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Relationships between white-footed mice and logging residue: Informing the sustainability of potential wood bioenergy harvests

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ABSTRACT

We examined local and site-scale relationships between white-footed mice (*Peromyscus leucopus*) and logging residue after timber harvests to assess potential effects of expanding bioenergy markets in the southern Appalachian region of the United States. We sampled mice in 10 recent (2013–2015) clearcut or shelterwood harvests dominated either by white pine or hardwoods prior to harvest. We captured mice May–August, 2016 and 2017 using 10 grids of 60 Sherman traps spaced 15 m apart and set twice for five consecutive nights in each year. We categorized traps as either near (≤5 m) or far (>5 m) from coarse woody debris (CWD; woody debris ≥10 cm in diameter). We estimated site-level woody debris volumes using modified prism sweep sampling and determined vegetation, woody debris, and ground cover composition at each trap location. White-footed mouse occupancy increased with greater trap-level CWD cover in all stands, and greater site-level woody debris volume in white pine stands. Mouse abundance increased with greater site-level woody debris volume, and abundance was greater at white pine sites than hardwood sites. These results demonstrate that residual logging debris is important to white-footed mice, both at the local- and site-scale. Reductions in residual logging debris following harvests, including via removal of low value stems for wood bioenergy, likely will result in decreased white-footed mouse occupancy and abundance. We recommend developing proactive strategies to retain scattered logging residues following even-aged timber harvests, especially in cases where bioenergy harvests occur in the southern Appalachian region.

1. Introduction

Downed wood, an often overlooked component of forests, serves a number of important ecological roles, including providing food and cover for wildlife. Occurring as small (<10 cm, termed fine woody debris or FWD) and large (≥10 cm, termed coarse woody debris or CWD) branches, fallen trees, and logs, downed wood provides critical resources for various wildlife taxa. Specifically, downed wood provides cover from predators (e.g., eastern chipmunks; Zollner and Crane, 2003), perches for birds (Shackelford and Conner, 1997; Hagan and Grove, 1999; Grodsky et al., 2016a), foraging areas for various wildlife (e.g., shrews; Loeb, 1996), nesting cover (e.g., ruffed grouse (*Bonasa umbellus*); Tirpak et al., 2006), and thermoregulatory cover (e.g., toads; Fritts et al., 2015a).

Small mammals, including rats, mice, and shrews, serve as vital prey animals, seed dispersers, and consumers of plants and invertebrates and are known to associate with downed wood (Harmon et al., 1986; Loeb, 1999). Therefore, woody debris availability likely influences abundance of small mammals and their associated ecosystem services (e.g., seed dispersal). For example, white-footed mice (*Peromyscus leucopus*) may select areas with larger and more abundant downed logs than randomly available (Dueser and Shugart, 1978), and individuals may use CWD more than other microsites in canopy gaps and closed canopy forests (Greenberg, 2002). However, Greenberg et al. (2006) did not document a relationship between mouse captures and downed wood following fuel reduction treatments in the southern Appalachians of the United States. Similarly, studies of shrew relationships with CWD suggest variation among regions (Davis et al., 2010; Greenberg and Miller, 2004) and among species (Fritts et al., 2015b). Generalist species, such as deer mice (*Peromyscus maniculatus*), may be less impacted by woody

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debris reductions (Sullivan et al., 2017) or numbers of downed logs than specialist species (Bowman et al., 2000), and specialists, such as the southern red-backed vole (*Myodes gapperi*), may persist in piles of debris following timber harvest (Sullivan et al., 2012; Sullivan and Sullivan, 2017). As such, reductions in downed wood volumes following timber harvest may have detrimental effects on some small mammal taxa. Considerable research has been conducted on the impact of downed wood on small mammals in mature forests, but less is known about the potential impacts of post-harvest downed wood removal.

Volume of woody debris in forest landscapes follows a "U-Shaped Chronosequence" from stand establishment to old growth (Gore and Patterson, 1986; Harmon et al., 1986). After a disturbance (e.g., timber harvest, high wind event, or wildfire), the volume of downed wood is relatively high in a forest (Harmon et al., 1986; Grodsky et al., 2016b). Over time, the volume of disturbance-generated woody debris decreases with decay, then increases as trees mature, senesce, and die, eventually falling to become downed wood (Harmon et al., 1986; Gore and Patterson, 1986). Timber harvests contribute to this dynamic by creating a large pulse of downed wood as tree tops, unmerchantable stems, and branches are left after a harvest (i.e., logging residue). However, management activities post-harvest, including site preparation, movement of debris (e.g., windrows), and debris removal (i.e., chipping or burning) may further alter downed wood volumes (Fritts et al., 2014).

As the demand for renewable sources of energy increases, bioenergy markets have expanded to include wood biomass chipped or pelletized and used to produce heat and electricity. The European Union currently has renewable energy standards favorable for wood pellet use, increasing the demand for wood pellets from the United States and other countries (Joudrey et al., 2012; Goh et al., 2013). An abundant source of woody biomass is low value tree species, small diameter stems, and other material that otherwise would be left after timber harvests as logging residue (Galik et al., 2009). Domestic markets for bioenergy have not greatly increased in the United States (Joudrey et al., 2012). However, wood pellet markets have the capacity to develop locally in some regions, including the southern Appalachians, where the pellets can be used to heat greenhouses, poultry houses, and schools (Patton, 2018).

As bioenergy markets potentially expand in the future, it is necessary to determine the potential ecological impacts of removing logging residue during harvesting, especially effects on habitat for small mammals and other wildlife. Recent studies in the Coastal Plain in the southeastern United States indicated that biomass harvests did not affect small mammal abundance (Fritts et al., 2015b; Fritts et al., 2017). However, the effects of downed wood reductions may be much different in the southern Appalachians, where many wildlife species are adapted to cool, moist microclimates, and where fires that consume downed wood may have been less frequent historically than in the Coastal Plain (Fritts et al., 2017).

We sampled white-footed mice in 10 harvested sites to determine the relationships between mice and residual debris volumes and distribution, helping to inform the potential impact of bioenergy markets on residual logging debris and associated wildlife in the southern Appalachians. We focused on white-footed mice because of their abundance, and their potential to represent other small mammals that could be affected by manipulations in residual logging debris. We used Sherman traps to estimate white-footed mouse occupancy at individual traps and abundance at each of the 10 harvest sites, and investigated whether these metrics were related to residual logging debris. We hypothesized that white-footed mice would be positively associated with woody debris cover and volume at both the trap (occupancy) and site (abundance) levels, respectively. Our study was not conducted in the context of operational wood bioenergy harvesting, but was designed to inform ecological sustainability goals of woody biomass markets as they potentially expand into the southern Appalachians. Additionally, the study adds to the sparse research available on the relationships between wildlife and downed woody debris in forests of the eastern United States.

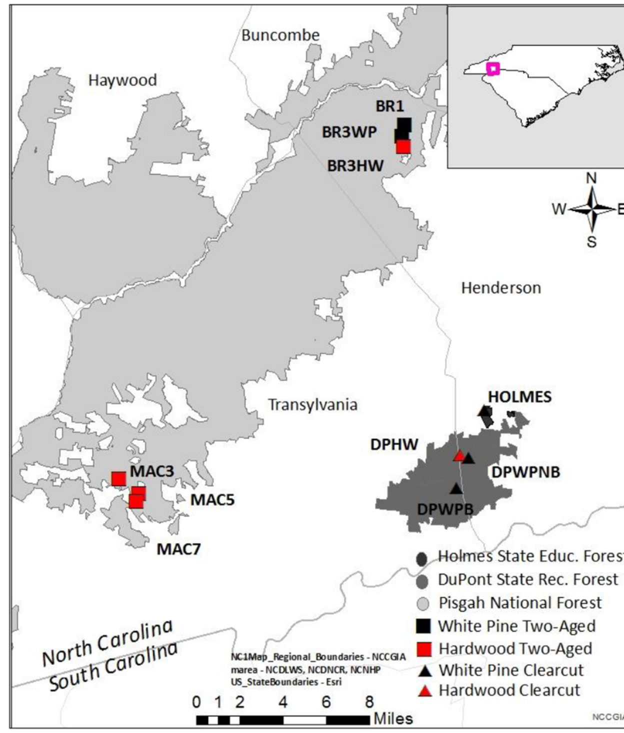

Fig. 1. Map of the 10 study sites sampled in western North Carolina, USA, in 2016 and 2017. BR1, BR3WP, BR3HW, MAC3, MAC5, and MAC7 were located in the Pisgah Ranger District of Pisgah National Forest. DPHW, DPWPNB, and DPWPB were located in DuPont State Recreational Forest. HOLMES was located in Holmes Educational State Forest.

2. Methods

2.1. Study area

The study area consisted of 10 harvested sites on public land in western North Carolina (Fig. 1). Harvests occurred between 2013 and 2015 and ranged in size from 3.2 ha to 16.6 ha. Six sites were located in Pisgah National Forest (PNF), 3 in DuPont State Recreational Forest (DSRF), and 1 in Holmes State Educational Forest (HSEF) (Fig. 1). The PNF sites were harvested using a 2-aged regeneration method, leaving a basal area averaging 4.98 m^2 ha^{-1} (Fig. 1). The DSRF and HSEF sites were harvested using the clearcut regeneration method (Fig. 1). We assigned forest type to each site based on the dominant tree species before harvest (US Forest Service; North Carolina Forest Service staff pers. comms.; Google Earth imagery). Five of the sites were previously dominated by white pine (*Pinus strobus*) (1 in HSEF, 2 in DSRF, and 2 in PNF) and five were previously dominated by hardwoods (4 in PNF and 1 in DSRF) (Fig. 1). Post-harvest site preparation treatments, involving the felling of trees < 20 cm in diameter and of non-target species along with herbicide treatment of stumps, were conducted in PNF before sampling began in 2016 for 4 sites (2 hardwood; 2 white pine) and after sampling was completed in 2016 for 2 hardwood sites (Fig. 1). All sites were allowed to naturally regenerate except the DSRF hardwood site, which was replanted with shortleaf pine (*Pinus echinata*). None of the harvests included a bioenergy component.

2.2. Mouse Capture

We captured white-footed mice in each harvested site using a trapping grid consisting of 60 Sherman traps with 15-m spacing between traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA). Traps were 7.62-cm wide, 8.89-cm high, and 22.86-cm long. We placed trapping grids at least 15 m from the edge of the harvested area to minimize potential effects of adjacent site types (Greenberg, 2002). We baited Sherman traps with oats and kept them open for five consecutive nights per trapping period. We sampled each site for two trapping periods between May and August in 2016 and 2017, with approximately six weeks between trapping periods each year. We noted proximity to coarse woody debris (debris with a diameter ≥ 10 cm; CWD) for each trap, with traps ≤ 5 m from CWD labeled as “near” CWD and traps > 5 m from CWD labeled as “far.” We tagged captured individuals in the right ear with a uniquely numbered tag (Monel size 1, style 1005-1P, National Band & Tag Company, Newport, KY, USA) and released individuals at the capture site immediately after marking. All trapping was conducted in accordance with the NCSU Institutional Animal Care and Use Committee protocol (IACUC ID# 16-035-O).

2.3. Vegetation structure

We measured vegetation structure and composition at plots centered on each Sherman trap location (600 total) once, between May and August of either 2016 or 2017. We used a 1-m height Weins pole to record contacts of grass, forb, and woody (trees, shrubs and woody vines) vegetation, FWD, CWD, bare ground, or leaf litter at 1-m intervals for 5 m in each cardinal direction, for a total of 20 points per Sherman trap location (Moorman and Guynn, 2001). We divided the number of points with a particular cover type recorded by the total number of points measured (20) to calculate the percent cover for each trap location.

2.4. Downed wood volumes

We estimated downed wood volumes in each of the 10 sites during winter 2016–2017, when live vegetation was less likely to impede the view of woody debris on the ground. We estimated debris volumes at 15 Sherman trap locations spaced systematically across each site and summed the estimates for scattered and piled debris to create an estimate of overall debris volume in m^3 ha^{-1} for each site. We conducted prism sweep sampling to estimate woody debris volume near Sherman trap locations by measuring the length of all FWD or CWD pieces close enough to the Sherman trap location to be considered “in” using a wedge prism (Bebber and Thomas, 2003; Osbourne et al., 2012). Volume estimates were taken separately for “scattered” and “piled” woody debris (Bebber and Thomas, 2003; Osbourne et al., 2012, Fritts et al., 2014).

2.5. Statistical analysis

We ran occupancy analysis (MacKenzie et al., 2002) using package Unmarked (Fiske and Chandler, 2011) in R (version 3.4.3) (R Core Team, 2017) to determine potential predictors of white-footed mouse presence at the trap level during the 10 days of sampling at each site in each year. This analysis allowed us to account for imperfect detection, and provided insight into the space use by individual mice along with the covariates that influenced the probability of the use of an individual trap. We used the corvif function in HighstatLibV10.R (Copyright Highland Statistics LTD) in R to test for multicollinearity (Zuur et al., 2009). Variance inflation factors for the covariates were less than 5, so we did not eliminate any covariates. We used the Dredge function (package MuMIn) (Barton, 2018) to examine all possible combinations of covariates separately for detection and occupancy. The covariates considered on detection in the global model included day of trapping and proximity to CWD. The covariates considered on occupancy in the global model included percent cover of woody vegetation, forbs, grass, CWD, and FWD, site-level woody debris volume, proximity to CWD (near or far), site type (white pine or hardwood), and year (2016 or 2017). Before initiating analysis, we standardized each of the covariates by subtracting the mean from each and dividing each by their standard deviation (Taillie et al., 2015). We completed model selection for the occupancy models created by the Dredge function (package MuMIn) and selected the most competitive model based on the lowest Akaike’s Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson, 2002). We created plots of predicted occupancy based on the best model using the predict method and ggplot2 (Fiske and Chandler, 2011; Wickham, 2016).

We conducted Closed Capture-Recapture analysis using RMark (Laake, 2013) in R (version 3.4.3) (R Core Team, 2017) to estimate mouse abundance at each of the 10 sites. Due to the low number of captures during 2016, we only ran Closed Capture-Recapture analysis on the 2017 data. We used the create.model.list function in RMark to create Closed Capture-Recapture models with combinations of either no covariate or time on capture and recapture probabilities and to select the best model (Otis et al., 1978; Laake, 2013). We used site as a grouping variable to obtain separate estimates of abundance for each site. We selected the best model as the one with the lowest AICc value (Burnham and Anderson, 2002). After obtaining abundance estimates for each site, we ran a generalized linear model (GLM) in R to determine if there was a relationship between estimated mouse abundance and site type or the standardized site-level woody debris volumes (or an interaction between site type and standardized woody debris volume) (R Core Team, 2017). Before running the generalized linear models, we used PROC ANOVA in SAS (version 7.15 HF3) (SAS Institute Inc., 2017) to determine if there was a significant association between site type and woody debris volume and determined there was no correlation. We selected the best GLM based on the lowest AIC value (Akaike, 1973). We used the predict method (Fiske and Chandler, 2011), ggplot2 (Wickham, 2016), and ggpubr (Kassambara, 2018) to predict abundance based on the top model.

We also examined apparent survival for white-footed mice within the 10 sites. Survival analysis was completed for only the 2017 data due to the relatively low number of captures in 2016. We used the create.model.list function in RMark (Laake, 2013) to complete model selection on Cormack-Jolly-Seber models (Cormack, 1964; Jolly, 1965; Seber; 1965), considering combinations of no covariates and time on capture probability and no covariates, time, and site on apparent survival (for a total of 6 models). We selected the most competitive model as the one with the lowest AICc value (Burnham and Anderson, 2002).

3. Results

3.1. Site-level woody debris volumes

Average ($\pm$ SE) site-level woody debris volume for the 10 study sites was 176.66 $\pm$ 28.71 m^3 ha^{-1} (range 56.05–376.61 m^3 ha^{-1}) (Table 1). Scattered woody debris volumes ranged from 40.39 m^3 ha^{-1} to 145.28 m^3 ha^{-1} (Table 1). Piled woody debris volumes ranged from 3.48 m^3 ha^{-1} to 293.26 m^3 ha^{-1} (Table 1).

3.2. Capture summary

We captured 491 individual white-footed mice a total of 1632 times in 12,000 trap nights during the 2 field seasons (2016 and 2017) (Table 2). We captured 84 individual white-footed mice a total of 270 times in 2016, and 416 individual white-footed mice a total of 1362 times in 2017. Nine white-footed mice captured in 2016 were recaptured in 2017. Other species captured were golden mouse (*Ochrotomys nuttalli*), cotton rat (*Sigmodon hispidus*), woodland vole (*Microtus pinetorum*), meadow vole (*Microtus pennsylvanicus*), woodland jumping mouse (*Napaeozapus insignis*), unidentified shrews (Soricidae), eastern chipmunk (*Tamias striatus*), eastern cottontail (*Sylvilagus floridanus*), and eastern gray squirrel (*Sciurus carolinensis*) (Table 2). We did not

Table 1
Scattered, piled, and overall woody debris volumes at each recently harvested study site in western North Carolina, USA. We classified each site as white pine or hardwood based on the overstory present before harvest.

Site	Site type	Scattered Woody Debris Volume (m^3 ha^{-1})	Piled Woody Debris Volume (m^3 ha^{-1})	Overall Woody Debris Volume (m^3 ha^{-1})
BR1[b]	White Pine	81.06	72.76	153.82
BR3WP[b]	White Pine	60.92	32.13	93.05
DPWPB	White Pine	76.11	70.55	146.66
DPWPNB	White Pine	52.57	3.48	56.05
HOLMES	White Pine	145.28	75.86	221.14
BR3HW[b]	Hardwood	71.29	32.47	103.76
DPHW	Hardwood	40.39	133.65	174.05
MAC3[b]	Hardwood	102.32	112.51	214.83
MAC5[a]	Hardwood	93.10	133.49	226.59
MAC7[a]	Hardwood	83.34	293.26	376.61
White Pine	**Mean**	83.19	50.96	134.14
	Standard Error	16.35	14.30	28.20
Hardwood	**Mean**	78.09	141.08	219.17
	Standard Error	10.74	42.36	44.84
Overall	**Mean**	80.64	96.02	176.66
	Standard Error	9.26	25.88	28.71

[a] Site preparation was conducted after sampling began in 2016
[b] Site preparation was conducted before sampling began in 2016

Table 2
Number of individual and total small mammal captures by year (2016 and 2017) and species within 10 recently harvested sites in western North Carolina, USA.

Species	Number of Individuals		Number of Captures	
	2016	2017	2016	2017
Peromyscus leucopus	84	416	270	1362
Ochrotomys nuttalli	10	89	16	163
Sigmodon hispidus	14	12	21	36
Microtus pinetorum	3	5	3	5
Microtus pennsylvanicus	0	8	0	11
Soricidae	3	4	3	4
Napaeozapus insignis	0	1	0	1
Neotoma floridana or *Rattus* spp.	0	2	0	2
Tamias striatus	1	Unknown*	1	15
Sylvilagus spp.	2	3	2	3
Sciurus carolinensis	0	1	0	1

*We did not mark eastern chipmunks (*Tamias striatus*) in 2017, so the number of individuals could not be determined.

analyze responses of other species to debris retention because captures were too few.

3.3. Trap-level occupancy

The detection model with the lowest AICc score indicated that detection was greater near CWD and increased over the 10 days of trapping (Table 3). Mean detection was 0.286 (mean SE = 0.009) at traps near CWD and 0.204 (mean SE = 0.012) at traps far from CWD.

Each of the five occupancy models with the lowest AICc scores included CWD cover, grass cover, site-level woody debris volume, site type, year, and the interaction between site type and woody debris volume (Table 3). The most competitive occupancy model contained CWD cover, grass cover, forb cover, site-level woody debris volume, site type, year, and the interaction between site type and woody debris volume on occupancy (Table 3). Two models had AICc values within 2 units of the top model. However, the additional parameters in these 2 models had high standard errors and p-values > 0.05, so model averaging was not used. The top model indicated that occupancy probability increased with greater CWD cover at the trap ($b = 0.26$, SE = 0.08) and greater woody debris volume at the site ($b = 0.10$, SE = 0.10); however, the positive relationship between occupancy probability and site-level woody debris volume was predominantly in white pine stands ($b = 0.70$, SE = 0.20) (Table 4; Fig. 2). The top model also indicated that occupancy probability declined as forb cover increased ($b = -0.20$, SE = 0.07) and declined as grass cover increased ($b = -0.31$, SE = 0.08) (Table 4). Predicted occupancy was high regardless of site type and woody debris volumes, ranging between 65% at 50 m^3 ha^{-1} of woody debris and 100% at 400 m^3 ha^{-1} of woody debris on white pine sites, and ranging between 65% and 75% on hardwood sites for the same range of woody debris volumes (Fig. 2).

3.4. Site-level abundance

The top Capture-Mark-Recapture model included time on both initial capture (p) and recapture (c) probabilities. Because the last capture probability was not estimable, we exported the model to Program MARK (White and Burnham, 1999) and used the parameter index matrices to manually set the last p equal to the last c. Initial capture probability ranged from 0.14 (95% CI: 0.09–0.20) to 0.35 (95% CI: 0.21–0.52) and, for the most part, increased over time. Recapture probability ranged from 0.28 (95% CI: 0.23–0.34) to 0.74 (95% CI: 0.62–0.83) and had a negative trend over time. We obtained abundance estimates separately for each site, ranging from 14 individual white-footed mice (95% CI:14–21) to 125 individuals (95% CI: 120–137) (Table 5). After obtaining the abundance estimates, we used GLMs to determine the relationship between abundance and the covariates site type, site-level woody debris volume, and the interaction between site type and woody debris volume. The model with the lowest AIC score included all covariates, including the interaction term; abundance increased with greater site-level woody debris volume, with a greater increase at white pine sites than hardwood sites (Table 6; Fig. 3).

3.5. Apparent survival

The Cormack-Jolly-Seber model with the lowest AICc score included the variable for time on detection, but no covariate on apparent survival. Monthly apparent survival probability for white-footed mice during the 2017 field season was estimated to be 50.0% (95% CI: 43.5% − 56.5%). The top model did not include an effect of site on apparent survival, indicating that apparent survival had limited variability across sites and, therefore, a limited relationship with site-level covariates.

4. Discussion

White-footed mice were influenced by retention of downed wood at the local (trap level) and site level, and the probability of mouse presence at an individual trap increased with greater CWD cover around the trap and with greater overall woody debris volume across the harvest site. Similarly, estimated mouse abundance increased with greater volume of downed wood at harvested sites. Proximity to CWD did not impact the probability that white-footed mice were present at a trap, but detection of white-footed mice was greater closer to CWD. The absence of a relationship between proximity to CWD and mouse use of individual trap locations may be related to CWD being scattered across each of the sites, allowing mice to move relatively freely and occupy trap locations more distant from CWD.

The positive relationships between captures and downed wood volume and cover likely are because of the associated resource benefits provided to the white-footed mice. Mice may travel along CWD to avoid auditory or visual detection by predators (Barnum et al., 1992; Roche

Table 3
Top five (based on AICc) occupancy models including number of parameters (K), AICc, ΔAICc, and model weight. The detection model for each was day of trapping + proximity. Occupancy models were based on white-footed mice captures in western North Carolina, USA (2016–2017).

Model	K	AICc	ΔAICc	Model Weight
Detection				
Day + Proximity	4	8379.99	0.00	0.97
Occupancy				
CWD % Cover + Forb % Cover + Grass % Cover + Site Type + Year + Woody Debris Volume + Site Type*Woody Debris Volume	9	8091.62	0.00	0.44
CWD % Cover + Forb % Cover + Grass % Cover + Site Type + Woody Vegetation % Cover + Year + Woody Debris Volume + Site Type*Woody Debris Volume	10	8092.76	1.15	0.25
CWD % Cover + Forb % Cover + Grass % Cover + Proximity + Site Type + Year + Woody Debris Volume + Site Type*Woody Debris Volume	10	8093.64	2.03	0.16
CWD % Cover + Forb % Cover + Grass % Cover + Proximity + Site Type + Woody Vegetation % Cover + Year + Woody Debris Volume + Site Type*Woody Debris Volume	11	8094.80	3.18	0.09
CWD % Cover + Grass % Cover + Site Type + Year + Woody Debris Volume + Site Type*Woody Debris Volume	8	8097.57	5.95	0.02

Table 4
Parameter estimates with standard errors and p-values for the occupancy model with the lowest AICc based on white-footed mouse captures in western North Carolina, USA (2016–2017). Site type (white pine) indicates that hardwood is the reference site type.

Covariate	Parameter estimate	Standard error	P-Value
Detection			
Day	0.03	0.01	< 0.01
Proximity	0.40	0.07	< 0.01
Occupancy			
CWD % Cover	0.26	0.08	< 0.01
Forb % Cover	−0.20	0.07	< 0.01
Grass % Cover	−0.31	0.08	< 0.01
Site Type (White Pine)	1.14	0.18	< 0.01
Year (2017)	2.18	0.15	< 0.01
Woody Debris Volume	0.10	0.10	0.32
Site Type (White Pine)*Woody Debris Volume	0.70	0.20	< 0.01

et al., 1999) or to search for seed and insect foods. Based on measurements taken on our study sites for a related study of invertebrate relationships with downed wood, the maximum temperature under CWD was lower (mean: 27.47 °C, SE: 4.32, $p < 0.0001$) than away (5 m) from CWD (mean: 46.54 °C, SE: 12.20), and minimum humidity was greater under CWD (mean: 90.08%, SE: 13.16) than away from CWD (mean: 47.08%, SE: 25.03), indicating that white-footed mice may use CWD as refuge from hot and dry conditions (Boggs, 2019).

Table 5
Estimated abundance of white-footed mice in 2017 at each harvested site in western North Carolina, USA, based on the closed Capture-Mark-Recapture model with the lowest AICc, with corresponding site type and woody debris volume.

Site	Estimated abundance (95% CI)	Site type	Woody debris volume (m^3 ha^{-1})
BR1	42 (41–50)	White Pine	153.82
BR3WP	28 (27–35)	White Pine	93.05
DPWPB	36 (34–43)	White Pine	146.66
DPWPNB	19 (18–25)	White Pine	56.05
HOLMES	125 (120–137)	White Pine	221.14
BR3HW	14 (14–21)	Hardwood	103.76
DPHW	41 (40–49)	Hardwood	174.05
MAC3	34 (32–41)	Hardwood	214.83
MAC5	35 (33–42)	Hardwood	226.59
MAC7	37 (35–44)	Hardwood	376.60

Results of other studies on the relationship between mice and CWD cover or volume are inconsistent, likely a result of different geographic regions, vegetation types, seral stage of individual research sites, or background noise due to fluctuations in mice populations. Multiple studies involving white-footed mice or closely related deer mice (*Peromyscus maniculatus*) and cotton mice (*Peromyscus gossypinus*) show a positive relationship between mice and CWD or quantities of downed

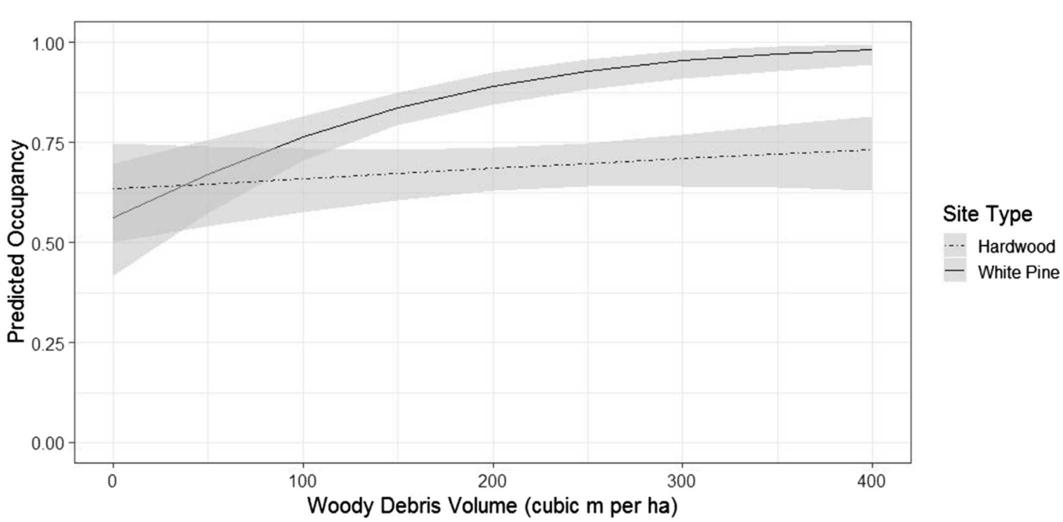

Fig. 2. Predicted white-footed mouse occupancy probability (with 95% confidence intervals) for 2017 related to site-level woody debris volume and site type across 60 trapping locations at each of 10 sites in western North Carolina, USA (2016–2017). All other covariates (e.g., forb cover, grass cover) were set to their median values.

Table 6
Parameter estimates with standard errors and p-values for the Generalized Linear Model (GLM) with the lowest AICc of the top abundance model. The GLM used the estimated white-footed mouse abundance at the 10 harvested sites in western North Carolina, USA (2017). Site type (white pine) indicates that hardwood is the reference site type.

Covariate	Parameter estimate	Standard error	P-value
Site Type (White Pine)	0.82	0.11	< 0.01
Woody Debris Volume	0.16	0.08	0.03
Site Type (White Pine)*Woody Debris Volume	0.97	0.13	< 0.01

wood (Goodwin and Hungerfod, 1979; Loeb, 1999; Moses and Boutin, 2001; Greenberg, 2002; Fauteux et al., 2012; Kellner and Swihart, 2014; Sollmann et al., 2015). Conversely, other studies documented no association with CWD (Osbourne, 2002; Craig et al., 2006; Jones and Lindquist, 2012; Marshall et al., 2012; Farrell, 2013; Homyack et al., 2014; Fritts et al., 2017), or reported mixed results at the trap and site level (Urban and Swihart, 2011). These studies occurred across a range of sites with various downed wood volumes, management histories, stand ages, and geographic regions, confounding generalizations about the relationship between mice and downed wood. That said, our research indicates that in the southern Appalachians of the eastern US, woody debris volume and percent cover are important aspects of habitat for white-footed mice in recently harvested forest stands. However, the relative effect of site-level woody debris volume in our study was small compared to other covariates, leaving the possibility that other factors, such as site type, are more important than woody debris volumes for white-footed mouse abundance and distribution in the region.

Site type had a strong influence on white-footed mouse distribution and abundance, possibly because of micro-environmental factors associated with white pine forests. Occupancy probability was greater in white pine than hardwood sites, and increasing woody debris volume had a greater, positive influence on white-footed mouse abundance in white pine sites than in hardwood sites. This variation may be due to the specific characteristics of downed wood present in the sites, such as species or decay class, or due to a greater positive population response to timber harvesting in coniferous sites than in deciduous sites (Kirkland, 1977; Kirkland, 1990; Zwolak, 2009). Other possible causes of variation between the two site types include differences in elevation, slope position, leaf litter depth, seed availability, or composition or richness of understory plants (Brooks et al., 1998; Brannon, 2005; Craig et al., 2006; Kaminski et al., 2007; Lindemann et al., 2015). Because white-footed mouse occupancy increased at a greater rate on white pine sites than hardwood sites as woody debris volume increased, site type should be considered when determining how much woody debris to leave after a timber harvest.

The negative association between white-footed mouse occupancy and vegetation cover, specifically grass and forb percent cover, was unexpected. Other studies documented a negative relationship between *Peromyscus* spp. and grass cover (Kaufman et al., 1983; Kaminski et al., 2007), whereas others documented a positive relationship with forb cover (Barnum et al., 1992; McMurry et al., 1996) or mixed grass-forb cover (Martin and McComb, 2002). Because dense grass cover rustles with movement, allowing for potential detection by predators, white-footed mice may avoid it (Getz, 1961; Barnum et al., 1992). Although forbs provide food and cover under which white-footed mice can generally travel silently (Barnum et al., 1992), it is possible that forbs in our sites may have been too tall or too short to provide adequate cover or so dense that they reduced the ability of white-footed mice to move quietly.

Capture rates and associated occupancy probability increased substantially between 2016 and 2017, which highlights the importance of multi-year studies when working with mice and other rodents. The dramatic increase in mice in the second year of the study may be attributable to a variety of factors, including increased availability of hard and soft mast during the fall of 2016 compared to the fall of 2015 (Buckner and Shure, 1985; Elias et al., 2004; Fantz and Renken, 2005; Clotfelter et al., 2007; Greenberg et al., 2007; Olfenbuttel, 2016), or natural population fluctuations (Deitloff et al., 2010). Weather, including temperature and precipitation, also may have played a role by providing conditions optimal for recruitment or survival between 2016 and 2017.

The best Cormack-Jolly-Seber model indicated apparent monthly survival in our study area (50.0%; 95% CI: 43.5% − 56.5%) was similar to survival in other regions, including the Central Hardwood Forest region (44% to 86%; Nelson et al., 2019) and the upper Hudson Valley region (50%; Collins and Kays, 2014). Survival of white-footed mice may be improved with greater availability of downed wood, as is the case for deer mice (Manning and Edge, 2004). However, apparent survival rates in this study showed little variation among sites,

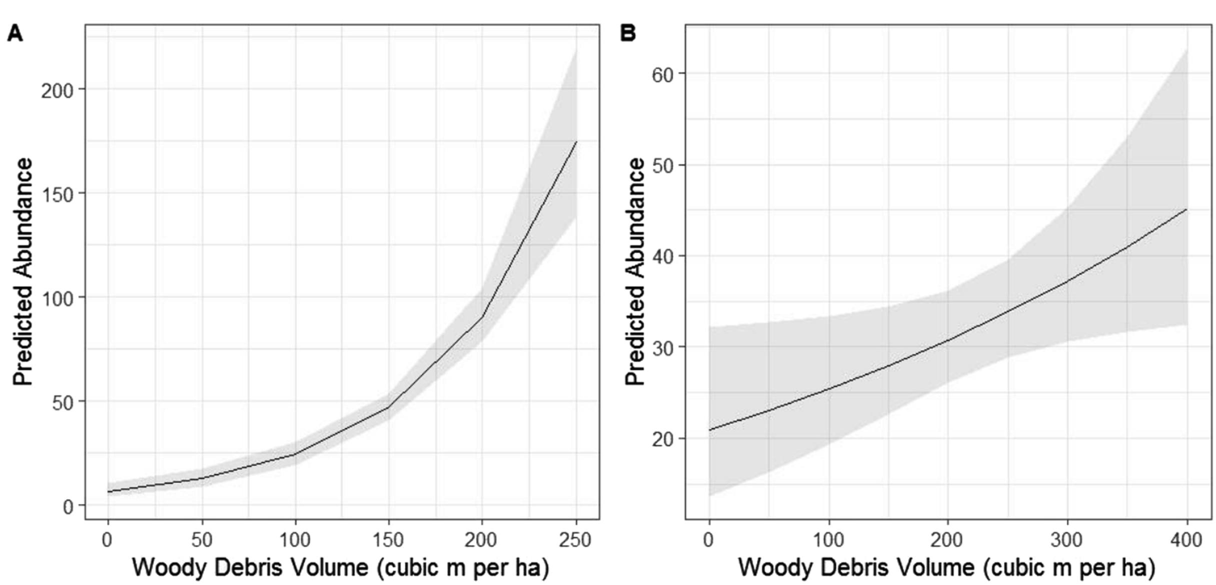

Fig. 3. Predicted white-footed mouse abundance (with 95% confidence intervals) in 2017 at five white pine sites (A) and five hardwood sites (B) in western North Carolina, USA, as a function of woody debris volume based on closed Capture-Mark-Recapture analysis and linear regression of captures.

indicating that site-level covariates, such as woody debris volume, did not influence survival.

Our study was conducted outside of the context of operational woody biomass harvesting, but the relationships we documented between mice and residual logging debris should help inform sustainability practices should a wood bioenergy market arise in the region. In the Coastal Plain of the southeastern United States, woody biomass harvesting reduced residual downed wood volume by more than 80% (Fritts et al., 2014). If the same percentage held for the southern Appalachians, debris volumes after biomass harvesting in our sites would drop from 56.05 m^3 ha^{-1} to 10.65 m^3 ha^{-1} at the site with the lowest debris volume, and from 376.60 m^3/ha to 71.55 m^3 ha^{-1} at the site with the greatest debris volume. Such a drastic decrease in woody debris volume could decrease white-footed mice abundance, especially at sites that had low initial debris levels. However, efficacy of woody debris removal may be lower in the southern Appalachians than in the Coastal Plain. Due to steep slopes and other logistical challenges (e.g., access, road conditions) in the mountainous terrain, it is likely that the recovery rate of woody debris in the southern Appalachians would be similar to values reported for temperate and boreal forests of Canada, France, Finland, and Sweden (53%) (Thiffault et al., 2015) or Maine, USA (55%) (Briedis et al., 2011). It is also important to note that the average woody debris volume was greater at sites in this study (176.66 m^3 ha^{-1}) than in Coastal Plain sites without a biomass harvest (108.20 m^3 ha^{-1}) (Fritts et al., 2014).

The white-footed mouse is a common and widespread generalist species, but relationships we documented between its abundance or occupancy and retention of downed wood may be similar for other less common wildlife species, including Allegheny woodrat (*Neotoma magister*), long-tailed shrew (*Sorex dispar*), and even plethodontid salamanders. However, other species may respond to differences in downed wood volume at scales different than mice, or these other species may be affected differently by environmental factors, including aspect (e.g., plethodontid salamanders) and leaf litter cover (e.g., *Sorex* spp.). Because the relationships between white-footed mice and woody debris varied between the two site types, site type should be considered when determining how much woody debris to leave on a site. We recommend leaving as much woody debris as possible without greatly reducing potential income in both white pine and hardwood sites where operational removal of woody debris is to occur, and more woody debris if possible in white pine sites. Specifically, our results indicate that woody debris removal greater than 50% (in line with the average recovery rate in Thiffault et al., 2015) on a white pine site with 176.66 m^3 ha^{-1} of woody debris, would result in a 68.7% (67 to 21 individuals) decrease in white footed mouse abundance, and a 14.9% (0.87 to 0.74%) decrease in occupancy probability. On a hardwood site with 176.66 m^3 ha^{-1} of woody debris, occupancy would decrease from 0.69 to 0.63 and abundance would decrease from 30 to 25. Because occupancy probability increases with CWD percent cover, we also recommend that any retained debris be scattered across the site. However, this recommendation is only for white-footed mice or wildlife with similar habitat requirements, as other, larger species of wildlife may benefit from retaining woody debris in piles. Biomass Harvesting Guidelines often recommend retention of 15–30% of merchantable woody biomass, though these retention thresholds have not been widely tested in an operational setting (Evans et al., 2013; Fritts et al., 2014). Future research should involve the experimental manipulation of logging residues or operational removal of debris to better identify thresholds that optimize economic harvest of woody biomass and conservation of wildlife in the southern Appalachians and other areas of the eastern United States.

5. Conclusion

The use of low value woody biomass for bioenergy is imminent in the southern Appalachians. Before biomass harvesting becomes a common practice in the region, it is important to determine its environmental impacts. Our research indicates that both the abundance and distribution of white-footed mice in harvested sites in the region is positively associated with the cover and volume of downed wood left following timber harvest. Where conservation of mice and other ground-dwelling wildlife is a management goal, managers should retain as much woody debris as economically feasible on sites where operational harvest of the woody debris is to occur. Debris left after a biomass harvest should be scattered across the site to provide cover for white-footed mice and other wildlife with similar habitat requirements.

Declaration of Competing Interest

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

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