

Rodent population and community responses to forest based biofuels production

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Abstract:

Intensively managed forests in the southeastern United States are a potential source of cellulosic bioenergy and, as conversion technologies improve and demand increases, a greater land area may be required to produce biofuel feedstocks. However, responses of wildlife to forest-based biofuel production are largely unknown. We examined the 4-year response of rodent populations and assemblages to a range of biofuel production regimes, including harvesting residual woody debris and intercropping switchgrass (*Panicum virgatum*), in an intensively managed loblolly pine (*Pinus taeda*) forest in eastern North Carolina, USA. We investigated abundance, demography, and community response of rodents in a randomized and replicated field experiment using mark-recapture techniques during 2009–2012. Whereas removal of downed woody biomass did not affect abundance, diversity, or demography of rodents, we detected species-specific effects of incorporating switchgrass. After switchgrass was well established, invasive house mice (*Mus musculus*) were most abundant in plots with switchgrass. In contrast, white-footed mice (*Peromyscus leucopus*) were commonly captured in plots without switchgrass and other rodents were not affected by biofuel treatments. Across the study, natural succession exerted greater effects on rodent species and the rodent community than biofuel production regimes. As remaining logs and stumps decay and become limiting, downed wood may become more important to rodents. Our results indicate that intercropping switchgrass and harvesting residual woody material had limited effects on rodents in the Coastal Plain of North Carolina, USA within 4 years of stand establishment.

Keywords: house mouse | intensive forestry | *Mus musculus* | North Carolina | *Peromyscus leucopus* | pine plantation | *Pinus* spp. | small mammal | switchgrass | white-footed mouse

Article:

As the scope, scale, and number of potential sources of cellulosic-based liquid transportation fuels (i.e., biofuels) continue to grow globally, so does the debate regarding land sharing versus land sparing. This paradigm focuses on whether sustainable biofuels production increases are best met from multiple use landscapes (land sharing) versus maximizing production on marginal lands and setting aside other lands for conservation (land sparing; Anderson-Teixeira et al. **2012**, Fargione et al. **2008**). In short, scientists and policy makers have been evaluating sustainability trade-offs for converting either crop-producing or fallow lands for intensive management of biofuel production. Potential effects on sustainability from biofuel production include losses of wildlife habitat, net carbon sequestration, and changes to water use (Alcamo et al. **2005**, Searchinger et al. **2008**, King et al. **2013**, Rupp et al. **2012**). Effects on sustainability likely depend on biofuel feedstock (e.g., corn [*Zea mays*], woody residuals, or perennial grasses), landscape context, production management regime, geographic region, and/or other factors (Abbasi and Abbasi **2010**, Riffell et al. **2012**, Berger et al. **2013**, Duke et al. **2013**). First generation biofuels primarily are produced from food crops such as corn, sugar cane (*Saccharum officinarum*), or vegetable oils. Second generation sources of bioenergy, such as perennial grasses and agricultural or forest residues, are produced from a variety of agricultural and managed forest systems (Naik et al. **2010**). Recently, more emphasis has been placed on second generation feedstock sources, which may avoid food security issues, generate fewer greenhouse gases, and require lower nutrient inputs (Fargione et al. **2008**, Sedjo and Sohngen **2009**, Wright and Turhollow **2010**).

Gleaning of harvest residuals (tops, limbs, and/or unmerchantable hardwoods removed during or following a harvest) in intensively managed pine (*Pinus* spp.) stands has a long history of use for producing energy (Watson et al. **1986**, Puttock **1987**). Sustainability recommendations for forest-based energy products have focused primarily on growing short-rotation woody crops (e.g., *Populus* spp., *Eucalyptus* spp.; Riffell et al. **2011a**), forest thinning (Verschuyl et al. **2011**), or harvesting residual woody materials after a final harvest (Riffell et al. **2011b**, Forest Guild Southeast Biomass Working Group **2012**, Otto et al. **2013**). More recently, Europeans have increased proportion of energy produced from forest-based sources. The southeastern United States is meeting much of this demand through exportation of wood pellets to the European market (Sedjo and Sohngen **2009**, Goh et al. **2013**). Further, new technologies are being implemented to convert woody biomass into liquid transportation fuels (Kirilenko and Sedjo **2007**). The southeastern United States will be a primary source of biomass for the expected 60% increase in demand for woody energy over the next 10–15 years (Sedjo and Sohngen **2009**).

In addition to harvesting woody biomass, great potential exists for growing energy crops planted between tree rows in intensively managed pine stands (Albaugh et al. **2012**, Blazier et al. **2012**, Riffell et al. **2012**). Intercropping switchgrass (*Panicum virgatum*) or other perennial grasses in pine plantations does not increase the overall footprint of production area and may positively increase biodiversity by increasing vegetation heterogeneity and abundance of grass-associated species in the community (Riffell et al. **2012**). Alternatively, timing of harvesting of intercropped grasses could negatively affect reproduction of grassland nesting birds or small mammals (Riffell et al. **2012**). Thus far, intercropping switchgrass between tree rows has been implemented primarily at a plot scale. Given the 16 million ha of intensively managed forests in the southeastern United States prospectively available for biofuels production, intercropping

switchgrass has potential to influence wildlife populations over a large area (Wright and Turhollow **2010**, Riffell et al. **2012**, Zhang et al. **2012**).

Determining effects of biofuel production on intensively managed pine stands, including both gleaning harvest residuals and intercropping energy grasses, on ecological sustainability has received surprisingly little research (Riffell et al. **2011b**, **2012**; Rupp et al. **2012**). Rodents are excellent study animals for examining effects of forest-based biofuels because many species need downed, woody debris to meet their life-history requirements, and they use logs and stumps as nesting sites, resting sites, foraging areas, or for below-ground access (Maser et al. **1978**, Loeb **1999**, Mengak and Guynn **2003**, Pearce and Venier **2005**). Further, members of the rodent community in the southeastern United States, such as hispid cotton rats (*Sigmodon hispidus*) and eastern harvest mice (*Reithrodontomys humulis*) are associated with grassy or complex understory structure (Atkeson and Johnson **1979**, Browne et al. **1999**, Mengak and Guynn **2003**). Therefore, although removal of woody residuals might be expected to have negative effects on rodent demographics, abundant grasses interspersed with early successional pine trees may positively influence some rodent species (Marshall et al. **2012**). Further, the length of time a pine plantation exists in an early successional state may be lengthened by intercropping switchgrass, especially if wider row spacing is used to facilitate switchgrass management, which could positively influence a subset of species dependent on this increasingly rare structural condition (Litvaitis **1993**, Askins **2001**, Fuller and DeStefano **2003**, King and Schlossberg **2014**).

To better understand influence of biofuel production on biodiversity, we examined effects of harvesting woody residuals and intercropping switchgrass in loblolly pine (*Pinus taeda*) plantations on metrics of rodent community diversity, abundance, and population performance to 4 years post-treatment in a randomized and replicated field experiment in eastern North Carolina, USA. In prior research at this site over 2 years post-treatment, we determined that 1) rodents exhibited species-specific responses to biofuel feedstock production options, with native white-footed mice (*Peromyscus leucopus*) being most abundant in treatments without switchgrass and invasive house mice (*Mus musculus*) being most abundant in treatments with switchgrass (Marshall et al. **2012**); 2) white-footed mice maintained their functional role in intercropped treatments (Briones et al. **2013**); and 3) rodent community composition did not change in response to treatments (Marshall et al. **2012**). Only white-footed mice exhibited treatment effects on demography, with survival higher in treatments without switchgrass, but we found no effects on survival from harvesting woody residuals (Marshall et al. **2012**).

The above results were only to 2 years post-treatment. However, we predict that rodent responses may change through time as switchgrass becomes well established, downed woody debris is further decayed, and pine trees grow. Herein, we extend our previous research to 4 years post-treatment to determine effects of harvesting woody residuals and intercropping switchgrass in loblolly pine plantations on rodents. We hypothesized that changes to vegetation and near-ground cover from intercropping switchgrass and removing coarse woody debris would manifest in species-specific differences in rodent populations, demography, and community assemblages. Specifically, we predicted that switchgrass monocultures would be associated with decreased diversity of small mammals through time because of reduced heterogeneity of vegetation structure (King et al. **2014**). We also expected to observe species-specific responses of rodents to biofuel treatments, with more individuals of early successional and grass-associated species (e.g.,

cotton rats) where switchgrass was present and well established. Lastly, because residual biomass serves as potential escape cover and nest sites, we predicted that species associated with downed woody debris (e.g., white-footed mice) would have lower survival and reproduction in treatments where biomass was removed.

STUDY AREA

The Lenoir 1 Intercropping Sustainability Study was a collaborative experiment established and maintained by Weyerhaeuser Company and Catchlight Energy LLC, a joint venture between Chevron and Weyerhaeuser Company, to examine effects of potential sources of forest-based biofuels on ecological sustainability. The study site, located in Lenoir County, North Carolina, USA, on land owned and managed by Weyerhaeuser Company, was established in 2008 on a 109-ha loblolly pine plantation planted in 1974. As was typical for the region, a series of linear drainage ditches, which improve the hydrologic conditions for pine growth and survival in plantations, were present. The surrounding landscape was a mixture of row-crop agriculture, forest, and rural housing.

The study was a complete randomized block design, with 5 treatments replicated and randomly applied within 4 blocks on approximately 1.11-ha plots, the unit of replication ($n = 20$ plots). A full description of the study area can be found in Leggett and Sucre (2012) with maps in Marshall et al. (2012) and Briones et al. (2013). The 5 treatments were 1) traditional operational pine establishment with biomass left in place (non-merchantable material left on site), which served as the control for this study (PB+); 2) traditional pine establishment with biomass of materials that could potentially be used for biofuel production removed (PB-); 3) pine plantation with switchgrass intercropped between pine rows and biomass left in place ($P \times SB+$); 4) pine plantation with switchgrass intercropped and biomass removed ($P \times SB-$); 5) switchgrass production with only residual biomass removed (S).

The study area was clear cut and loblolly pine seedlings planted during winter 2008. Switchgrass was planted during June 2009. Following clear cutting, loblolly pines were established using standard Weyerhaeuser methods including site preparation and planting (approx. 1,100 trees/ha), vegetation management, and fertilization. For treatments where biomass was removed, an excavator moved residual woody debris from plots after clear-cut harvesting occurred. Although excavators are not standard equipment for biomass harvests, they facilitated an intense biomass removal, resulting in an average reduction in downed, woody biomass from 9.4 Mg/ha to 1.5 Mg/ha, based on measuring down, woody material ≥ 5 cm in diameter (Beauvais 2010). Fine woody material was left on site. Site preparation for planting varied by treatment, with pine treatments being V-sheared and bedded using a bulldozer with required attachments to create a raised planting surface for pines. Additionally, Weyerhaeuser's liquid suspension-based fertilizer with 3% nitrogen, 6.2% phosphorus, 2.5% potassium, 4.5% magnesium, and 2% calcium was incorporated into beds to promote pine seedling root development and establishment. Intercropped switchgrass treatments incurred additional V-shearing to prepare a 3.1-m strip between crop tree rows to plant switchgrass. Switchgrass only plots had the entire plot V-sheared and roots raked after biomass was removed from the sites, so that no large woody material remained. Prior to planting pines, Chopper® (Research Triangle Park, NC), a pre-emergent herbicide, was used to temporarily control competing vegetation. Pines were planted at 6.1-

m × 1.5-m spacing and switchgrass was planted at 9 kg/ha of pure live seed using a modified corn planter. Switchgrass was fertilized when planted with a liquid suspension fertilizer and with Arborite® fertilizer (Weyerhaeuser, Federal Way, WA) during the second and fourth growing season (Jun 2010 and Apr 2012). Further, during summer 2010, switchgrass plots were treated with 2,4-D and a post-emergent herbicide (Basagram, BASF Corporation, Cary, NC) to control competing vegetation. Switchgrass was harvested annually during winter. Prior to the start of the second growing season (Apr 2010), switchgrass was mowed and left on site, but thereafter it was mowed, raked, and baled using standard agricultural equipment (Dec 2010, Dec 2011).

METHODS

Livetrapping

During Jul–Dec of 2009–2012, we used standard capture-mark-recapture methods to sample rodent populations and community dynamics. We established a 30-m × 60-m grid of 28 live traps at 10-m spacing. Each row of 7 trap stations included 6 Sherman traps (H.B. Sherman Traps Inc., Tallahassee, FL) and 1 randomly placed Longworth trap (Rogers Manufacturing Company, Peachland, British Columbia, Canada). We used Longworth traps to increase probability of capturing juvenile rodents and smaller bodied species on site (Anthony et al. **2005**). We set traps at dusk (1700–2030) and checked them at dawn (0600–0830) for 3 consecutive nights, which we termed a trapping period. Generally, we trapped 2 blocks of all 5 treatments simultaneously and then sampled the remaining 2 blocks for the next 3 consecutive nights. We baited traps with rolled oats and sunflower seeds and added cotton to traps when the weather was predicted to be <10°C. Upon capture, we identified each individual rodent to species, marked them with a uniquely numbered ear tag (Monel Numeric size 1005-1; National Band and Tag Co, Newport, KY), assessed them for sex, age (juvenile or adult), and reproductive condition, weighed (g) them, measured hind foot length (mm), and released them at the capture site (Marshall et al. **2012**). We assigned juvenile or adult age classes based on body mass and pelage characteristics, considering white-footed mice as adults when they had completed their post-juvenile molt (Layne **1968**) and hispid cotton rats as adults when they weighted >80 g (Chipman et al. **1965**). All rodent livetrapping and handling protocols were approved by the North Carolina Wildlife Resources Commission (09-SC00162, 10-SC00162, 11-SC00162, 12-SC00162) and the University of North Carolina at Greensboro Institutional Animal Care and Use Committee (Protocol Numbers 09-09, 10-04, 11-13).

Statistical Analyses

We examined annual changes in mean population and diversity metrics for years 1–4 post-treatment establishment. We followed the methods of Marshall et al. (**2012**) and used our livetrapping data to estimate population metrics, including population abundance, apparent survival, and recruitment. With Pollock's robust design model (Huggins closed capture estimator) in Program MARK, we estimated population abundance during each trapping period and apparent survival for each inter-trapping period interval (Pollock et al. **1990**, White and Burnham **1999**). We selected the best model for each species-year grouping based on the lowest corrected Akaike's Information Criterion (AIC_c) values (Burnham and Anderson **2002**). We calculated recruitment from births and immigration using a robust design Pradel survival and

recruitment model and the Huggins closed capture estimator (Huggins 1991, Pradel 1996). We parameterized encounter capture and recapture probabilities (p and c) for year-species models based on the best-fit model from the adult population abundance models. Because sample sizes were small after we separated number of individuals by species, plot, and year, we limited models to those assuming constant recruitment. Therefore, recruitment estimates represent recruitment/individual/plot. With our livetrapping data, we calculated richness, Shannon's diversity index, and Simpson's diversity index ($1/D$) for each plot-year combination (McCune and Grace 2002) using package Vegan (Oksanen et al. 2013) in Program R (R Core Team 2013).

We tested for differences in population metrics (abundance, survival, recruitment) and diversity (richness, Shannon's diversity index, Simpson's index to diversity) among plots for effects of treatment, year, or a treatment \times time interaction using a repeated-measures analysis of variance (ANOVA) that incorporated a block for plots sampled over time. Prior to analysis, we examined data for normality with a Kolmogorov-Smirnov test and for homogeneous variance with a modified Levene's test. We rank-transformed data that violated parametric assumptions. We made post-hoc pairwise comparisons using Tukey-adjusted P -values.

To evaluate how rodent communities changed through years and across treatments, we used nonmetric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity. We examined multivariate normality with a modified Shapiro–Wilks test. We used 2-dimensional solutions for each NMDS based on scree plots. For each NMDS, we conducted 50 random starts. We used 1-way analysis of similarities (ANOSIM), each with 999 permutations, to test for significant differences among treatments and years. We used a similarity percentage (SIMPER) procedure to identify which species were contributing the most to dissimilarity between treatments and years. We conducted ANOVAs using Proc Mixed in SAS (SAS 9.3, Cary, NC). We used Program R (R Core Team 2013) with ecodist (Goslee and Urban 2007), MASS (Venables and Ripley 2002), and Vegan (Oksanen et al. 2013) packages for NMDS and SIMPER analyses, and we used the PAST (version 3) data analysis package for ANOSIM and subsequent Bonferroni corrected pairwise comparisons (Hammer et al. 2001). For all analyses, we considered $P < 0.05$ as significant.

RESULTS

Our livetrapping resulted in 7,777 captures of 3,401 rodents (mice, rats, and voles) across 45,730 trap nights and 5–8 trapping periods/year (2009: 8 trapping periods, 2010: 6 trapping periods, 2011: 5 trapping periods, 2012: 6 trapping periods). Across the 4 years of study, we captured 781 white-footed mice, 751 house mice, 1,559 hispid cotton rats, 281 eastern harvest mice, 17 woodland voles (*Microtus pinetorum*), 12 marsh rice rats (*Oryzomys palustris*), and had 1 capture of a southeastern shrew (*Sorex longirostris*), 38 captures of least shrews (*Cryptotis parva*), 15 captures of northern short-tailed shrews (*Blarina brevicauda*), and 15 captures of southern short-tailed shrews (*Blarina carolinensis*) (Table 1). Capture and recapture rates were large enough to use mark-recapture methods for house mice, white-footed mice, and cotton rats in all 4 years of the study, and for eastern harvest mice in 2011 and 2012.

Table 1. Number of individual rodents captured or number of shrew captures with live traps by year across biofuels treatments (woody debris removal and/or switchgrass intercropping) at the Lenoir 1 Sustainability Study Site in eastern North Carolina, USA, 2009–2012

	Year			
	2009	2010	2011	2012
White-footed mouse (<i>Peromyscus leucopus</i>)	267	297	179	38
House mouse (<i>Mus musculus</i>)	248	310	126	67
Cotton rat (<i>Sigmodon hispidus</i>)	122	1,030	294	113
Eastern harvest mouse (<i>Reithrodontomys humulis</i>)	11	15	59	196
Marsh rice rat (<i>Oryzomys palustris</i>)	0	6	2	4
Woodland vole (<i>Microtus pinetorum</i>)	0	0	10	7
Southeastern shrew (<i>Sorex longirostris</i>)	0	0	1	0
Least shrew (<i>Cryptotis parva</i>)	0	0	0	38
Southern short-tailed shrew (<i>Blarina carolinensis</i>)	0	0	0	15
Northern short-tailed shrew (<i>Blarina brevicauda</i>)	0	0	0	15

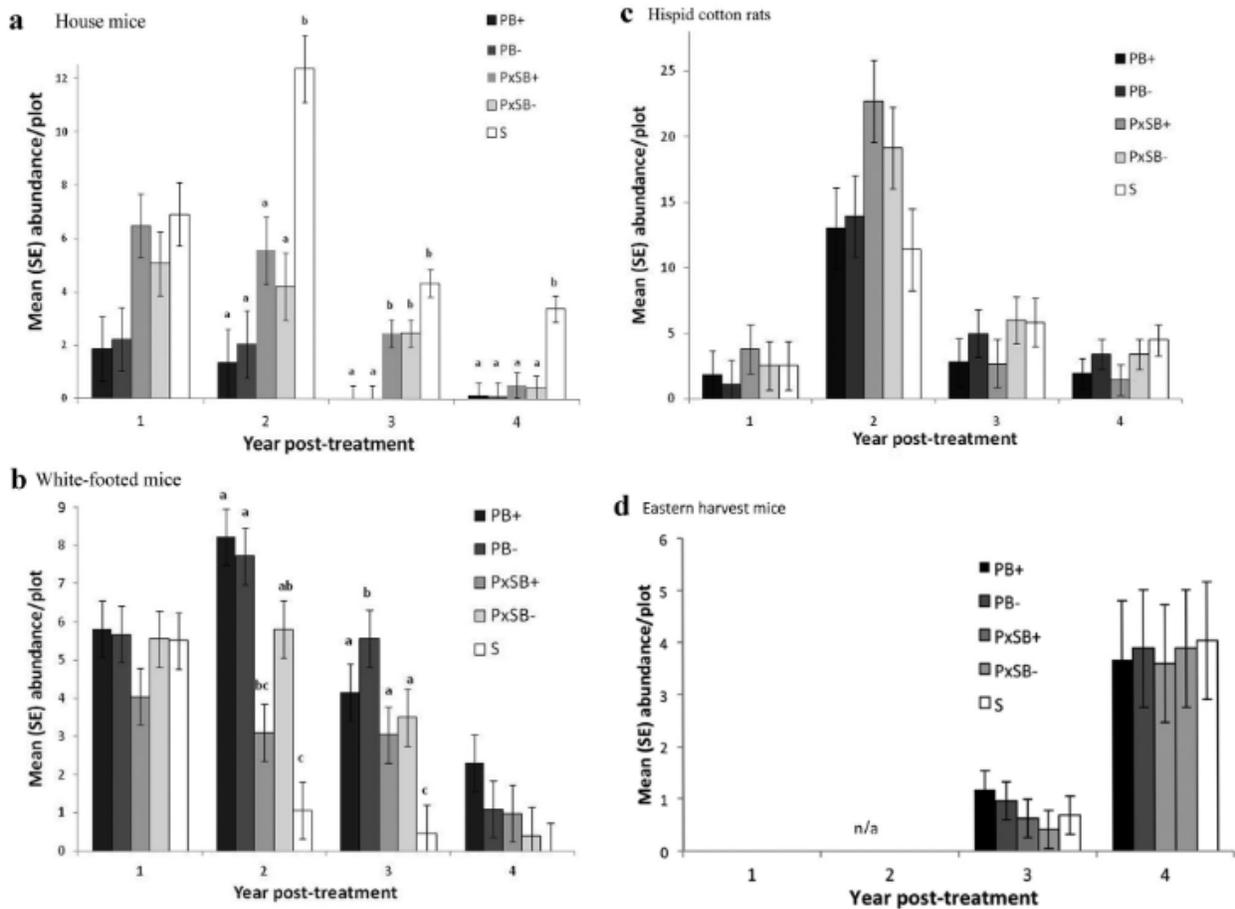


Figure 1. Response of (a) house mice (*Mus musculus*), (b) white-footed mice (*Peromyscus leucopus*), (c) hispid cotton rats (*Sigmodon hispidus*), and (d) eastern harvest mice (*Reithrodontomys humulis*) to biofuels treatments at the Lenoir 1 Sustainability Study in Lenoir 1, North Carolina, USA, 2009–2012. Treatments included pine plantation with residual woody biomass in place (PB+), pine plantation with a harvest of residual woody biomass (PB-), pine intercropped with switchgrass (*Panicum virgatum*) and residual woody biomass in place (P × SB+), pine intercropped with switchgrass and a harvest of residual woody biomass (P × SB-), and a switchgrass monoculture with all residual woody biomass removed (S). Different letters indicate statistical differences ($P < 0.05$) among treatments within a year.

Abundance

We found a treatment \times year interaction ($F_{12, 45} = 2.79$, $P = 0.006$) for abundance of house mice (Fig. 1a). House mouse populations did not differ across years in PB+, PB-, or P \times SB- plots, ($P > 0.079$), but abundances in P \times SB+ were an order of magnitude greater in year 1 and 2 compared to year 4 ($P < 0.037$), and abundances in switchgrass plots were 184–265% greater in year 2 compared to year 3 or 4 ($P < 0.001$). Across treatments, abundances of house mice in S were 2 \times greater than abundances of house mice in other treatments in both year 2 and 4 post-treatment ($P < 0.044$), and greater than both pine only plots (PB+, PB-) in year 3 ($P < 0.001$), where no house mice were captured.

We also found a treatment \times year interaction ($F_{12, 45} = 3.55$, $P = 0.001$) for abundance of white-footed mice (Fig. 1b). The effect of treatment was inconsistent across years, with no effect of treatments in either year 1 ($P > 0.973$) or 4 ($P > 0.785$). In year 2, however, both pine only treatments and intercropped plots with biomass removed had 5.4–7.7 \times greater abundance of white-footed mice than S plots ($P < 0.009$). Intercropped plots with biomass in place (P \times SB+) were intermediate to pine or switchgrass plots (Fig. 1b). At 3 years post-treatment, PB- plots had 12.1 \times more white-footed mice than S plots. Further, abundance of house mice declined through time and was lower in year 4 than previous years across all treatments ($P < 0.035$) except for in P \times SB+.

Abundance of hispid cotton rats was affected by year ($F_{3, 45} = 82.56$, $P < 0.001$) but not treatment ($F_{4, 12} = 0.30$, $P = 0.871$) and we did not find evidence of a year \times treatment interaction ($F_{12, 45} = 0.70$, $P = 0.744$; Fig. 1c). We estimated 3.6–6.8 \times more cotton rats in year 2 than other years. During years 3 and 4, abundance of eastern harvest mice was not affected by treatment ($F_{4, 12} = 0.06$, $P = 0.992$), but we found a year effect ($F_{1, 15} = 143.15$, $P < 0.001$), with abundances 5.0 \times greater in year 4 compared to year 3 ($P < 0.001$; Fig. 1d).

Survival

Not all plots had resident house mice in each year so we did not estimate demographic metrics for every plot \times year combination. Survival of house mice did not differ among treatments ($F_{4, 12} = 3.17$, $P = 0.054$) and we did not find an effect of year on house mouse survival ($F_{3, 30} = 1.80$, $P = 0.170$; Table 2). Survival of white-footed mice was affected by treatment ($F_{4, 12} = 6.46$, $P = 0.005$) and year ($F_{3, 12} = 15.10$, $P < 0.001$), but we did not find a treatment \times year interaction ($F_{11, 12} = 2.21$, $P = 0.095$; Table 2). However, post-hoc comparisons of pair-wise differences between treatments and years were not significant ($P > 0.149$). Survival of hispid cotton rats did not differ across treatments ($F_{4, 12} = 1.01$, $P = 0.441$) but was affected by year ($F_{3, 12} = 62.69$, $P < 0.001$), with survival estimates 1.3–1.8 \times higher in year 2 compared to all other years ($P \leq 0.012$; Table 2). We did not find an interaction between treatment and year ($F_{12, 12} = 1.54$, $P = 0.232$). Survival of eastern harvest mice was affected by year ($F_{1, 6} = 51.38$, $P < 0.001$) and was 1.8 \times higher in year 4 than in year 3 (Table 3). We did not find an effect of treatment ($F_{4, 12} = 0.96$, $P = 0.464$) or an interaction ($F_{4, 6} = 1.37$, $P = 0.347$) between treatment and year for survival of eastern harvest mice.

Table 2. Mean least squares (SE) estimates of apparent survival by treatment and year for rodents captured at the Lenoir 1 Sustainability Site, North Carolina, 2009–2012. We estimated survival from mark-recapture data of rodents using the Pollock's robust design model and the Huggins closed capture estimator in Program MARK. Some treatments or years did not have enough captures to produce estimates. We show non-transformed values for comparisons and different letters indicate statistically different post-hoc comparisons with Tukey's adjustments. Treatments: PB+ = pine biomass in place; PB- = pine biomass removed; P × SB+ = pine intercropped with switchgrass, biomass in place; P × SB- = pine intercropped with switchgrass, biomass removed; S = switchgrass only

	White-footed mouse (<i>Peromyscus leucopus</i>)	House mouse (<i>Mus musculus</i>)	Hispid cotton rat (<i>Sigmodon hispidus</i>)	Eastern harvest mouse (<i>Reithrodontomys humulis</i>)
Treatments				
PB+	0.89 (0.03)		0.72 (0.06)	0.56 (0.06)
PB-	0.88 (0.03)		0.66 (0.06)	0.56 (0.07)
P × SB+	0.78 (0.03)	0.52 (0.04)	0.67 (0.07)	0.50 (0.07)
P × SB-	0.84 (0.03)	0.55 (0.04)	0.78 (0.06)	0.65 (0.07)
S		0.70 (0.04)	0.75 (0.07)	0.64 (0.07)
Year				
2009	0.92 (0.02)	0.56 (0.04) ^{ab}	0.52 (0.03) ^a	
2010	0.84 (0.03)	0.61 (0.04) ^a	0.96 (0.01) ^b	
2011	0.84 (0.03)		0.71 (0.06) ^a	0.41 (0.04) ^a
2012		0.48 (0.05) ^b	0.67 (0.07) ^a	0.75 (0.03) ^b

Table 3. Mean least squares (SE) estimates of recruitment by treatment and year for rodents captured at the Lenoir 1 Sustainability Site, North Carolina, 2009–2012. We calculated recruitment from births and immigration using a robust design Pradel survival and recruitment model and the Huggins closed capture estimator in Program MARK. Some treatments or years did not have enough captures to produce estimates. We show non-transformed values for comparisons and different letters indicate statistically different post-hoc comparisons with Tukey's adjustments. Treatments: PB+ = pine biomass in place; PB- = pine biomass removed; P × SB+ = pine intercropped with switchgrass, biomass in place; P × SB- = pine intercropped with switchgrass, biomass removed; S = switchgrass only

	White-footed mouse (<i>Peromyscus leucopus</i>)	House mouse (<i>Mus musculus</i>)	Hispid cotton rat (<i>Sigmodon hispidus</i>)	Eastern harvest mouse (<i>Reithrodontomys humulis</i>)
Treatments				
PB+	0.07 (0.34)		0.52 (0.39)	0.11 (0.14)
PB-	0.09 (0.32)	0.56 (0.11)	0.76 (0.40)	0.38 (0.12)
P × SB+	0.19 (0.34)	0.35 (0.09)	0.31 (0.41)	0.55 (0.14)
P × SB-	1.00 (0.34)	0.29 (0.09)	0.47 (0.40)	0.37 (0.12)
S		0.11 (0.09)	0.32 (0.40)	0.27 (0.14)
Year				
2009	0.03 (0.27)	0.25 (0.06) ^{ab}	0.41 (0.30)	
2010	0.10 (0.27)	0.15 (0.06) ^a	0.04 (0.27)	
2011	0.17 (0.28)		0.29 (0.31)	0.57 (0.11) ^a
2012		0.46 (0.08) ^b	1.16 (0.29)	0.10 (0.07) ^b

Recruitment

Mean recruitment of house mice differed among years ($F_{3, 32} = 4.13$, $P = 0.014$) but not among treatments ($F_{4, 12} = 2.92$, $P = 0.067$) and we did not find a treatment × year interaction ($F_{11, 32} = 0.38$, $P = 0.956$). Mean recruitment of house mice in year 4 was 2.97× greater than recruitment in year 2 ($P = 0.006$; Table 3). We did not find an effect of treatment ($F_{4, 12} = 1.88$, $P = 0.179$) or year ($F_{3, 38} = 1.89$, $P = 0.148$) on mean recruitment of white-footed mice (Table 3). Mean recruitment of cotton rats was affected by year ($F_{3, 36} = 3.35$, $P = 0.029$) but not treatment ($F_{4, 12} = 1.06$, $P = 0.418$), and we did not find a treatment × year interaction ($F_{12,$

$\lambda_6 = 1.52, P = 0.164$). Recruitment estimates for cotton rats were very low (0.041 recruitment per individual per plot) at 2-years post-treatment, but between-year pairwise comparisons were not significant ($P > 0.055$; Table 3). Lastly, recruitment for eastern harvest mice was affected by year ($F_{1,7} = 8.87, P = 0.021$) and was 1.9× higher in year 4 compared to year 3. We did not find an effect of treatment ($F_{4,12} = 2.23, P = 0.127$) or a treatment × year interaction ($F_{4,7} = 1.52, P = 0.200$) for recruitment of eastern harvest mice (Table 3).

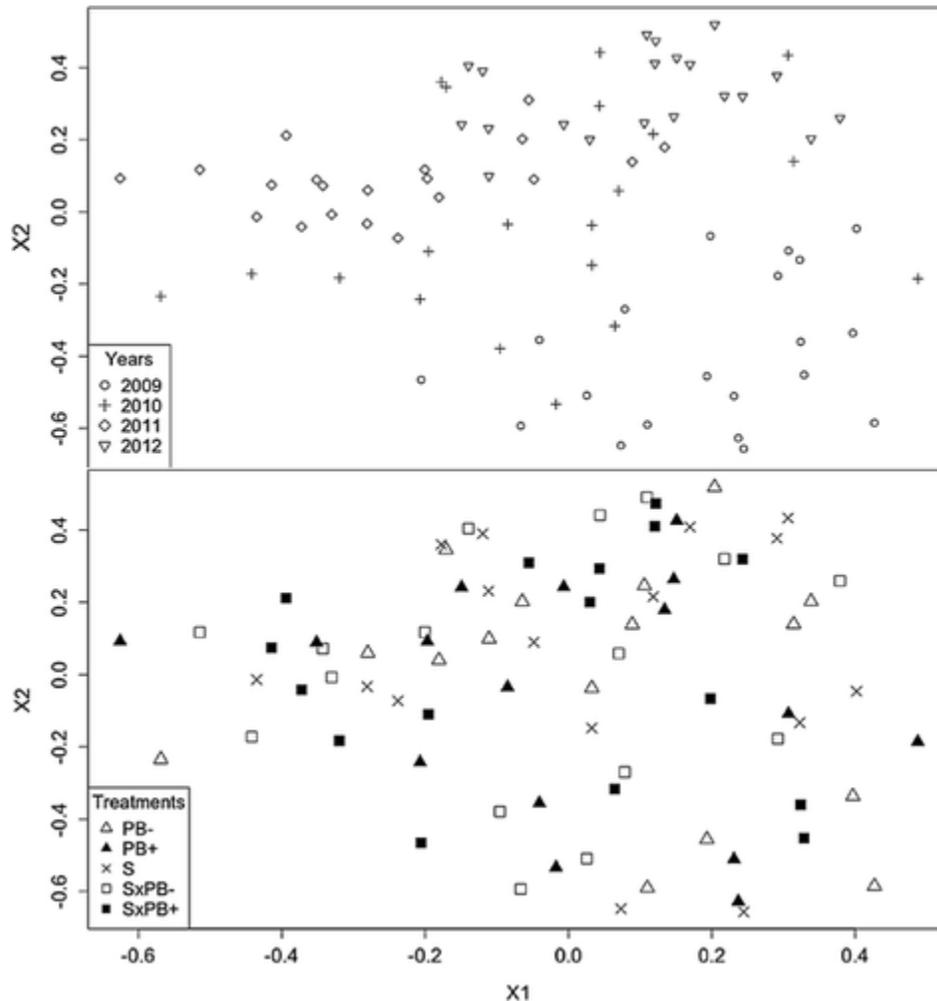


Figure 2. Non-metric multi-dimensional scaling of rodent communities indicated that rodent communities separated across years (top), but were similar across biofuels production treatments (bottom). Treatments included pine plantation with residual woody biomass in place (PB+), pine plantation with a harvest of residual woody biomass (PB-), pine intercropped with switchgrass (*Panicum virgatum*) and residual woody biomass in place (P × SB+), pine intercropped with switchgrass and a harvest of residual woody biomass (P × SB-), and a switchgrass monoculture with all residual woody biomass removed (S). We sampled rodents using livetrapping and mark-recapture techniques at the Lenoir 1 Sustainability Site in North Carolina from 1–4 years post-treatment, 2009–2012.

Community Metrics

Richness, Shannon–Wiener index, and Simpson's index were not affected by treatment ($F_{4,12} \leq 0.99, P > 0.45$) or year ($F_{3,45} \leq 1.88, P > 0.147$). The community matrix for the NMDS was not normally distributed ($W = 0.58, P < 0.001$). Final stress for the NMDS scaling treatment was

0.18. Consideration of our ANOSIM analyses and NMDS plots indicated higher dissimilarity among communities when compared across years ($R = 0.55$, $P = 0.001$) rather than biofuel treatments ($R = 0.07$, $P = 0.007$; Fig. 2). However, post-hoc pairwise comparisons showed that S treatments differed only from PB- ($P = 0.012$) and PB+ ($P = 0.003$) treatments with overall average pairwise dissimilarity of 60.67 and 64.26, respectively (Appendix A). Cotton rats contributed most to dissimilarity between S and PB- treatments and house mice contributed most to dissimilarity between S and PB+ treatments. Post-hoc pairwise comparisons showed that all years differed from each other (in all cases $P < 0.001$; Appendix B). Overall average dissimilarity ranged from 50.8% between years 1 and 2 of the study to 75.6% between years 1 and 4 of the study. With the exception of white-footed mice between years 1 and 4 of the study, cotton rats contributed most to dissimilarity for pairwise comparisons across years.

DISCUSSION

Increasing the intensity of forest management with biofuels production did not negatively affect rodent populations or communities, suggesting that multiple use landscapes can sustainably contribute to cellulosic energy needs. We found that removal of approximately 85% of downed woody material (Beauvais 2010) had little influence on rodents. Further, incorporating switchgrass into regenerating pine plantations or growing switchgrass alone produced species-specific effects on rodent abundance that varied through the first 4 post-treatment years. Through years 3 and 4 post-treatment, invasive house mice and native white-footed mice continued to have divergent patterns of abundance related to presence of planted switchgrass. However, forest succession was also important in explaining temporal trends in rodent populations (Marshall et al. 2012). Despite differences in abundances for some species, community diversity of rodents was not affected by biofuel treatments in any year. Thus, we determined that forest-based biofuel production had limited effects on rodent abundance and community structure during 4 years post-establishment as compared to standard pine silviculture.

Although intercropping can change vegetative structure of the understory, our results in conjunction with previous research indicate that wildlife communities in pine plantations are often similar despite whether switchgrass was intercropped or biomass was harvested. For example, rodent, herpetofauna, and avian richness and diversity were either unaffected by intercropping switchgrass, or converged to that of pine plantations by 3 years after switchgrass establishment (Marshall et al. 2012, Homyack et al. 2013, Loman et al. 2014). Further, the ecological role and trophic position of omnivorous white-footed mice was not affected by intercropping a potential food source, switchgrass (Briones et al. 2013). Similarly, harvesting of residual woody biomass did not have strong negative effects on either abundance or diversity of herpetofauna or rodents (Marshall et al. 2012, Homyack et al. 2013). However, planting switchgrass in a monoculture often changed the community structure of specific taxa and resulted in lower abundance of several species (Marshall et al. 2012, Homyack et al. 2013, Loman et al. 2014). Other aspects of sustainability such as water use, landscape context, or invasive species still need to be considered with intercropping switchgrass or other potential biofuels sources (Riffell et al. 2012, King et al. 2013).

Despite being commensal with humans, house mice commonly occur at low densities in managed forests of the southeastern United States (Mitchell et al. 1995, Iglay 2010, Lane et

al. 2010). In fall 2009 (year 1), we observed house mice immigrating across all treatment types into the research site from adjacent, recently harvested agricultural fields (Marshall et al. 2012; Fig. 1a). By year 4 when planted pines were >3 m tall and dominated intercropped and pine only plots, house mice were abundant only in S plots, suggesting they used all pine treatments similarly. We did not observe a concomitant treatment effect on house mouse survival or recruitment so that S plots with abundant house mice were not operating as either sink populations or ecological traps for this species (Van Horne 1983, Robertson and Hutto 2006; Table 2). Because recruitment of house mice was highest in year 4 when overall rodent abundances were lowest, populations may have been stabilizing and responding more to vegetative succession than biofuels treatments (Table 3). We conclude that intercropping switchgrass in young pine plantations did not facilitate presence of house mice in young pine plantations, and instead the mixed agricultural-forest landscape may have contributed to this pattern. A companion study in a forested matrix in east-central Mississippi, USA had no house mouse captures across 3 intercropped and 3 traditionally managed pine plantations sites (King et al. 2014).

Prior research documented lower abundances of native white-footed mice in treatments with switchgrass by year 2 (Marshall et al. 2012). In this study, by year 3 post-treatment, abundances of white-footed mice were lower in switchgrass only plots when compared to PB- plots, and by year 4 we were unable to detect a treatment effect (Fig. 1b). White-footed mice responded positively as an early successional species, but overall abundances declined across treatments over the 4 years. Based on our demographic analyses, survival of white-footed mice in 2012 was lowest in S plots, the treatment where abundance of house mice, a potential competitor, was greatest (Caldwell and Gentry 1965, Caut et al. 2007). Thus, despite potential negative effects to survival from house mice, white-footed mice were not extirpated through 4 years post-treatment, indicating that biofuel treatments did not alter inter-specific interactions significantly and allowed for coexistence of both species.

Cotton rats and eastern harvest mice, 2 species strongly associated with early successional habitat conditions with grassy cover, were affected by forest succession (Kincaid et al. 1983, Mengak and Guynn 2003) but not by biofuel treatments. The dense, herbaceous vegetation that dominates young pine plantations or pocosins provides adequate cover and easily exploitable food resources that sustain rapid population growth for both rodent species (Kincaid et al. 1983, Randolph and Cameron 2001). Abundance and demographic metrics of cotton rats and eastern harvest mice were strongly affected by year. We are unclear why cotton rat abundances decreased precipitously from year 2 to year 3 post-treatment; however, either the >30 cm of rainfall from Hurricane Irene on 26–27 August 2011 may have caused mortalities or cotton rats responded to forest succession and/or larger-scale population processes (Krebs and Myers 1974, Wilson et al. 2004). Similarly, nearly 18-fold increases in abundances of eastern harvest mice along with increases in survival and recruitment of eastern harvest mice further indicate that vegetative succession had a greater influence on abundance and demography than intercropping switchgrass or harvesting residual woody biomass.

In contrast to our prediction that S plots would have lower community diversity, we did not detect treatment or year effects on diversity. Rodent communities examined in ordination space were similar across treatments (Fig. 2b) but followed an expected successional trajectory across

years with year 1 (2009) being most different from year 4 (2012; Fig. 2a). Thus, in concordance with our analyses of single species, rodent assemblages were affected more by temporal changes in vegetation structure than by biofuel treatments. Other studies of young, managed pine forest in the southeastern United States have identified rapid changes to vegetation structure that occur between stand establishment and crown closure and subsequent indirect effects on small mammals (Mitchell et al. **1995**, Mengak and Guynn **2003**, Lane et al. **2011**, Hanberry et al. **2013**). As plantations age, we expect a more static rodent community in S plots where successional effects on vegetation structure will be minimal. We are unsure whether rodent diversity metrics will change at our study area as crown closure occurs, but intercropped stands may retain an understory layer of herbaceous vegetation longer than traditionally managed pine stands (Loman et al. **2014**). Increasing the length of time with abundant understory grasses could positively influence a suite of early successional species, including cotton rats, eastern harvest mice, and songbirds, at larger scales (King and Schlossberg **2014**, Loman et al. **2014**).

Downed woody debris helps rodents meet requirements for reproduction, foraging, and movement (Maser et al. **1978**, Mengak and Guynn **2003**, Loeb **1999**), yet our experimental removal of residual woody biomass did not negatively affect rodents. Most research linking downed woody material to small mammals is from the northwestern or northeastern United States. However, studies from the southeastern United States have positively linked *Peromyscus* (Loeb **1999**, Mengak and Guynn **2003**) or shrews (Soricidae; Davis et al. **2010**) to abundance of woody debris at varying spatial scales. Strength and existence of relationships between small mammals and woody debris appears to be context specific, with geographic location, landscape context, sampling duration, and species-specific requirements for downed wood likely contributing to variation (Riffell et al. **2011b**). Our results suggest that volume of retained downed wood following a biomass harvest in the Atlantic Coastal Plain may have been sufficient to avoid negative effects on rodents. At our study site, 1.5 Mg/ha of biomass remained on the treatments where biomass was removed (Beauvais **2010**), less than the 2.24 Mg/ha retention recommended by the Forest Guild (Forest Guild Southeast Biomass Working Group **2012**). Rodents possibly were using residual fine woody debris retained following clear-cut harvesting and mechanical site preparation. As retained woody debris deteriorates in the hot and humid climate of eastern North Carolina, downed logs, stumps, and fine woody debris may become more limiting and negative effects on rodents may materialize (Riffell et al. **2011b**).

At a broader scale, open canopy pine plantations with a vigorous understory vegetation layer that were historically maintained by fire, represent a condition currently rare on the landscape (Mitchell et al. **2006**). Intercropping switchgrass may extend the period that rapidly growing pine plantations provide this structural condition by slowing encroachment of woody vegetation between rows of planted pines (Loman et al. **2014**). Considering that early successional habitat conditions are limiting and many early successional associated species are in decline (Litvaitis **1993**, Askins **2001**, Fuller and DeStefano **2003**, King and Schlossberg **2014**), intercropping switchgrass may have an important role in providing this stand condition across managed forest landscapes.

MANAGEMENT IMPLICATIONS

Intercropping switchgrass in pine plantations and harvesting biomass had short-term and limited effects on rodent populations and community diversity. Therefore, intensively managed pine stands managed for production of forest-based biofuel feedstocks may contribute to meeting requirements for sustainable sources of cellulosic energy. Future research should aim to evaluate effects of operationally scaled biofuel treatments on rodent diversity and demographics and to elucidate relationships between rodents and down woody debris at larger spatial and longer temporal scales.

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APPENDIX A. Results of simpler analyses for significant ($P < 0.05$) pairwise comparison for rodent communities in biofuels treatments at the lenoir 1 sustainability site, North Carolina, USA, 2009–2012. We found significant differences between S (Switchgrass only) and A) PB- (Pine with biomass removed) and B) PB+ (Pine, with biomass in place) treatments with overall average pairwise dissimilarity of 60.67 and 64.26, respectively. abbreviations refer to species as follows: SIHI (*Sigmondon hispidus*), MUMU (*Mus musculus*), PELE (*Peromyscus leucopus*), REHU (*Reithrodontomys humulis*), MIPI (*Microtus pinetorum*), And ORPA (*Oryzomys palustris*).

Comparison	Species	Average % abundance in PB-	Average % abundance in S	Cumulative percent contribution to difference
S vs. PB-				
	Sihi	16.19	16.25	32.32
	Mumu	4.06	19.25	63.20
	Pele	13.75	7.31	88.43
	Rehu	3.69	3.38	98.81
	Mipi	0.38	0.00	99.66
	Orpa	0.00	0.19	100.00
S vs. PB+				
	Mumu	2.69	19.25	32.39
	Sihi	12.81	16.25	62.52
	Pele	13.44	7.31	87.33
	Rehu	3.75	3.38	98.50
	Mipi	0.38	0.00	99.41
	Orpa	0.13	0.19	100.00

APPENDIX B. Results of simpler analyses for significant pairwise comparisons of rodent communities at the lenoir 1 sustainability site, North Carolina, USA, 2009–2012. We found significant differences ($P < 0.05$) between all years. abbreviations refer to species as follows: SIHI (*Sigmondon hispidus*), MUMU (*Mus musculus*), PELE (*Peromyscus leucopus*), REHU (*Reithrodontomys humulis*), MIPI (*Microtus pinetorum*), AND ORPA (*Oryzomys palustris*). Overall average dissimilarity presented in bold under the list of species for each comparison.

Comparison	Species	Average % abundance in 2012	Average % abundance in 2011	Cumulative percent contribution to difference
2012 vs. 2011	Sihi	6.2	15.9	34.6
	Pele	2.35	9.55	56.53
	Rehu	10.05	3.15	78.31
	Mumu	3	6.55	96.69
	Mipi	0.35	0.6	99.17
	Orpa	0.2	0.15	100
	62.26			
2012 vs. 2009	Pele	2.35	19.4	38.61
	Mum	3	13.95	62.63
	Rehu	10.05	0.55	84.16
	Sihi	6.2	7.45	98.8
	Mipi	0.35	0	99.55
	Orpa	0.2	0	100
	75.56			
2012 vs. 2010	Mumu	6.2	40.05	38.61
	Sihi	3	15.25	62.63
	Pele	2.35	11.15	84.16
	Rehu	10.05	0.6	98.8
	Mipi	0.35	0	99.55
	Orpa	0.2	0	100

Comparison	Species	Average % abundance in 2012	Average % abundance in 2011	Cumulative percent contribution to difference
	74.45			
2011 vs. 2009	Sihi	15.9	7.45	32.62
	Pele	9.55	19.4	62.48
	Mumu	6.55	13.95	88.93
	Rehu	3.15	0.55	97.82
	Mipi	0.6	0	99.69
	Orpa	0.15	0	100
	50.58			
2011 vs. 2010	Sihi	15.9	40.05	54.54
	Mumu	6.55	15.25	78.3
	Pele	9.55	11.15	92.1
	Rehu	3.15	0.6	98.44
	Mipi	0.6	0	99.76
	Orpa	0.15	0	100
	50.92			
2009 vs. 2010	Sihi	40.05	0.5855	58.55
	Mumu	15.25	0.7985	79.85
	Pele	11.15	0.9847	98.47
	Rehu	0.6	1	100
	Mipi	0	1	100
	Orpa	0	1	100
	50.78			