of population abundance (calculated as MNKA) and recruitment (calculated as juveniles per

reproductive female per plot) among treatments, year, and a possible interaction of treatment and year. We used an overall split-plot model to analyze the repeated measures, randomized block design ANOVA with stand as block, treatment as whole-plot, and year as sub-plot, with degrees of freedom adjusted for non-independence across years. We conducted a Fisher's exact test to assess for effects of treatment and year separately on survival. We only completed population level analyses for cotton rats as this species had sufficient data to estimate abundance, recruitment, and survival.

We used repeated measures, randomized block design ANOVA to test the null hypothesis that there were no differences in treatment plot means of community diversity, richness, and evenness indices among treatment, year, and possible interaction of treatment and year. We used NMDS to compare rodent community assemblage within and among treatment plots. We used a two-way PerMANOVA with interaction and stand as a blocking factor to assess differences in rodent assemblages among treatments and years.

For all NMDS procedures, we used 2-dimensional solutions based on scree plots and the minimal reduction in stress with additional dimensions. For each NMDS, we conducted 50 random starts. For each PerMANOVA, we generated 999 permutations and made post-hoc comparisons using Bonferroni-corrected p-values. For all vector-fitting procedures, we generated 999 random permutations. Given the large number of zeros in the dataset, we used Bray-Curtis dissimilarity matrices for all multivariate tests.

For all repeated measures ANOVAs, we checked normality and sphericity to ensure assumptions were met (Logan, 2010). We rank transformed data that did not meet the normality assumption as either raw or log transformed data. When the sphericity assumption was violated, we used the Greenhouse-Geisser correction. We investigated pairwise contrasts if the omnibus test was statistically significant using a Tukey HSD. We used Program R (R Core Team, 2014) for all analyses except the PerMANOVA post-hoc tests, which we performed in Paleontological Statistics Software Package for Education and Data Analysis (PAST) (Hammer et al., 2001).

3. Results

3.1. Vegetation

Within each treatment plot we measured microhabitat characteristics at 49 trap stations resulting in 196 subsamples for intercrop and monocrop plots and 392 subsamples for control plots each year. Microhabitat structure varied by treatment and year based on a NMDS plot and two-way PerMANOVA with interaction (stress = 0.13, treatment; $F_{2,27} = 57.66$, $R^2 = 0.67$, $p < 0.01$ and year; $F_{2,27} = 11.15$, $R^2 = 0.13$, $p < 0.01$; Fig. 2). There was no significant interaction of treatment and year ($F_{4,27} = 1.98$, $R^2 = 0.05$, $p = 0.10$). Monocrop plots had more grass cover and less woody debris, woody vegetation, and other debris compared to control and intercrop plots (based on vectors having $r > 0.92$ and $p < 0.01$; Fig. 2). All years differed from each other in microhabitat structure (2013 vs. 2014 $p = 0.01$; 2013 vs. 2015 $p < 0.01$; and 2014 vs. 2015 $p = 0.04$). The primary vegetation components each year were woody debris in 2013, woody vegetation in 2014, and other debris in 2015 (Fig. 2).

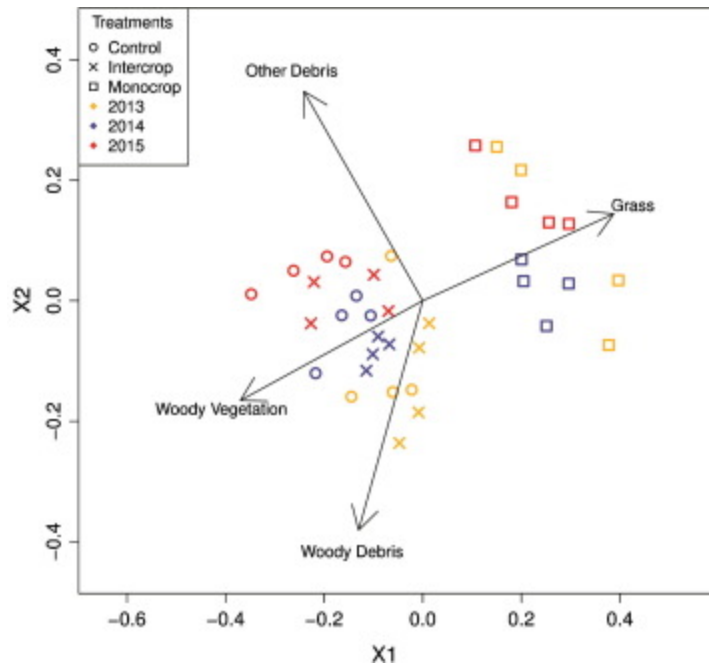


Fig. 2. Non-metric dimensional scaling (NMDS) plot of microhabitat characteristics (ground cover measured at each trapping station and averaged per plot) by treatment with vectors (black lines) fit to explain separation. We collected microhabitat data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Based on a two-way permutation multivariate analysis of variance (PerMANOVA), microhabitat characteristics varied by treatment ($F_{2,27} = 57.66$, $R^2 = 0.67$, $p < 0.01$) and year ($F_{2,27} = 11.15$, $R^2 = 0.13$, $p < 0.01$). Stress = 0.13.

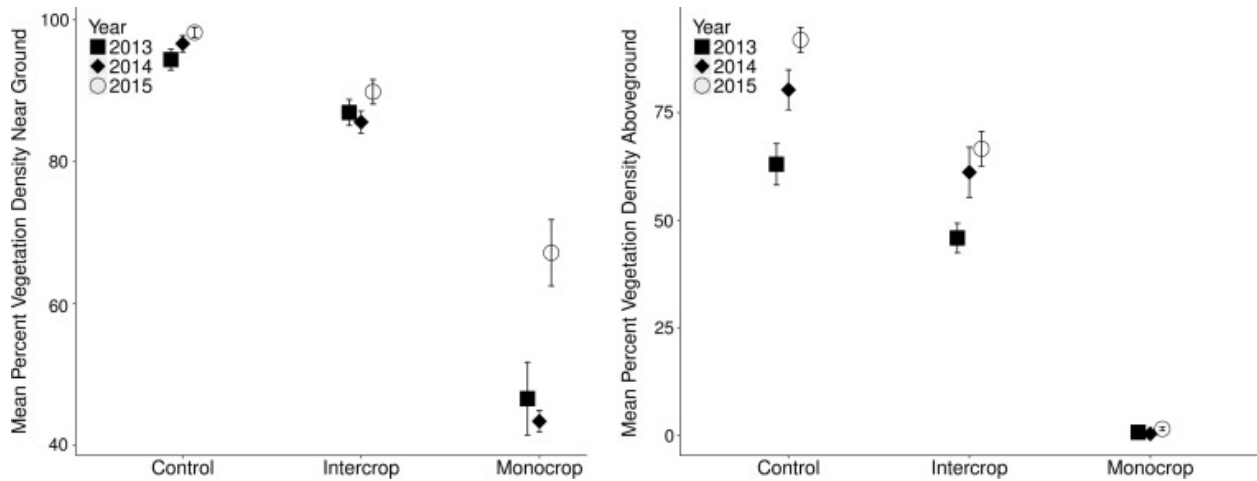


Fig. 3. Mean (\pm SE) percent vertical vegetation density from both near ground (A) and aboveground (B) sections of a cover board measured at each trapping station and averaged per plot. We collected vertical vegetation estimates in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Overall density was greater for the near ground (A) section when compared to the aboveground (B) section. In both sections, control plots had the greatest, intercrop had intermediate, and monocrop had the lowest density. In the near ground (A) section, density was lower in 2013 and remained lower in 2014 in both intercrop and monocrop plots compared to 2015. In the aboveground (B) section control plots increased in vertical density throughout the years while intercrop and monocrop plots did not differ across years.

We detected a significant interaction of treatment and year ($F_{4,18} = 3.18$, $p = 0.04$) for vertical vegetation density near the ground. Overall, control plots had the greatest (mean \pm SE; 96.41 ± 0.77), intercrop had intermediate (87.45 ± 1.05), and monocrop had the least vertical vegetation density near the ground (52.37 ± 3.83 ; Fig. 3). Vegetation density was less in 2013 in each treatment and remained significantly less in 2014 in both intercrop and monocrop plots compared to 2015. There was also a significant interaction of treatment and year ($F_{4,18} = 5.48$, $p < 0.01$; Fig. 3) for vegetation density in the aboveground section. Similar to the near-ground section, overall, control had the greatest (78.41 ± 4.20), intercrop had intermediate (57.87 ± 3.55), and monocrop had the least vegetation density above the ground (0.85 ± 0.23). However, while control plots increased (63–91%) in vertical density from 2013 to 2015, intercrop and monocrop plots did not significantly differ across years (46–67% and 0.7–1.5%, respectively). Monocrop plots had the most grass and least vertical vegetation density in both sections throughout our study.

3.2. Population

Using 14,112 trap nights per year (3,528 per replicate per year), we marked and captured 1,036 unique individuals 2,543 times in 2013; 385 unique individuals 728 times in 2014; and 535 unique individuals 979 times in 2015. Across all years, trapping sessions, and plots, we captured 1,733 cotton rats, 102 marsh rice rats (*Oryzomys palustris*), 31 house mice (*Mus musculus*), 28 fulvous harvest mice (*Reithrodontomys fulvescens*), 22 eastern harvest mice (*Reithrodontomys humulis*), 20 white-footed mice, 9 woodland voles (*Microtus pinetorum*), 9 cotton mice (*Peromyscus gossypinus*), and 2 eastern woodrats (*Neotoma floridana*).

Table 1. Mean (\pm SE) number of minimum known alive (calculated to represent robust design model of population abundance) averaged across trapping sessions per plot by treatment. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Rodent species captured include SIHI: *Sigmodon hispidus*; ORPA: *Oryzomys palustris*; MUMU: *Mus musculus*; REFU: *Reithrodontomys fulvescens*; REHU: *Reithrodontomys humulis*; PELE: *Peromyscus leucopus*; MIPI: *Microtus pinetorum*; PEGO: *Peromyscus gossypinus*.

	SIHI	ORPA	MUMU	REFU	REHU	PELE	MIPI	PEGO
<i>2013</i>								
Control	17.48 \pm 3.45	1.48 \pm 0.55	0.10 \pm 0.10	0.00 \pm 0.00	0.00 \pm 0.00	0.08 \pm 0.06	0.02 \pm 0.02	0.02 \pm 0.02
Intercrop	17.79 \pm 3.21	0.25 \pm 0.25	0.29 \pm 0.17	0.00 \pm 0.00	0.00 \pm 0.00	0.88 \pm 0.88	0.00 \pm 0.00	0.00 \pm 0.00
Monocrop	17.13 \pm 6.91	0.33 \pm 0.18	1.33 \pm 0.98	0.00 \pm 0.00	0.08 \pm 0.05	0.21 \pm 0.21	0.00 \pm 0.00	0.00 \pm 0.00
<i>2014</i>								
Control	4.19 \pm 2.42	0.56 \pm 0.15	0.00 \pm 0.00	0.06 \pm 0.04	0.04 \pm 0.04	0.02 \pm 0.02	0.04 \pm 0.02	0.00 \pm 0.00
Intercrop	5.46 \pm 1.76	0.13 \pm 0.08	0.00 \pm 0.00	0.17 \pm 0.07	0.04 \pm 0.04	0.08 \pm 0.08	0.04 \pm 0.04	0.00 \pm 0.00
Monocrop	8.88 \pm 2.99	0.17 \pm 0.10	0.08 \pm 0.05	0.00 \pm 0.00	0.21 \pm 0.10	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
<i>2015</i>								
Control	6.46 \pm 1.73	0.46 \pm 0.18	0.00 \pm 0.00	0.46 \pm 0.20	0.02 \pm 0.02	0.00 \pm 0.00	0.06 \pm 0.04	0.08 \pm 0.08
Intercrop	5.29 \pm 2.13	0.21 \pm 0.13	0.00 \pm 0.00	0.25 \pm 0.08	0.13 \pm 0.08	0.17 \pm 0.17	0.25 \pm 0.25	0.08 \pm 0.05
Monocrop	11.04 \pm 2.10	0.38 \pm 0.24	0.00 \pm 0.00	0.08 \pm 0.08	0.42 \pm 0.20	0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00

3.2.1. Abundance

The cotton rat was the most abundant species followed by the marsh rice rat (Table 1). We also captured 2 juvenile eastern woodrats in a single control plot in 2015. We only conducted population analyses on the cotton rat, the only species with sufficient captures to warrant further analyses. The interaction of year and treatment for relative abundance of adult cotton rats was not significant ($F_{4,18} = 2.56$, $p = 0.07$; Fig. 4). However, relative abundance of adult cotton rats was about 3 times greater in all plots in 2013 than the control and intercrop plots in 2014 and 2015 ($F_{2,18} = 32.51$, $p < 0.01$). Monocrop plots also had about 1.5 times greater adult cotton rat relative abundances than control plots ($F_{2,6} = 6.77$, $p = 0.03$; Fig. 4).

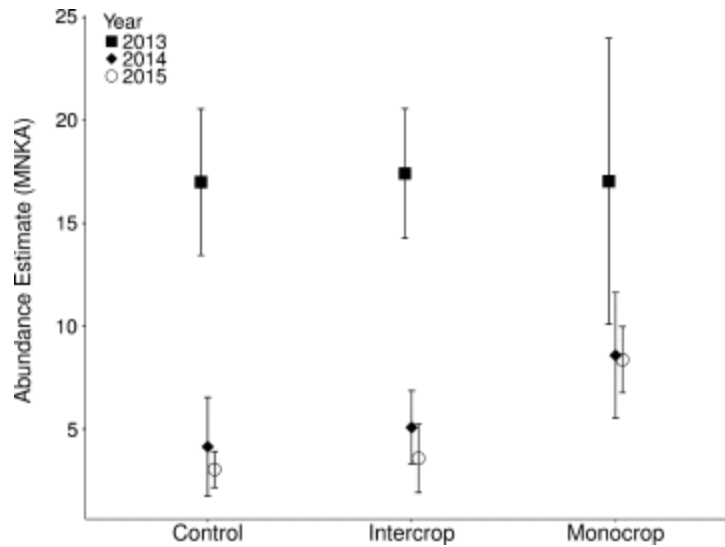


Fig. 4. Adult *Sigmodon hispidus* mean population abundance estimates (\pm SE) based on minimum known alive (MNKA) averaged across replicates and plotted by treatment per year. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Both treatment ($F_{2,6} = 6.77$, $p = 0.03$) and year ($F_{2,18} = 32.51$, $p < 0.01$; 2013 significantly greater than 2014 and 2015) effects were significant. Letters denote significant treatment pairwise comparisons.

3.2.2. Survival

In 2013, we radiomarked 18 resident, female cotton rats (6 per treatment; Table 2) with no evidence of predation in that summer. In 2014 and 2015, we radiomarked 33 and 31 resident female cotton rats, respectively (minimum of 10 per treatment). Of the 64 individuals radiomarked in 2014 and 2015, 6 of the 33 radiomarked individuals were eaten in 2014 (2 by snakes, 3 by unidentified predators and 1 by possible coyote (*Canis latrans*)), and 3 of the 31 radiomarked individuals were eaten in 2015 (2 by snakes and 1 by an unidentified predator). We radiotracked individuals for an average of 22.51 (\pm 1.23) days overall (range: 1–50 days). The length of time we radiotracked each individual depended on whether or not (and when) (1) the animal was eaten, (2) the radiomark was lost by the animal, and (3) the animal was easily recaptured for radiomark removal. Survival did not differ among treatments ($p = 1.00$) or years ($p = 0.15$). We calculated survival analyses using known predation events of radiomarked individuals (Table 2). We did not detect any other natural sources of mortality during our study.

3.2.3. Recruitment

Cotton rat recruitment was 3 times lower in monocrop (0.14 ± 0.05) than control plots (0.46 ± 0.07 ; $F_{2,6} = 6.42$, $p = 0.03$). Recruitment also was 2 times greater in 2013 (0.45 ± 0.08) than 2014 (0.18 ± 0.06 ; $F_{2,18} = 6.06$, $p = 0.01$; Fig. 5).

Table 2. Adult, female *Sigmodon hispidus* depredation data based on fate of radiomarked individuals. We collected radiotelemetry data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Numbers to the left of brackets are the number of individuals that were eaten out of all radiomarked adult, females within each year and treatment (the number in brackets). We did not detect any other natural sources of mortality during our study.

	2013	2014	2015
Control	0 [6]	3 [10]	0 [10]
Intercrop	0 [6]	1 [11]	2 [11]
Monocrop	0 [6]	2 [12]	1 [10]

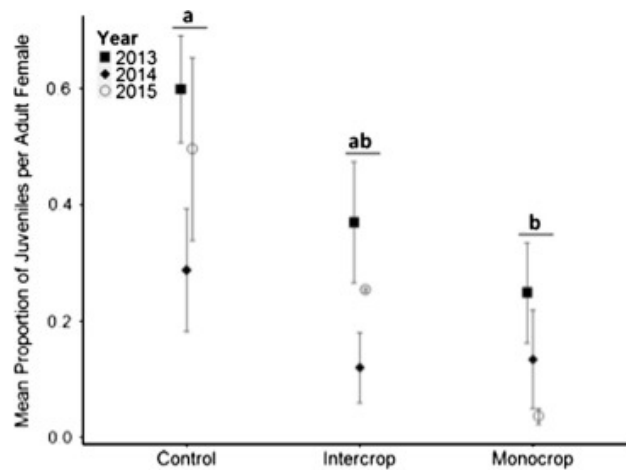


Fig. 5. Mean recruitment estimates (\pm SE) of *Sigmodon hispidus* (juveniles per reproductive female captured) plotted by treatment per year. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Both treatment ($F_{2,6} = 6.42$, $p = 0.03$) and year ($F_{2,18} = 6.06$, $p = 0.01$; 2013 significantly greater than 2014) were significant. Letters denote significant treatment pairwise comparisons.

3.3. Community

Richness and evenness did not differ among treatments ($F_{2,6} = 2.94$, $p = 0.13$; $F_{2,6} = 3.57$, $p = 0.10$, respectively). Rodent assemblages did not vary by treatment, but 2013 was different from 2014 and 2015 based on a NMDS plot and two-way PerMANOVA with interaction (stress = 0.10, treatment; $F_{2,27} = 1.47$, $R^2 = 0.06$, $p = 0.12$ and year; $F_{2,27} = 5.80$, $R^2 = 0.26$, $p < 0.01$; Fig. 6). Overall, 2013 had 2.5 times more captures of cotton rats compared to 2014 and 2015. In 2014 and 2015, we captured more woodland voles and fulvous harvest mice than in 2013 (Fig. 6). There was no significant interaction of treatment and year ($F_{4,27} = 0.93$, $R^2 = 0.08$, $p = 0.39$). Control plots had a greater Shannon and Simpson's diversity than both intercrop and monocrop plots ($F_{2,6} = 7.28$, $p = 0.02$ and $F_{2,6} = 7.92$, $p = 0.02$, respectively; Table 3). There were no significant ($p > 0.05$) interactions of treatment and year, nor were there any year effects for diversity, richness, and evenness indices.

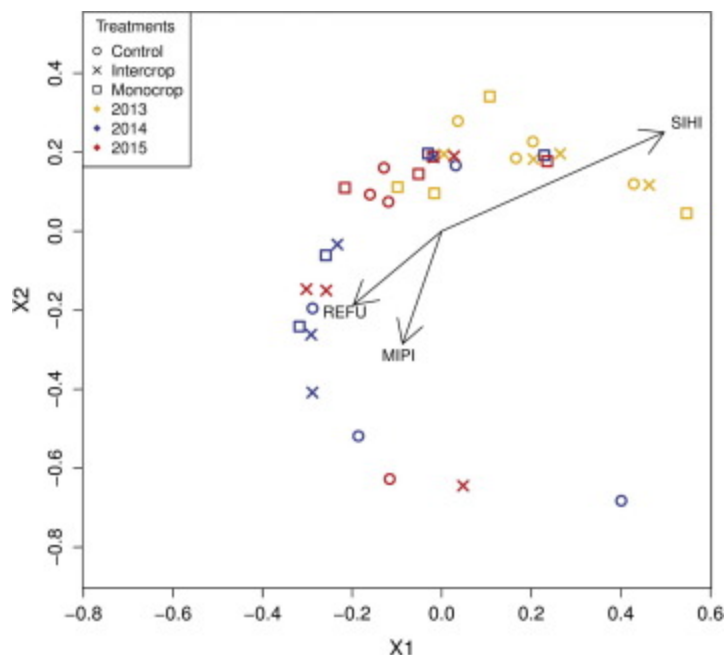


Fig. 6. Non-metric dimensional scaling (NMDS) plot of rodent assemblages by treatment with vectors (black lines) fit to explain separation. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Based on a permutation multivariate analysis of variance (PerMANOVA), rodent assemblages did not vary by treatment ($F_{2,27} = 1.47$, $R^2 = 0.06$, $p = 0.12$), but they did vary by year ($F_{2,27} = 5.80$, $R^2 = 0.26$, $p < 0.01$); 2013 was different from 2014 and 2015. Stress = 0.10. Vector codes are SIHI: *Sigmodon hispidus*; REFU: *Reithrodontomys fulvescens*; and MIPI: *Microtus pinetorum*.

Table 3. Mean diversity indices (\pm SE) averaged across replicates and years. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Richness and evenness indices did not significantly differ among treatments. Shannon and Simpson's indices of diversity were significantly greater in control than monocrop plots (different letters and bold text indicate significant differences among treatments).

	Shannon	Simpson's	Richness	Evenness
Control	0.54 ± 0.09a	0.28 ± 0.05a	3.58 ± 0.29	0.42 ± 0.07
Intercrop	0.44 ± 0.12ab	0.21 ± 0.06ab	3.00 ± 0.39	0.35 ± 0.07
Monocrop	0.34 ± 0.08b	0.17 ± 0.04b	2.75 ± 0.28	0.29 ± 0.06
	$F_{2,6} = 7.28$, p = 0.02	$F_{2,6} = 7.92$, p = 0.02	$F_{2,6} = 2.94$, $p = 0.13$	$F_{2,6} = 3.57$, $p = 0.10$

4. Discussion

Our results suggest that intercropping switchgrass in pine plantations can both produce biofuel feedstocks and maintain similar rodent population metrics and community structure to traditional pine plantations. Thus, switchgrass could be considered a feasible alternative fuel that can be planted on land not used for food crops while maintaining a diverse rodent community, which provides environmental benefits such as a food source for predators and effective seed and spore dispersal. Although we hypothesized that intercropping would change the understory and therefore would affect rodent populations and communities, we found intercrop plots were consistently intermediate and not significantly different from control and monocrop plots. Further, our predictions regarding cotton rat populations were not supported consistently as abundance was greater in monocrop than control plots, but the opposite result was found for

recruitment. Lastly, our predictions of community responses were partially supported as diversity was found to be least in monocrop plots, but richness and evenness did not differ among treatments.

Treatments varied in vegetation heterogeneity, and vegetation composition changed over time. Monocrop plots were the most homogeneous as switchgrass and other grasses were dominant cover types. Woody debris remained from site preparation in intercrop and control plots and decomposed during our study, whereas it was removed from all monocrop plots during site preparation in 2013. Leaving woody debris provides additional structure for wildlife (Loeb, 1999), which is an additional benefit of the intercropping system compared to monocrops when producing a biofuel feedstock. Other debris was greater in percent cover by 2015 because vegetation from previous years died and pine trees continuously lost needles. Vertical vegetation density was least in monocrop plots and increased throughout the years as switchgrass established. However, it is important to note that vertical vegetation density also increased throughout each summer, especially in intercrop and monocrop plots as switchgrass and other vegetation grew.

Switchgrass is not only a biofuel feedstock, but is a cover and potential food resource for cotton rats so, in areas where it was planted, it was expected that cotton rat population abundance and recruitment would be high (Kincaid and Cameron, 1982a, Rehmeier et al., 2005). Interestingly, planting switchgrass in a monocrop setting resulted in high cotton rat abundance, but low recruitment in comparison to control pine plots. One explanation is cotton rat dispersal could have occurred at younger ages than normal in monocrop plots because of high population abundance and limited habitat availability. Cotton rats have been shown to readily disperse and are able to easily move through landscapes (Bowne et al., 1999). If juvenile cotton rats dispersed as soon as they were capable, abundance of juveniles, and therefore recruitment, would decrease. Detection in our study may also have been particularly low given we had relatively low captures and recapture rates, particularly in 2014 and 2015. Because young cotton rats are less likely to enter traps that have been used by older, more dominant cotton rats, it is possible our results are simply due to known trap bias (Summerlin and Wolfe, 1973).

Alternatively, monocrop plots could be sinks, and control plots along with older surrounding pine stands could be sources. Cotton rats are grassland specialists and may perceive monocrop plots as quality habitat (Cameron and Spencer, 1981). However, the homogeneous habitat structure may reduce survival of adults, offspring, or both. In fact, one study found that female cotton rats preferred a mixture of monocot and dicot vegetation (Cameron and Spencer, 1985) as was present in our control pine and intercrop plots. However, we cannot make that conclusion based on our data. Even with detailed population data, it is difficult to account for temporal variation that could change areas previously described as sinks to sources (Kreuzer and Huntly, 2003). Additionally, well documented social dominance of cotton rats affects population abundance and recruitment, particularly in preferred habitat conditions (Cameron and Spencer, 1985, Doonan and Slade, 1995, Fleharty and Mares, 1973). Dominant cotton rat individuals may be less tolerant of home range overlap with other individuals and have more offspring, leading to low adult abundance yet high recruitment on a plot level.

Our estimates of cotton rat survival for females may be an overrepresentation of true survival given that rodents are common prey species for many predators. In Barrett et al. (2001), 5 of 72 cotton rats (4 male and 1 female) were preyed upon in one summer (Barrett et al., 2001). Comparing these results to our own, and considering we only radiomarked females, it is possible that we detected low levels compared to actual levels of predation. To reduce predation risk, cotton rats use habitat structure with dense, tall understory vegetation and low overstory canopy cover (Bowne et al., 1999, Fleharty and Mares, 1973). Although vegetation was relatively dense in all of our treatments, homogeneity of vegetation type in monocrop plots may have provided fewer refugia to rodents seeking protection from predators. Further, vegetation density would be most relevant to decreasing success of predators that use visual cues. Some predators of rodents, however, do not strictly rely on visual cues. Snakes, including black rat snakes (*Pantherophis obsoletus*) and timber rattlesnakes (*Crotalus horridus*), which were both common on our plots, mainly use vibrations as cues (Friedel et al., 2008, Young, 2003) and use vegetation cover themselves to ambush prey while being protected from their own predators (Kotler et al., 1992). In cases where predators are using different cues, dense vegetation may be detrimental as it would give prey less time to visually detect a predator (Schooley et al., 1996). Future research should evaluate differences in survival and dispersal in cotton rats among age classes and compare to the potential predator community.

Rodent community diversity was affected by planting switchgrass, particularly in monocrop plots. Switchgrass monocrops have been shown to have greater diversity of herpetofauna species when compared to pine and intercrop plots (Homyack et al., 2013). However, this greater diversity was likely due to a decrease in abundance of a common species, the southern toad (*Anaxyrus terrestris*) (Homyack et al., 2013). In our study, monocrop plots contained high abundances of the dominant species (the cotton rat), leading to low diversity (Brady and Slade, 2001, Tuomisto, 2012). The cotton rat is an ecologically dominant species, particularly at high densities. Therefore, high cotton rat abundances lead to reduced abundances of smaller species, such as western harvest mice (*Reithrodontomys megalotis*) and deer mice (*Peromyscus maniculatus*) (Brady and Slade, 2001). Similarly in our study, it was not until cotton rat abundances decreased in 2014 and 2015 that we captured greater abundances of smaller species such as fulvous harvest mice and woodland voles. The marsh rice rat was the second most commonly captured species in our study and had a particularly high abundance in control plots in 2013, but their abundance declined from 2013 to 2014. Marsh rice rats and cotton rats do not highly overlap in diet (16.7% overlap), which may explain why both populations could have had relatively high abundances in 2013 (Kincaid and Cameron, 1982b). However, marsh rice rats and fulvous harvest mice have an average of 97.8% overlap in diet (Kincaid and Cameron, 1982b). Therefore, as fulvous harvest mice abundance increased, marsh rice rats may have experienced increasing competition for food resources. Heterogeneous habitat conditions provide a variety of resources and therefore are capable of supporting more species (MacArthur and MacArthur, 1961). Throughout the years our control and intercrop plots became more heterogeneous and were therefore able to support more of the rare species. The increase in rare species may have caused a decrease in common species abundances.

Previous studies of switchgrass intercropping suggested a possible association between switchgrass and non-native, invasive house mice (Homyack et al., 2014, Marshall et al., 2012). Although our study detected house mice in initial years in plots where switchgrass was planted,

by year three, we no longer detected house mice in any plots. House mice are associated with humans and disturbance and by year three there was limited disturbance in our plots. There were also native species in the area that may have competed for resources. However, one study that investigated interspecific competition with house mice and old field mice (*Peromyscus polionotus*) found that house mice were more aggressive (King, 1957). Furthermore, house mice are seminomadic and may have simply immigrated to an area of newly disturbed land given the landscape is a matrix of actively managed pine plantations (Caldwell and Gentry, 1965). Therefore, house mice are more likely associated with initial disturbance of planting switchgrass and with agricultural fields that surrounded plots in a previous study than with switchgrass directly (Homyack et al., 2014, Marshall et al., 2012).

4.1. Conclusions

In conclusion, planting switchgrass as a monocrop within a managed pine plantation landscape reduced rodent diversity. However, it is unlikely that this management regime would be implemented in managed pine plantation landscapes and results may differ in agricultural or other forested landscape settings. Intercropping systems, however, are well suited for managed pine plantation landscapes and, as our study shows, appear capable of providing heterogeneous habitat conditions to support a diverse community of rodents. Therefore, intercrop plots would be recommended as a management practice in pine plantations to increase biofuel feedstock production while maintaining rodent diversity.

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