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Intensively managed pine forests provide habitat for a diversity of wildlife species, including bats and rodents. In Kemper Co., MS, USA, Weyerhaeuser Company and Catchlight Energy LLC, on land owned and managed by Weyerhaeuser, intercrops 'Alamo' switchgrass (*Panicum virgatum* L.) between rows of pines in managed loblolly pine (*Pinus taeda*) plantations. I considered whether switchgrass intercropping in pine plantations results in differences in understory vegetation density, affects propagation of ultrasound, and affects acoustic signals of bats and rodents when compared to non-intercropped pine plantations. Treatments included traditionally managed pine plantations (P), pine plantations intercropped with switchgrass (PxS), and a no vegetation control (C). I measured understory vegetation density to determine if switchgrass intercropping increased understory vegetation density. I used broadcasting experiments to determine if treatment influences the absorption of sound energy and the distance ultrasound travels. I recorded bat and rodent ultrasound to determine if they are altering the spectral and temporal characteristics of their vocalizations in response to treatment. Understory vegetation density was higher in the PxS treatment, but both treatments had dense vegetation in the understory. The absorption coefficient was largest and sounds travelled the shortest distance in the PxS treatment plots, where vegetation density was highest. In P treatment plots, the absorption coefficient and the distance sound travelled were both intermediate. The absorption coefficient was smallest and sounds travelled the longest distance in the C treatment, where there was no vegetation present. I found no evidence

to suggest that either bats or rodents are altering the spectral and temporal characteristics of vocalizations. Increased vegetation density could affect rodents living in the understory, because sound produced in habitat with dense vegetation are attenuated quickly. Rodents may respond to increased vegetation density by altering the spectral and temporal characteristics to improve sound transmission. Rodents may also respond to increased vegetation density by reducing the amount of ultrasonic vocalizations they produce and/or stop producing ultrasonic vocalizations, due to reduced signal effectiveness. Failure to detect signals in my system may or may not lead to decreased reproductive success of individuals, but more research needs to be done to fully understand the implications of reduced signal transmission on rodents.

INFLUENCE OF INTERCROPPING SWITCHGRASS IN INTENSIVELY MANAGED PINE FORESTS ON ULTRASOUND PRODUCED BY BATS AND RODENTS

by

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CHAPTER I

INTRODUCTION

Vegetation density influences sound propagation, with attenuation of sound happening more quickly in habitats with greater vegetation density (Smith 1979; Wiley and Richards 1982; Patriquin et al. 2003; Boncoraglio and Saino 2007). In general, the attenuation of sound is due to the physical properties of sound, including spreading loss, acoustic impedance, scattering, and absorption (Wiley and Richards 1982; Bradbury and Vehrencamp 1998). Vegetation increases scattering and absorption of sound, and increases the acoustic impedance in the medium the sound wave propagates through. Therefore decreasing the sound energy of the wave more quickly, resulting in faster attenuation of the acoustic signal (Wiley and Richards 1982; Bradbury and Vehrencamp 1998). The physical property of spreading loss is a function of distance from the sound source, and remains the constant regardless of the presence or absence of vegetation (Wiley and Richards 1982; Bradbury and Vehrencamp 1998).

It has been shown that the distance that animal vocalizations can be detected is influenced by the presence of vegetation and the frequency of sound (Naguib 2003; Morrill et al. 2013). Increased vegetation density decreases the transmission of sound (Smith 1979; Wiley and Richards 1982; Naguib 2003; Patriquin et al. 2003; Padgham 2004; Van Dongen and Mulder 2006; Boncoraglio and Saino 2007; Morrill et al. 2013). The distance vocalizations travel is shorter in habitats with dense vegetation cover,

whereas in habitat with little vegetation cover sound travels a longer distance (Morrill et al. 2013). Additionally, the frequency at which vocalizations are produced also influences the distance that sound travels (Naguib 2003; Van Dongen and Mulder 2006; Morrill et al. 2013). Higher frequency vocalizations travel a shorter distance than lower frequency vocalizations (Morrill et al. 2013), because vegetation becomes more effective at scattering and absorbing sound energy as the frequency of the sound increases (Smith 1979; Wiley and Richards 1982).

The acoustic behavior of animals can be impacted by anthropogenic changes in habitat (Laiolo 2010). Anthropogenic habitat change often results in changes to an animal's acoustic environment, which can decrease the effectiveness of acoustic communication by reducing an animal's ability to detect acoustic signals (Laiolo 2010; Francis and Barber 2013). Increased vegetation density can impair the detection of acoustic signals by animals (Mathevon et al. 1996; Slabbekoorn and Smith 2002; Naguib 2003; Padgham 2004; Nicholls and Goldizen 2006; Van Dongen and Mulder 2006; Boncoraglio and Saino 2007; Morrill et al. 2013). If animals are unable to detect acoustic signals then acoustic communication, predator/prey interactions, and orientation can be compromised (Francis and Barber 2013). Failure to detect acoustic signals can lead to changes in temporal patterns of behavior, spatial distribution and movement of individuals, mate attraction or territory defense, decreased foraging or provisioning of resources, and increased vigilance and anti-predator behavior (Francis and Barber 2013). Ultimately, such behavioral changes in animals could lead to physiological stress,

associated with decreased immune responses and fitness costs, affecting survival and reproduction (Francis and Barber 2013).

Plasticity of spectral and temporal characteristics of bat echolocation calls allows a bat to alter their echolocation calls to better suit their habitat (Kalko and Schnitzler 1993; Schaub and Schnitzler 2006; Gillam and McCracken 2007; Adams et al. 2009; Gillam et al. 2009; Brinkløv et al. 2010). Generally, bats flying near dense vegetation use short, broadband, high frequency echolocation calls, because echolocation calls with these characteristics provide the bat with more information about it's surroundings (Kalko and Schnitzler 1993; Schaub and Schnitzler 2006; Gillam et al. 2009). Bats flying in relatively open habitats use long, narrowband, low frequency echolocation calls (Kalko and Schnitzler 1993; Schaub and Schnitzler 2006; Gillam et al. 2009). An example of such plasticity in echolocation calls can be seen in three European *Pipistrelle* bat species (Kalko and Schnitzler 1993). When flying in cluttered habitat these bats emit broadband, frequency modulated echolocation calls, and when flying in open habitat they echolocate using narrowband, frequency modulated echolocation calls (Kalko and Schnitzler 1993).

Rodents can produce ultrasonic vocalizations with different spectral and temporal characteristics to better suit their habitat (Dempster and Perrin 1991). Closely related gerbil species, occupying habitats with different amounts of vegetation cover produce vocalizations with different spectral and temporal characteristics (Dempster and Perrin 1991). Species living in grassland savannah habitat produce vocalizations that are longer in duration and lower in frequency, when compared to closely related species living in habitat with little vegetation cover (Dempster and Perrin 1991).

Intensively managed pine forests in the Southeastern United States are ecologically important for plant and animal community biodiversity (Wear and Greis 2002; Miller et al. 2009). Common residents of managed pine forests in the Southeast include bats and rodents (Loeb 1999; Miller 2003; Mengak and Guynn Jr. 2003; Constantine et al. 2004; Constantine et al. 2005; Morris et al. 2010). Loblolly pine (*Pinus taeda*) plantations in Mississippi provide habitat for several species of mammals, birds, reptiles, amphibians, invertebrates, and plants (Miller et al. 2009).

Intercropping 'Alamo' switchgrass (*Panicum virgatum* L.) between rows of loblolly pines in intensively managed pine plantations has the potential to be a sustainable method of biofuel feedstock production that does not encumber arable lands (Miller et al. 2009; Riffell et al. 2012). Switchgrass is a promising cellulosic biofuel feedstock (McLaughlin and Walsh 1998; Schmer et al. 2008; Riffell et al. 2012) because it is a fast growing perennial plant with an extensive root system that reduces soil erosion (Dale et al. 2010). Switchgrass also thrives across a vast geographic region and is adapted to grow in a wide range of environmental conditions (McLaughlin and Walsh 1998; Hill et al. 2006; Dale et al. 2010). Lastly, switchgrass can provide habitat for native wildlife (Hill et al. 2006; Dale et al. 2010), especially grassland associated species.

Growing switchgrass in intensively managed pine forests has the potential to impact biodiversity (Miller et al. 2009; Riffell et al. 2012). The presence of switchgrass changes the composition of plant species present, and increases grassy vegetation cover in the understory of pine plantations (Marshall et al. 2012). As described above, vegetation cover alters sound propagation by decreasing the distance sound can travel

(Mathevon et al. 1996; Slabbekoorn and Smith 2002; Naguib 2003; Padgham 2004; Nicholls and Goldizen 2006; Van Dongen and Mulder 2006; Boncoraglio and Saino 2007; Morrill et al. 2013). The effects of vegetation on sound propagation are more pronounced for high frequency sound (Morton 1975; Smith 1979). Therefore intercropping switchgrass has the potential to reduce the effectiveness of ultrasonic acoustic signals. If acoustic signals are no longer effective, bats and rodents living in managed pine plantations intercropped with switchgrass could alter behavior with respect to how often they produce calls and the spectral and temporal structure of their vocalizations.

Objective

The objective of my study was to examine how intercropping switchgrass in managed pine forests influences vegetation density and the propagation of sound, including the distance sound travelled and the amount of absorption that occurs over that distance. I also determined if the spectral and temporal characteristics of ultrasound produced by bats and rodents are influenced by intercropping switchgrass.

Hypothesis

Intercropping switchgrass will change vegetation density in the understory. This change in vegetation density will have an effect on sound propagation and influence the spectral and temporal characteristics of ultrasound produced by bats and rodents.

Aims and Predictions

Aim 1 – Compare understory vegetation density in managed pine forests intercropped with switchgrass (PxS treatment) to managed pine forests that are not intercropped with switchgrass (P treatment).

Prediction 1 – The understory vegetation density will be higher in managed pine forests intercropped with switchgrass (PxS).

Aim 2a – Compare the distance pure tone and animal produced ultrasound travels in managed pine forests intercropped with switchgrass (PxS treatment), managed pine forests that are not intercropped with switchgrass (P treatment), and a no vegetation control (C treatment).

Prediction 2a – Pure tone and animal produced ultrasound will travel the shortest distance in managed pine forests intercropped with switchgrass (PxS).

Aim 2b – Compare the absorption coefficients obtained from modeling attenuation of sound broadcasted in managed pine forests intercropped with switchgrass (PxS treatment), managed pine forests that are not intercropped with switchgrass (P treatment), and a no vegetation control (C treatment).

Prediction 2b – The absorption coefficient will be largest for pure tone and animal produced ultrasound broadcasted into managed pine forests intercropped with switchgrass (PxS).

Aim 3 – Compare the spectral and temporal characteristics of rodent and bat ultrasound recorded in managed pine forests intercropped with switchgrass (PxS treatment) to rodent and bat ultrasound recorded in managed pine forests that are not intercropped with switchgrass (P treatment).

Prediction 3 – Both bats and rodents will alter the spectral and temporal characteristics of their vocalizations. Rodents will produce vocalizations with lower frequency and longer duration in managed pine forests intercropped with switchgrass (PxS), when compared to vocalizations recorded in managed pine forests that are not intercropped with switchgrass (P). Bats will produce short, frequency modulated echolocation calls in managed pine forests intercropped with switchgrass (PxS), when compared to vocalizations recorded in managed pine forests that are not intercropped with switchgrass (P).

CHAPTER II

METHODS

Study Area

My study site was located in the Upper Coastal Plains Region of east central Mississippi, in Kemper Co. The landscape is rural, and is predominantly composed of an operational, managed pine forest matrix. Located within this matrix of pine forests are my study plots. Study plots were established and maintained by Catchlight Energy LLC (CLE), a Chevron | Weyerhaeuser joint venture, and Weyerhaeuser Company, on land owned and managed by Weyerhaeuser Company. These plots consisted of the Alamo variety of switchgrass (*Panicum virgatum* L.) intercropped between rows of loblolly pines (*Pinus taeda*) in intensively managed pine forests. The intercropped switchgrass was harvested annually for use as a biofuel feedstock. My study was conducted on six 10 hectare plots (Figure 1). Three plots were managed pine forests intercropped with switchgrass (PxS treatment), and three plots were managed pine forests that were not intercropped with switchgrass (P treatment). The P treatment plots were used as a vegetation control. On all experimental plots, site preparation included V-shearing stumps and roots, followed by planting pine trees on raise beds at approximately 1.5 m intervals in 2005. Rows of pines were spaced 6.1 m apart. Woody residuals were left on the plots, after clear cutting pines. On the PxS treatment plots switchgrass was

intercropped between the rows of pines using drill seeding methods in 2009. All site preparation was completed by Weyerhaeuser Company.

Vegetation Density

I sampled vegetation density using a cover board in July and August of 2012, in all six experimental plots (Figure 1). I randomly generated six points within each plot using random point generator in ArcGIS 10 (Esri, Redlands, California, USA), and loaded the points on to a Garmin Rino 650 (Garmin International Inc., Olathe, Kansas, USA) GPS device to locate the vegetation sampling points within each plot (Figure 2). The cover board was 1.83 m tall, 15.24 cm wide, and divided in to six 30.48 cm sections of alternating orange and white colors (Braun 2005). At each sampling site the board was held by a field assistant or staked into the ground. I viewed the board from 14 m away from each cardinal direction. I recorded the percentage of each of the six sections that was visually obstructed by vegetation. I calculated the mean percentage of vegetation that was visually obstructing each section of the board across all four directions, which was used as a measure of vegetation density.

Broadcasting

Propagation of Sound: Distance

Between 18 June and 3 August 2012, I used a transect of microphones to record broadcasted sound (Figure 1). Sound was broadcasted from the edge of the forest towards the interior of the forest (Figure 3). In addition to the experimental plots, I also conducted broadcasting experiments on a gravel road adjacent to the P treatment plots, to be used as a no vegetation control (C treatment). Experimental plots were paired as follows: PxS 1

with P 1, PxS 3 with P 3, and PxS 7 with P 5. To ensure that my broadcasting experiments were not influenced by weather conditions, on any given night of broadcasting, I conducted my experiments in one P treatment plot, one C treatment, and one PxS treatment plot. On each night, for logistical reasons, I began broadcasting in the P treatment plot, followed by the C treatment site, and ended at the PxS treatment plot. I broadcasted at all plot pairs and nearby road on three consecutive nights (i.e. night 1 broadcasting at P 1, C near P 1, and PxS 1, night 2 at P 3, C near P 3, and PxS 3, and night 3 at P 5, C near P 5, and PxS 7). The three consecutive nights were considered as one round of sampling. I conducted five rounds of broadcasting throughout the summer, for a total of fifteen nights of broadcasting, with equal sampling at each P treatment plot, C treatment site, and PxS treatment plot. I chose new locations within plots or along the roads for a broadcasting experiment at the start of every night.

Before the start of each round, I tested all ultrasonic microphones (Avisoft-Electret EP3, Avisoft Bioacoustics, Berlin, Germany) to insure they were working. I used an AT-100 ultrasound speaker (Binary Acoustic Technology LLC. Tucson, Arizona, USA), and PLAY'R with G'Tools version 1.6 ultrasonic generation software (Binary Acoustic Technology LLC. Tucson, Arizona, USA) to broadcast 20kHz pure tone ultrasound at 80 and 90 dB sound pressure level (dB) for the tests. Before testing, I set gain to "high" on all 12 channels of the Avisoft UltraSoundGate 1216H (Avisoft Bioacoustics, Berlin, Germany), and plugged a microphone directly into each channel of the Avisoft-UltraSoundGate. During testing, I used Avisoft-RECORDER, version 4.2.10 (R. Specht, 2012, Avisoft Bioacoustics, Berlin, Germany) to record a sound file from

each channel. After testing, I used Avisoft-SASLab Pro, version 5.2.06 (R. Specht, 2012, Avisoft Bioacoustics, Berlin, Germany) to view recorded sound files from the test. I noted the sound pressure level (dB) at which each microphone detected the broadcasted pure tone sound. For a microphone to be considered as "working" I ensured that the microphone was detecting sound at approximately the same sound pressure level as the other microphones, and that there was no interference or noise that was not attributed to the broadcasted tone. Any microphones that were not clearly detecting sound appropriately were not used in the experiment. I tested all microphones in the same way before the start of each round.

I broadcasted pure tone sound that were generated using G'Tools ultrasonic generation software, and previously recorded bat and rodent vocalizations at four different frequencies. The four frequencies chosen were 20, 30, 40, and 60 kHz. These frequencies were chosen because they are common frequencies used by bats and rodents. Rodent ultrasonic vocalizations and bat echolocation calls were selected from a library of previously recorded sound files, the 20 and 30 kHz rodent ultrasonic vocalizations were recorded at the Hastings Natural History Reserve, CA in 2008, and the 60 kHz rodent ultrasonic vocalization and all bat echolocation calls were recorded in Kemper Co., MS in 2011 (Figure 4). Although bats are not flying through the switchgrass, bat echolocation calls were broadcasted at the same height as pure tone sound and rodent vocalizations were broadcasted at. The reason for using bat echolocation calls was to have animal produced ultrasound that was short in duration. Our recording library did not include a suitable rodent ultrasonic vocalization at 40 kHz, therefore no 40 kHz rodent was used in

broadcasting experiments. Individual sound files typically included multiple syllables (rodents) or sound pulses (bats), so I used the "cut" feature in Avisoft-SASLab Pro to select only one syllable within a sequence of vocalizations. The duration of rodent ultrasonic vocalizations at 20, 30, and 60 kHz were 0.298 s, 0.108 s, and 0.060 s, respectively. The duration of bat echolocation calls at 20, 30, 40, and 60 kHz were 0.022 s, 0.022 s, 0.020 s, and 0.015 s, respectively. I also eliminated as much ambient noise from the file as possible using the "bandpass" feature in Avisoft-SASLab Pro. The one syllable was broadcasted in a loop, so that when broadcasted it would repeat the one syllable over again until broadcasting was stopped. The interval between looped rodent ultrasonic vocalizations at 20, 30, and 60 kHz were 0.08 s, 0.009 s, and 0.008 s, respectively. The interval between looped bat echolocation calls at 20, 30, 40, and 60 kHz were 0.009 s, 0.012 s, 0.010 s, and 0.014 s, respectively. Pure tone sound were broadcast at frequencies to match the rodent and bat frequencies used, and they were generated by the G'Tools software (Figure 4). All sound were broadcasted at two different sound pressure levels, 80 and 90 dB.

Before broadcasting began, I arrived at a P treatment plot approximately 15 minutes before sunset to set up equipment. I used a measuring tape to determine the placement of nine ultrasonic microphones along an18 m long transect at 2 m intervals. The AT-100 ultrasound speaker was placed 0 m, the first microphone in the transect was placed 2 m from the AT-100, and the last microphone was placed 18 m from the AT-100 (Figure 3). Microphones were individually connected to cables that plugged into separate channels on the Avisoft-UltraSoundGate. The Avisoft-UltraSoundGate was connected to

a laptop that ran Avisoft-RECORDER. I used the PLAY'R/G'Tools ultrasonic generation software, on a different laptop, to select the ultrasound type (pure tone, rodent, or bat), frequency (20, 30, 40, or 60 kHz), and sound pressure level (80 or 90 dB) that was broadcasted through the AT-100. I broadcasted pure tone ultrasound at 20, 30, 40, and 60 kHz, rodent ultrasound at 20, 30, and 60 kHz, and lastly bat ultrasound at 20, 30, 40, and 60 kHz, at a sound pressure level of 80 dB. This sequence was repeated three times at 80 dB and three times at 90 dB in the P treatment plot, the C treatment site, and the PxS treatment plot. I recorded a new sound file each time the frequency (kHz), sound type, and sound pressure level was changed. I used an external hard drive to store all recorded files. All broadcasting equipment was powered by a 12 V battery.

I determined the distance sound travelled by determining which microphone was the last microphone to detect the broadcasted sound, using Avisoft-SASLab Pro. In Avisoft-SASLab Pro display settings were as follows: auto gain on, color table gray.pal and contrast char1.grd, and spectrograph parameters in the frequency resolution section were as follows: FFT length of 256, frame size at 100%, and FlatTop window. Each recorded sound file displayed nine recorded channels. Each channel corresponded to a microphone that was placed at a known distance from the sound source, and had a spectrograph associated with it. I viewed each spectrograph individually to first, determine if the sound was recorded on the channel or not, and second, at what sound pressure level was the sound detected at. I determined the distance sound travelled in the following way. I viewed the spectrograph recorded at the shortest distance (i.e. 2 m). If I could clearly see the sound I moved on to the next channel/distance (i.e. 4 m). If I could

not see the sound on the 4 m spectrograph I considered the longest distance the sound travelled to be at the previous channel/distance (i.e. 2 m). If I could see the sound on the 4 m spectrograph but the quality of the recorded sound was poor, I looked to see if the integrity of the sound was maintained. If not maintained the previous channel/distance (i.e. 2 m) was used as the longest distance the sound travelled. If the integrity or quality of the sound was maintained, I measured the sound pressure level. If the sound pressure level was smaller than -50 dB (i.e. -55 dB) I used the previous channel/distance (i.e. 2 m). If the sound pressure level was larger than -50 dB (i.e. -40 dB) the longest distance the sound was considered to travel was increased to the current channel (i.e. 4 m). In all cases, I made sure that the last recorded sound had a sound pressure level that was larger than -50 dB.

Propagation of Sound: Absorption Coefficient

Obtaining the sound pressure level of a broadcasted sound at a known distance allowed me to fit a model to determine how much absorption was occurring as the sound wave propagated through the medium. I used Avisoft-SASLab Pro to automatically measure the sound pressure level of the broadcasted sound, to determine how loud the sound was detected at each 2 m interval. I used the automatic parameter measurements batch processing feature in Avisoft-SASLab Pro to measure the peak amplitude, meaning the loudest sound pressure level of the sound that had been recorded. I enabled dynamic data exchange with Excel (Microsoft Excel ®; Microsoft Corporation, Redmond, Washington, USA), so sound pressure level information measured from sound files was transferred to the open, blank Microsoft Excel ® sheet. Batch processing of the sound

files produced an output of sound pressure levels. I chose the loudest sound pressure level that was recorded on each channel, within each sound file, and averaged the sound pressure level over the three trials. The average sound pressure level was used as the actual sound pressure level value when modeling the absorption coefficient.

Steps used in the derivation of the equation I used for modeling sound propagation are as follows.

The standard definition of sound pressure level β in decibels (dB) is

$$\beta = 10 \log\left(\frac{I}{I_{ref}}\right) \tag{1}$$

where I is the sound intensity in joules/(seconds*area) or Watts/m^2 and I_{ref} is a reference intensity.

The energy for the broadcasted sound spreads over a larger area as distance from the source increases $\left(\frac{1}{r^2}\right)$, and the sound energy is absorbed and scattered (e^{-kr}). The function for intensity is therefore

$$I = \left(\frac{P_0}{r^2}\right) e^{-kr}$$

$$\text{J/(sec*m}^2\text{)} \tag{2}$$

where P_0 depends on the sound source.

Combining equation (2) with equation (1) gives the equation for sound pressure level

$$\beta = 10\log\left(\frac{P_0\frac{e^{-kr}}{r^2}}{I_{ref}}\right) = 10\log\left(\frac{P_0}{I_{ref}}\right) + 10\log(e^{-kr}) - 20\log(r) \quad (3)$$

Using $\log(e) = 0.434$ and defining a constant $\mathrm{Z} = 10\log\left(\frac{P_0}{I_{ref}}\right)$ gives

$$\beta = \mathrm{Z} - 4.34kr - 20\log(r) = \mathrm{Z} - ar - 20\log(r) \quad (4)$$

where β is sound pressure level (dB), Z is a constant, a is absorption in dB/m, and r is distance from the broadcasting speaker. The equation contains a constant Z, which is dependent on experimental set-up, which may vary from night to night.

I used the Microsoft Excel® add-in solver for all parts of the model (Eq. 4) fitting. The steps used in model fitting are as follows. First, I randomly selected 5 nights for each combination of frequency, sound type, and sound pressure level (i.e. 5 nights from 20 kHz pure tone sound broadcasted at 80 dB, 5 nights from 20 kHz rodent sound broadcasted at 80 dB, etc.). I used data from the same night across treatments (C treatment site, PxS treatment plot, and P treatment plot). Second, I graphed the sound pressure level (y-axis) and distance sound travelled (x-axis) data in Microsoft Excel®. Third, I used solver to find the constant (Z) and absorption (a) for the C treatment data from any given randomly selected night by minimizing the standard error between the actual sound pressure level values and the predicted model values (Eq. 4; Tables 1-3;

Figure 5). Fourth, I used the solver to find absorption (a) for the P and PxS treatment plot data, while the constant (Z) was held to the value determined for the C treatment site (Figures 6 and 7).

Recording

I recorded rodent and bat ultrasound in P and PxS treatment plots from June to August 2012. I paired experimental plots as follows: PxS 1 with P 1, PxS 3 with P 3, PxS 7 with P 5 (Figure 1). I used Pettersson D240x ultrasound detectors (Pettersson Elektronik AB, Uppsala, Sweden) and an Avisoft-UltraSoundGate for recording. The D240x detectors and the Avisoft-UltraSoundGate allowed me to maximize the number (with the D240x detectors) and quality (with the Avisoft-UltraSoundGate) of recordings. I used SonoBat NE 3.1 (SonoBat, Arcata, California, USA) to find bat and rodent vocalizations in all of the recordings. I analyzed spectral and temporal characteristics of bat echolocation calls using SonoBat and rodent ultrasonic vocalizations using Avisoft-SASLab Pro.

I recorded acoustic data using D240x detectors from 22 June to 8 August 2012, sampling every night except for 1 August 2012. I sampled two experimental treatment plot pairs at a time (i.e. PxS 1 and P 1, and PxS 3 and P3). In each plot, one sampling tree was selected. I attached two detectors to each sampling tree. Trees were selected based on areas deemed appropriate for bat flight. On each tree one detector was placed approximately 0.5 m high, to detect rodents, and another detector approximately 1.7 m high, to detect bats. The settings on the D240x detectors placed at approximately 0.5 m high, to record rodents, were as follows: NORMAL, TIME EXP (time expanded), HIGH

GAIN, TRIG AUTO (auto trigger), MEM SIZE (memory size) 3.4 s, TRIGGER LEVEL LOW and TRIGGER SOURCE HF. The settings on the D240x detectors placed at approximately 1.7 m high, to record bats were the same, except that MEM SIZE was set to 1.7 s. The D240x detectors were turned on at approximately 19:30 every evening. I returned at approximately 01:00 to replace batteries and change SD cards. I collected all detectors and SD cards in the morning.

I recorded sound at four different locations/sampling trees within each experimental treatment plot over a six week time period. To do this, I recorded at any given sampling tree for one week. After one week at a given sampling tree I chose a new sampling tree in each plot. I rotated the detectors from plot to plot, until all plots had been equally sampled. Sampling trees always had two D240x detectors present at two different heights, as explained above. For example, during week one of recording, I chose the first sampling tree in each of the following treatment plots PxS 1, P 1, PxS 3, and P 3. During week two of recording, I chose a second sampling tree in PxS 3 and P 3 treatment plots, and chose the first sampling tree in PxS 7 and P 5 treatment plots. During week three of recording, I chose a second sampling tree in each of the following treatment plots PxS 1, P 1, PxS 7, and P 5. This rotation process was repeated and at the end of six weeks I had recorded at four different sampling trees in all six experimental treatment plots (Figure 2).

In addition to the D240x detectors, I recorded acoustic data using an Avisoft UltraSoundGate from 22 July to 9 August 2012. The Avisoft-UltraSoundGate and the computer running Avisoft-RECORDER were powered using a 12 V battery. I did not use

the Avisoft-UltraSoundGate for recording bat and rodent ultrasound during a broadcasting round. Therefore, recording was more infrequent with the Avisoft-UltraSoundGate, when compared to the D240x detectors. I recorded with the Avisoft-UltraSoundGate at a given sampling tree within each plot for one night. I recorded at all four sampling trees in the P treatment plots and three of the four sampling trees in the PxS treatment plots. Similarly to D240x detectors, I recorded with the Avisoft-UltraSoundGate at two heights. To do this, I used two of the twelve channels on the Avisoft-UltraSoundGate. The microphone associated with channel one was placed at approximately 0.5 m high, and channel two was placed at approximately 1.7 m high. I began recording at approximately 19:00 and stopped recording at approximately 03:00.

Analysis of all recorded calls was conducted using a combination of Avisoft-SASLab Pro and SonoBat software packages. Recordings from D240x detectors were recorded as time expanded .wav sound files. To accurately view D240x recordings in Avisoft-SASLab Pro I restored the original time scale of the time expanded recordings. I batch processed the D240x sound files using the 'restore original time scale of time expanded recordings' function in Avisoft-SASLab Pro. The settings to restore the original time scale were as follows: time expansion 10:1, check box to perform subsequent sample rate conversion, and convert from 441000 Hz to 2500000 Hz. Additionally, I batch processed the Avisoft-UltraSoundGate sound files using the 'split multi-channel file into mono files (into separate folders)' function in Avisoft-SASLab Pro. I ran sound files, from both recording methods, through SonoBat using SonoBatch 'Scrubber' to reduce the number of sound files that contained non-bat and non-mouse

sound (i.e. wind and insects). I then used Avisoft-SASLab Pro to manually examine all sound files that were not removed during the scrubbing process. Sound files that had rodent or bat calls present were further analyzed as follows.

To identify bat echolocation call sequences to species, I used SonoBatch 'Classify' in SonoBat to identify the calls with the following settings: max # of calls to consider per file at 8, acceptable call quality at 0.80, acceptable quality to tally passes at 0.20, and decision threshold at 0.90. I accepted all species identifications based on the 'By Vote' criterion in SonoBat. To ensure that only high quality recordings of bat echolocation call sequences would be included in my subsequent analyses. I used the reference call library in SonoBat to examine each identified echolocation call sequence manually. I used a SonoBatch 'Parameterize' in SonoBat to obtain spectral and temporal characteristics for all high quality identified echolocation call sequences from each sound pulse within an echolocation call sequence. As some sound files had multiple echolocation sound pulses, I decided to use the spectral and temporal characteristics from the second sound pulse in the sequence for my spectral and temporal analysis of echolocation call characteristics. I chose the second pulse in the sequence because the first sound pulse was often not a high quality recording, and not all files had more than two sound pulses in a sequence. Spectral and temporal parameters analyzed were bandwidth (kHz), characteristic frequency (kHz), highest apparent frequency (kHz), lowest apparent frequency (kHz), frequency at maximum amplitude (kHz), call duration (ms), upper slope (kHz/ms), lower slope (kHz/ms), slope at characteristic frequency (kHz/ms) and total slope (kHz/ms).

To obtain spectral and temporal characteristics for recorded rodent vocalizations, I used Avisoft-SASLab Pro. I examined the spectrographs containing rodent vocalizations with the following display settings: auto gain on, color table gray.pal and, contrast char1.grd, and spectrograph settings: FFT length of 256, frame size at 100%, and FlatTop window. I individually selected each a syllable of a recorded rodent vocalization. The automated parameter measurements in Avisoft-SASLab Pro provided me with the following spectral and temporal characteristics of rodent vocalizations, the peak frequency at maximum amplitude (kHz), the duration of the syllable (s), and the time interval between syllables (s).

Statistical Analysis

I checked normality of all data using Shapiro-Wilk tests. If data were not normally distributed, I attempted to normalize the data using standard transformations. Transformed data were only used if a transformation was able to normalize data. When the data did not conform to parametric assumptions and the data set was small I used non-parametric tests. When the data did not conform to parametric assumptions and the data set was large I used parametric tests.

For vegetation density analysis, I used a permutation ANOVA with 5000 repetitions with treatment a factor. To determine an F-value I used the mean of the 5000 F-values from the permutation ANOVA. For broadcasting analyses, I used full factor parametric ANOVA tests on distance sound travelled and absorption coefficient data, with treatment (PxS, P, and C), sound type (pure tone, rodent, and bat), sound pressure level (80 and 90 dB) and frequency (20, 30, 40, and 60kHz) as factors. I used Bayesian

information criterion (BIC) backward/forward model selection criterion for selecting the best model (Ellison 2004, Kuha 2004, Xin and Song 2010). The ANOVA model selected for by the BIC model selection criterion was then used in reduced ANOVA tests (Tables 4-5). I used Tukey HSD tests for all post-hoc comparisons. All data in figures are presented as mean ± 1 standard error. For all statistical tests, I used a 0.05 rejection criterion to determine whether or not a result was statistically significant. I used one-way MANOVA tests to compare spectral and temporal characteristic variables for echolocation calls associated with the recorded bat species in the P and PxS treatment plots.

I used Microsoft Excel ® add-in solver (Microsoft Corporation, Redmond, Washington, USA) for absorption coefficient model fitting. I used Program R version 2.15.3 (R Development Core Team 2013) for all vegetation density and sound propagation (both distance and absorption coefficient) ANOVA statistical tests, and I used SPSS (IBM Corporation, Armonk, New York, USA) for MANOVA statistical tests.

CHAPTER III

RESULTS

Vegetation Density

Standard transformations on vegetation density data were unable to normalize the data. Therefore, original data were used in the analysis. Due to the small sample size (n = 36) of my vegetation density data I used a non-parametric ANOVA. Vegetation density was influenced by treatment ($F_{1,214}$ = 1.02, p = 0.002; Figure 8), with vegetation being significantly more dense in the PxS treatment plots (94.1%) when compared to the vegetation density in the P treatment plots (88.5%).

Broadcasting

Propagation of Sound: Distance

Standard transformations on the distance sound travelled data were unable to normalize the data. Therefore, original data were used in all analyses. Due to the large sample size (n = 957) of my distance sound travelled data I used a parametric ANOVA. The best model selected by BIC criterion had distance sound travelled with treatment, frequency, sound type, sound pressure level, an interaction between treatment and frequency, and an interaction between treatment and sound pressure level as factors (Table 4). All distance sound travelled data results are reported from the reduced ANOVA model described above.

The distance sound travelled was significantly influenced by an interaction between treatment and frequency ($F_{6,940} = 9.695$, $p < 0.001$; Table 6, Figure 9). Sound broadcasted at 20, 30, and 40 kHz was detected at a longer distance than sound broadcasted at 60 kHz. The following distances reported are the approximate mean distance sound travelled averaged over all sound types and sound pressure levels. On the C treatment sites the distance 20, 30, and 40 kHz sound travelled was 17.9 m, and 60 kHz sound travelled 11.5 m. In the P treatment plots 20, 30, and 40 kHz sound travelled 11.1 m, and 60 kHz sound travelled 5.6 m. In the PxS treatment plots 20, 30, and 40 kHz sound travelled 6.9 m, and 60 kHz sound travelled 3.6 m (Figure 9).

The distance sound travelled was significantly influenced by an interaction between treatment and sound pressure level ($F_{2,940} = 23.28$, $p < 0.001$; Table 6, Figure 10). Sound broadcasted at 80 dB was detected at a shorter distance than sound broadcasted at 90 dB. The following distances reported are the approximate mean distance sound travelled averaged over all frequencies and sound types. In the C treatment, 80 dB sound travelled 15.8 m and 90 dB travelled 16.6 m. In the P treatment plots, 80 dB sound travelled 8.0m and 90 dB sound travelled 1.4 m. In the PxS treatment plots, 80 dB sound travelled was 4.9 m and 90 dB sound travelled 7.9 m (Figure 10). Tukey HSD post-hoc tests on the treatment and sound pressure level interaction showed significant differences in the distance sounds travelled when broadcasted at 80 and 90 dB in the P and the PxS treatment plots ($p < 0.001$), and in the C treatment ($p < 0.047$).

The distance sound travelled was significantly influenced by sound type ($F_{2,940} = 25.4$, $p < 0.001$; Table 6, Figure 11). The following distances reported are the

approximate mean distance sound travelled averaged over all treatments, frequencies, and sound pressure levels. Pure tone sound travelled 11.4 m, rodent sound travelled 10.3 m, and bat sound travelled 10.1 m. Pure tone sound travelled a significantly longer distance than bat sound ($p < 0.001$) and rodent sound ($p < 0.001$). Rodent sound travelled a significantly longer distance than bat sound ($p = 0.011$; Figure 11).

Propagation of Sound: Absorption Coefficient

Standard transformations on the modeled absorption coefficient data were unable to normalize data. Therefore, original data were used for analysis. Due to the large sample size (n = 330), I used a parametric ANOVA. The best model selected by BIC criterion had the absorption coefficient with treatment and frequency as factors (Table 5). All absorption coefficient results are reported from the reduced ANOVA model described above. Although not included in the reduced ANOVA model, I have provided a figure showing a non-significant interaction between treatment and frequency for the absorption coefficient data (Figure 12) to allow comparisons between the distance sound travelled results to the absorption coefficient results.

The absorption coefficient was significantly influenced by treatment ($F_{2,324} = 130.064$, $p < 0.001$; Table 7, Figure 13). The absorption coefficient was largest in the PxS treatment plots, intermediate in the P treatment plots, and smallest in the C treatment. The following absorption coefficients reported are the approximate mean absorption coefficient averaged over all frequencies, sound types, and sound pressure levels. In the PxS treatment plots the absorption coefficient was 3.9 dB/m, in the P treatment plots the absorption coefficient was 2.0 dB/m, and in the C treatment was 0.24 dB/m. The

absorption coefficient for sound broadcasted in the PxS treatment plots was approximately two times larger than the absorption coefficient in the P treatment plots, and was approximately 16 times larger than the absorption coefficient in the C treatment (Figure 13). Tukey HSD post-hoc tests showed that the absorption coefficient was significantly different for each combination of treatment ($p < 0.001$).

The absorption coefficient was significantly influenced by frequency ($F_{3,324} = 6.076$, $p < 0.001$; Table 7, Figure 14). The absorption coefficient was largest when sound was broadcasted at 40 and 60 kHz, intermediate at 30 kHz, and smallest at 20 kHz. The following absorption coefficients reported are the approximate mean absorption coefficient averaged over all treatments, sound types, and sound pressure levels. The absorption coefficient for 20 kHz sound was 1.5 dB/m, for 30 kHz sound it was 2.0 dB/m, for 40 kHz sound it was 2.6 dB/m, and for 60 kHz sound it was 2.3 dB/m (Figure 14). Tukey HSD post-hoc comparisons showed a significant difference in the absorption coefficient of sound broadcasted at 20 and 40 kHz ($p = 0.001$), and 20 and 60 kHz ($p = 0.004$; Figure 14). There was no significant difference in the absorption coefficient for sound broadcasted at 20 and 30 kHz ($p = 0.115$), 30 and 40 kHz ($p = 0.252$), 30 and 60 kHz ($p = 0.672$), and 40 and 60 kHz ($p = 0.836$).

Recording

I deployed the D240x detectors for 46 nights, and the Avisoft-UltraSoundGate for 22 nights. I recorded over 200,000 sound files. In total, 47,136 sound files potentially contained bat or rodent ultrasound. Of the 47,136 sound files I manually identified 3,024 sound files that contained bat echolocation calls or rodent vocalizations. Of the 3,024

sound files there were 708 sound files were identified to species. For my analysis, I obtained spectral and temporal characteristics from 385 high quality, echolocation calls. Five bat species were identified: *E. fuscus* (big brown bat, n = 38), *L. borealis* (Eastern red bat, n = 250), *L. cinereus* (Hoary bat, n = 4), *L. noctivagans* (silver-haired bat, n = 13), and *P. subflavus* (tri-colored bat, n = 80). I excluded *L. cinereus* from analysis due to the small sample size.

Between the P and PxS treatment plots bat echolocation call spectral and temporal characteristics produced by *E. fuscus* ($F_{10,27}$ = 1.058, p = 0.426), *L. borealis* ($F_{10,238}$ = 1.546, p = 0.124), *L. noctivagans* ($F_{10,2}$ = 1.093, p = 0.568), and *P. subflavus* ($F_{10,69}$ = 0.955, p = 0.49; Table 8) were not significantly different.

Using my methods, I was able to find 11 sound files containing rodent vocalizations (Table 9). All vocalizations recorded were of the syllable vocalization motif type (see Kalcounis-Rueppell et al. 2010). Syllable vocalizations are characterized by long, relatively constant frequency vocalizations. In the PxS treatment plots, the number of syllables recorded ranged from 2 to 3, and in the P treatment plots ranged from 1 to 6 syllables. In the PxS treatment plots, the time interval between syllables ranged from 0.08 s to 0.32 s, and in the P treatment plots ranged from 0.07 s to 0.28 s. In the PxS treatment plots, the duration of a syllable ranged from 0.046 s to 0.26 s, and in the P treatment plots ranged from 0.06 s to 0.48 s. In the PxS treatment plots, the frequency of the call at maximum amplitude of the vocalization ranged from 13.6 kHz to 49.8 kHz and in the P treatment plots ranged from 16.6 kHz to 29.2 kHz (Table 9).

CHAPTER IV

DISCUSSION

Vegetation Density

I demonstrated that intercropping switchgrass between rows of pine trees in managed pine forests increases understory vegetation density. Although vegetation density in the PxS treatment plots was significantly higher than vegetation density in the P treatment plots, both treatments had relatively high vegetation density. Increased vegetation density changes an animals' acoustic environment, by decreasing the distance at which acoustic signals can travel, and be detected (Naguib 2003; Morrill et al. 2013). Decreasing the distance at which acoustic signals travel could impact communication between individuals that live in the understory, by reducing the effectiveness of acoustic signals. Some animals respond to habitat change by altering vocalizations to improve transmission (Smith 1979; Wiley and Richards 1982; Naguib 2003; Patriquin et al. 2003; Padgham 2004; Van Dongen and Mulder 2006; Boncoraglio and Saino 2007; Morrill et al. 2013), however, I found no evidence of this in my study.

Broadcasting

Higher vegetation density reduced the distance that sound travelled by increasing absorption of sound. Regardless of sound type, sound pressure level, or frequency, all broadcasted sound travelled the shortest distance in the treatment with the highest

vegetation density. The interaction between treatment and frequency on the distance sound travelled is likely due to the differences in the distance sound travelled at 40 and 60 kHz, which was not consistent among treatments. In the C treatment, the difference in distance sound travelled between 40 and 60 kHz was a 6.5 m, whereas in the P treatment plots there was a difference of 5.5 m, and in the PxS treatment plots there was a difference of 3 m. Based on the pattern of how sound travelled in the C and P treatments at 40 and 60 kHz, I would have expected that 60 kHz sound broadcasted in the PxS treatment would travel approximately 1 m, as opposed to 3.5 m.

The interaction between treatment and sound pressure level on the distance sound travelled is likely due to how the distance sound travelled at 80 and 90 dB, which was not consistent among treatments. Along the gravel road, increasing the sound pressure level from 80 to 90 dB increased the distance sound travelled by 0.8 m, whereas in the P treatment the distance sound travelled increased by 3.4 m, and in the PxS treatment the distance sound travelled increased by 2.2 m. The interaction could also be an artifact of my experimental design. The microphone transect in the broadcasting experiment was 18 m long. If both 80 and 90 dB sound were travelling beyond the length of the transect I had no way of detecting the sound. It is likely that in the C treatment for 20, 30, and 40 kHz sound, the microphone transect was not long enough. Based on the patterns observed in the P and PxS treatment I would expect 90 dB sound to travel a distance between 18.8 and 20 m in the C treatment. By unintentionally clipping responses to a distance of 18m, I truncated the data set in the no vegetation control treatment (C).

I also demonstrated than an increase in the duration of the broadcasted sound resulted in an increase in the distance sound travelled. Of the sound types I broadcasted, pure tone sound was longest in duration and travelled the longest distance. Rodent sound was intermediate in duration and travelled an intermediate distance. Bat sound was shortest in duration and travelled the shortest distance. Broadcasted bat and rodent sound had a short time interval between the repeated sound pulse or syllable. Pure tone sound did not have an interval, as it was broadcasted continuously. Of the animal produced sound I broadcasted, rodent sound travelled a significantly longer distance than bat sound with a mean difference of approximately 0.2 m. The biological significance of this difference is unknown however it is likely to be important given minimum and maximum detection differences for echolocating bats and distances between vocalizing mice and conspecifics (Kalko 1995; Siemers and Schnitzler 2000; Briggs and Kalcounis-Rueppell 2011; Nørum et al. 2012; Stilz and Schnitzler 2012). At a distance of 5 cm from vegetation the Natterer's bat, *Myotis nattereri*, can localize and detect prey (Siemers and Schnitzler 2000). The estimated maximum detection distance for different bat species can range from 1.14 m to 2.4 m (Kalko 1995; Stilz and Schnitzler 2012). This distance is dependent on the species that produces the echolocation call, and frequency and intensity of the echolocation call produced at (Kalko 1995; Nørum et al. 2012; Stilz and Schnitzler 2012).

The absorption coefficient provides information about how much absorption and scattering is occurring as a sound propagates through a medium. The absorption coefficient takes into account both absorption of sound energy by vegetation and the

atmosphere, and scattering of sound energy due to vegetation present in the medium that the sound wave is propagating through. A large absorption coefficient means that sound will be attenuated more quickly due to absorption and scattering of sound energy. In the PxS treatment, where vegetation density was highest, the absorption coefficient was also highest. The P treatment had an intermediate absorption coefficient value. In the C treatment, where no vegetation was present, the absorption coefficient was small because there were no objects present to influence the propagating sound wave. However, the absorption coefficient in the C treatment was not zero, indicating that some absorption was occurring. Absorption that did occur in the C treatment was presumably due to atmospheric absorption (Wiley and Richards 1982; Snell-Rood 2012). The absorption coefficient was also influenced by frequency. The absorption coefficient was largest for 40 kHz sound, which was statistically the same as the absorption coefficient for 60 kHz sound, and the absorption coefficient was smallest for 20 kHz sound. I expected to see a similar pattern for the distance sound travelled and the absorption coefficient, because the distance sound can travel is related to the amount of sound energy absorbed. Instead, I found that the distance sound travelled was longest for 20, 30, and 40 kHz sound, and shortest for 60 kHz sound. I expected that 40 kHz sound would travel a similar distance to 60 kHz sound, because 40 and 60 kHz sound had similar absorption coefficients. Below, I will further discuss possibilities for pattern differences in the distance sound travelled and absorption coefficient data.

I found that the distance sound travels and the modeled absorption coefficients do not follow the same pattern for all frequencies. The presence of switchgrass has more of

an influence on high frequency sound than on low frequency sound. In all treatments, high frequency sound (i.e. 60 kHz sound) travelled the shortest distance. However, not all frequencies responded to treatment in the same way. The absorption coefficient was also largest for high frequency sound (i.e. 40 and 60 kHz). Regardless, my results agree with previous studies that have shown that lower frequency sound travels a longer distance, and is less impacted by vegetation, than higher frequency sound (Smith 1979; Patriquin et al. 2003; Padgham 2004; Nicholls and Goldizen 2006; Van Dongen and Mulder 2006; Nemeth and Brumm 2009; Morrill et al. 2013). High frequency sounds travel a shorter distance, and experience more absorption and scattering of sound energy, that low frequency sounds. In my study, lower frequency sounds (i.e. 20, 30, and 40 kHz) travelled a longer distance, potentially allowing individual animals to communicate across a larger area.

An explanation for difference in patterns of distance sound travelled and the absorption coefficient data could be related to the frequency response curves of the microphones or my microphone calibration methods. A frequency response curve is the sensitivity of a microphone at a given frequency. The Avisoft- Emkay FG Series microphones I used detect 20 kHz sound at -2 dB, 30 kHz sound at -12 dB, 40 kHz sound at -33 dB, and 60 kHz sound at -27 dB. When modeling the absorption coefficient I used the sound pressure level as a function of distance. If the sound pressure level was less intense due to the ability of the microphone to detect that frequency of sound it may appear that more absorption has occurred over a short distance. It is possible that the microphones were detecting 40 kHz sound at a longer distance but the intensity of the

sound that was detected was relatively low, when compared to 20 and 30 kHz sound. Therefore the distance 40 kHz sound travelled was long and absorption was high, which could have lead to differences in patterns of distance sound travelled and absorption coefficient data results. Future studies attempting to model absorption of sound should use microphones with flat frequency response curves, so that the microphones detect a wide range of frequencies at similar sound pressure levels. However, frequency response curves should not influence treatment results for distance sound travelled or the absorption coefficient because all frequencies were pooled when looking at treatment main effects. However, frequency response curves could potentially influence comparisons among frequencies.

In addition to frequency response curves, microphone calibration could be improved upon. I checked to see if the microphones were detecting sound at approximately the same sound pressure level, but not the same sound pressure level. Ideally, I should have calibrated all microphones I used so they would detect sound at the same sound pressure level, because this would have allowed for more accurate modeling of the absorption coefficient. Future studies should also calibrate the microphones so they detect sounds at the same sound pressure level.

I have shown that vegetation density influences sound propagation. The inability or reduced ability to detect sound may or may not have fitness consequences for bats and rodents living in a managed pine forest system with intercropped switchgrass. Other studies have shown that when individuals are unable to detect acoustic signals, communication, predator/prey interactions, spatial orientation, and other behaviors may

be impacted (Francis and Barber 2013). Anthropogenic noise, like vegetation, can influence the detection of acoustic signals (Warren et al. 2006) and traffic noise has been shown to reduce great tit reproductive success, by reducing clutch size and fledgling success (Halfwerk et al. 2011). Frequency overlap reduced the females' perception of male songs, influencing mate choice and investment, resulting in smaller clutch sizes (Halfwerk et al. 2011). Increased noise and frequency overlap may also impact communication between parents and offspring resulting in decreased fledgling success (Halfwerk et al. 2011). Whether or not similar effects would be seen in my study system would require further research to examine the consequences of decreased sound propagation in switchgrass by examining individual responses and reproductive success. If rodents are unable to improve sound transmission by altering characteristics of vocalizations I would predict that there would be some decrease in reproductive success.

In summary, acoustic signals are attenuated as they propagate (Wiley and Richards 1982; Mathevon et al. 1996; Bradbury and Vehrencamp 1998; Patriquin et al. 2003; Van Dongen and Mulder 2006; Snell-Rood 2012). The amount of attenuation and degradation of acoustic signals depends on habitat characteristics (Patriquin et al. 2003) and environmental conditions (Wiley and Richards 1982; Snell-Rood 2012). I demonstrated that intercropping switchgrass between rows of pine trees in managed pine forests increases the absorption coefficient and decreases the distance ultrasound travels. In order for communication to occur, the signal produced by the sender must be detected by the receiver (Bradbury and Vehrencamp 1998). When acoustic signals produced by the sender are unable to be detected by the receiver acoustic, communication will be

impacted. Animals producing sound for the purpose of acoustic communication, in habitats with dense vegetation cover, will either need to be in closer proximity for effective communication to occur, or will need to alter the spectral and temporal characteristics of their vocalizations to improve sound transmission.

Recording

There are many possible ways that animals, such as rodents, could improve signal transmission through dense vegetation. For comparison, birds can improve transmission of songs through habitats with varying amounts of vegetation cover by changing the frequency and duration of songs (Nicholls and Goldizen 2006). Birds also have the ability to increase the amplitude of their calls in response to increased background noise levels (Brumm and Todt 2002; Pytte et al. 2003; Brumm 2004). Rodents living in dense vegetation of the forest understory may be able to increase the amplitude of their vocalizations. Rodents could also increase the duration of their vocalizations in response to higher vegetation density to increase the distance sound can travel (Nicholls and Goldizen 2006; Van Dongen and Mulder 2006).

I predicted that rodents would produce vocalizations of longer duration and of lower frequency in the PxS treatment, when compared with the P treatment. However, I was unable to find evidence to support my prediction because I recorded too few rodent ultrasonic vocalizations in both treatments. I only recorded seven files containing rodent vocalizations in the P treatment and four files containing rodent vocalizations in the PxS treatment. Vocalizations recorded were all of the same motif type (i.e. single or multi-syllable vocalizations; see Kalcounis-Rueppell et al. 2010).

I may have had difficulty recording rodent vocalizations for multiple reasons. First, rodents may not have used vocalizations as often in habitat with dense vegetation cover, where sound travels a shorter distance due to the increased absorption of sound energy. Both treatments had relatively high vegetation density so rodents may not have produced many ultrasonic vocalizations. Second, the effectiveness of recording in high density vegetation may have been low in both treatments. If rodents were not in close proximity to the recording equipment, it is unlikely that I would have been able to detect their vocalizations, in either the P or PxS treatments. Third, it is possible that by using the SonoBatch scrubber in SonoBat to remove sound files containing mostly ambient noise, I could have removed quiet rodent vocalizations. Future studies should record rodent vocalizations near locations where rodent activity is known to be high, such as at the entrance of nest sites. If rodents are vocalizing, recording equipment needs to be near the vocalizing animal in order to record vocalizations.

I predicted that bats would alter their echolocation calls in response to increased vegetation cover, because short, frequency modulated echolocation calls are more informative than long, narrowband echolocation calls in cluttered habitat (Kalko and Schnitzler 1993). For example, the returning echoes from frequency modulated echolocation calls provide the bat with information about the texture and depth of objects in their habitat (Habersetzer and Vogler 1983). I did not find that the spectral or temporal characteristics of bat echolocation calls changed in response to intercropping switchgrass between rows of pine trees in managed pine forests.

The lack of a difference in echolocation call characteristics between treatments may be explained by how bats use the space between trees. Bats in both treatments fly above the vegetation between the rows of pine trees (personal observation). Even though vegetation composition is differs between rows of pine trees, bats in both treatments are flying along a vegetation canopy edge (either above woody and herbaceous vegetation in P or above switchgrass in P x S treatments). Intercropping switchgrass between the rows of pine trees in managed pine forests could create an additional edge that is relatively uniform in height, when compared to woody and herbaceous vegetation in the P treatment. Thus, intercropping switchgrass could be creating a clear edge for bats to fly along. Edges are important flight features for bats (Verboom and Huitema 1997; Hein et al. 2009; Kalcounis-Rueppell et al. 2013). Furthermore, if there were any difference between bat echolocation calls, they would have been right along the top edge of vegetation. To detect these differences my recorders should have been placed along the top edge of vegetation in each treatment.

CHAPTER V

CONCLUSIONS

I found that vegetation density was higher in pine forests intercropped with switchgrass when compared to traditionally managed pine forests. However, both treatments had high vegetation density. The amount of sound energy absorbed was largest in the PxS treatment plots, and for 40 and 60 kHz sound. Increased absorption contributed to the decrease in the distance that sound travelled in the PxS treatment plots compared to the other treatment plots. The distance sound travelled was influenced by treatment, frequency, sound type, and sound pressure level. Sound that was lower, longer, and louder travelled a longer distance in all treatment types. I found no evidence that bats changed their echolocation calls in the PxS treatment plots. I recorded very few rodent ultrasonic vocalizations and was not able to determine whether they changed their vocalizations in response to the presence of switchgrass. A small increase in vegetation density can have significant impacts on the distance sound travels due to the amount of absorption that occurs as the sound propagates through a medium. To determine the implications of a decrease in the distance that sound travels, and an increase in sound absorption, on vocalizing animals research would need to examine individual responses and reproductive success.

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APPENDIX A

TABLES

Table 1. The reference (Z) values for pure tone sound absorption coefficient model fitting for the C treatment. Shown are the reference values obtained during model fitting methods, each frequency (kHz) at either 80 or 90 dB has five reference values associated with the randomly selected night. Reference values may vary on the same night due to the methods I used during model fitting. I treated each randomly selected night as an independent event therefore leading to variation in reference values on the same night.

Sound Type	Pure Tone							
Sound Pressure Level	80				90			
Frequency	20	30	40	60	20	30	40	60
Night 1	4.17	3.89	6.29					
Night 2	-7.06	-3.33	4.14	-12.01	-0.29	3.51		-1.89
Night 3		-5.05	2.20					
Night 4	-7.16						2.86	-13.65
Night 5						4.35	11.47	
Night 6								-16.30
Night 7		-12.92	-8.00		-2.46			
Night 8			-7.74		-4.26	-5.49	3.62	
Night 9				-23.87		-3.32	1.26	
Night 10								
Night 11	-7.13				-1.08			
Night 12				-21.71	0.47			-14.47
Night 13				-14.70				-5.21
Night 14		-9.90				-1.95	3.03	
Night 15	-10.34			-15.80				

Table 2. The reference (Z) values for rodent sound absorption coefficient model fitting for the C treatment. Shown are the reference values obtained during model fitting methods, each frequency (kHz) at either 80 or 90 dB has five reference values associated with the randomly selected night. Reference values may vary on the same night due to the methods I used during model fitting. I treated each randomly selected night as an independent event therefore leading to variation in reference values on the same night.

Sound Type	Rodent					
Sound Pressure Level	80			90		
Frequency	20	30	60	20	30	60
Night 1		5.97	-5.87			
Night 2	-5.73	-3.50		1.68		
Night 3			-12.83	2.60	6.37	-0.57
Night 4	-8.25					
Night 5		-2.37				
Night 6					3.97	
Night 7	-8.63		-27.63			
Night 8				-2.56		
Night 9			-20.57	-1.04		-13.97
Night 10	-7.10	-9.24				-17.01
Night 11	-4.42					
Night 12			-19.09			-10.66
Night 13					2.82	
Night 14				1.23	0.40	-12.59
Night 15		-6.82			2.04	

Table 3. The reference (Z) values for bat sound absorption coefficient model fitting for the C treatment. Shown are the reference values obtained during model fitting methods, each frequency (kHz) at either 80 or 90 dB has five reference values associated with the randomly selected night. Reference values may vary on the same night due to the methods I used during model fitting. I treated each randomly selected night as an independent event therefore leading to variation in reference values on the same night.

Sound Type	Bat							
Sound Pressure Level	80				90			
Frequency	20	30	40	60	20	30	40	60
Night 1	4.06							
Night 2							12.19	
Night 3	-7.13			-11.37	2.11			3.73
Night 4			0.40			5.42		
Night 5		-2.00	3.87		2.10	8.74	11.86	
Night 6		-4.36						-12.94
Night 7	-8.11				-1.01		4.26	
Night 8			-5.74		-2.60			-11.61
Night 9	-11.26					-0.44		
Night 10		-9.11		-30.79		-1.18		
Night 11			-2.45				4.63	
Night 12		-5.46				2.54		
Night 13	-8.88		5.02	-10.43	0.80		9.26	
Night 14				-21.34				-12.45
Night 15		-5.98		-9.63				2.09

Table 4. BIC backward/forward model selection steps for distance sound travelled ANOVA model reduction. The chosen, reduced ANOVA model is in bold type font. In the table is dB is referring to the sound pressure level (dB) of broadcasted sound. Broadcasting data were collected from June to August 2012 in Kemper Co., MS.

Model	BIC	Δ BIC
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Treatment + Frequency:Treatment	1799	---
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Treatment + Frequency:Treatment	1815	16
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Treatment + Frequency:Treatment + dB:Frequency:Treatment	1820	21
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Treatment + Frequency:Treatment + Sound Type:Treatment + dB:Frequency:Treatment	1824	25
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + Frequency:Sound Type + dB:Treatment + Frequency:Treatment + Sound Type:Treatment + dB:Frequency:Treatment	1836	37
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Frequency:Treatment + Sound Type:Treatment + dB:Frequency:Treatment	1850	51
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Frequency:Treatment + Sound Type:Treatment + dB:Frequency:Treatment + dB:Sound Type:Treatment	1876	77
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Frequency:Treatment + Sound Type:Treatment + dB:Frequency:Sound Type + dB:Frequency:Treatment + dB:Sound Type:Treatment	1910	111
Distance ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Frequency:Treatment + Sound Type:Treatment + dB:Frequency:Sound Type+ dB:Frequency:Treatment + dB:Sound Type:Treatment + Frequency:Sound Type:Treatment	1967	168
Distance ~ dB * Frequency * Sound Type * Treatment	2033	234

Table 5. BIC backward/forward model selection steps for absorption coefficient ANOVA model reduction. The chosen reduced ANOVA model is in bold type font. In the table is dB is referring to the sound pressure level (dB) of broadcasted sound. Broadcasting data were collected from June to August 2012 in Kemper Co., MS.

Model	BIC	Δ BIC
Absorption ~ Frequency + Treatment	375.98	---
Absorption ~ dB + Frequency + Treatment	381.49	5.51
Absorption ~ dB + Frequency + Sound Type + Treatment	391.3	15.32
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Sound Type	401.74	25.76
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Sound Type + dB:Treatment	412.69	36.71
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + dB:Treatment	427.83	51.85
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + dB:Treatment + Sound Type:Treatment	449.75	73.77
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + dB:Treatment + Sound Type:Treatment + dB:Sound Type:Treatment	471.92	95.94
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Sound Type:Treatment + dB:Sound Type:Treatment	494.74	118.76
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Sound Type:Treatment + dB:Frequency:Sound Type + dB:Sound Type:Treatment	519.78	143.8
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Frequency:Treatment + Sound Type:Treatment T + dB:Frequency:Sound Type + dB:Sound Type:Treatment	548.39	172.41
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Frequency:Treatment + Sound Type:Treatment + dB:Frequency:Sound Type + dB:Frequency:Treatment + dB:Sound Type:Treatment	579.85	203.87
Absorption ~ dB + Frequency + Sound Type + Treatment + dB:Frequency + dB:Sound Type + Frequency:Sound Type + dB:Treatment + Frequency:Treatment + Sound Type:Treatment + dB:Frequency:Sound Type + dB:Frequency:Treatment + dB:Sound Type:Treatment + Frequency:Sound Type:Treatment	625.41	249.43
Absorption ~ dB * Frequency * Sound Type * Treatment	680.76	304.78

Table 6. The ANOVA table from the reduced distance sound travelled ANOVA model (Distance ~ dB + Frequency + Sound Type + Treatment + dB:Treatment + Frequency:Treatment). In the table is dB is referring to the sound pressure level (dB) of broadcasted sound. The reduced model was chosen based on BIC selection criterion, broadcasting data were collected from June to August 2012 in Kemper Co., MS.

	Df	SumSq	MeanSq	F	P
dB	1	1121.5	1121.5	189.998	<0.001
Frequency	3	4938.5	1646.2	278.88	<0.001
Sound Type	2	299.6	149.8	25.379	<0.001
Treatment	2	16834.5	8417.2	1425.984	<0.001
dB:Treatment	2	274.8	137.4	23.28	<0.001
Frequency:Treatment	6	343.4	57.2	9.695	<0.001
Residuals	940	5548.6	5.9		

Table 7. The ANOVA table from the reduced absorption coefficient ANOVA model (Absorption ~ Frequency + Treatment). The reduced model equation was chosen based on BIC selection criterion. Broadcasting data were collected from June to August 2012 in Kemper Co., MS.

	Df	SumSq	MeanSq	F	P
Frequency	3	52.2	17.4	6.076	<0.001
Treatment	2	745.0	372.5	130.064	<0.001
Residuals	324	928.0	2.9		

Table 8. The results of the four, one-way MANOVA tests with 10 dependent spectral and temporal characteristics of bat echolocation calls with treatment as the independent variable. The number of bat calls used in the analysis are reported by treatment. The degrees of freedom for the numerator (Df_{num}) and denominator (Df_{den}) are also reported. The MANOVA test statistic reported in the table is Wilks' Lambda (λ). Recording took place in Kemper Co., MS from June to August 2012.

Bat Species	N_{PxS}	N_P	Df_{num}	Df_{den}	λ	F	P
Eptesicus fuscus	23	15	10	27	0.719	1.058	0.426
Lasiurus borealis	147	103	10	238	0.939	1.546	0.124
Lasionycterus noctivagans	6	7	10	2	0.155	1.093	0.568
Perimyotis subflavus	39	41	10	69	0.878	0.955	0.490

Table 9. Summary table of the spectral and temporal characteristics of rodent vocalizations recorded in Kemper Co., MS. The treatment column indicates the treatment that the vocalization was recorded in. The motif column indicates the type of vocalization that was recorded; SV is a syllable vocalization. The syllable column indicates the number of vocalization syllables per sound file, and the interval column indicates the amount of time (seconds) between the vocalization syllables. The duration and frequency (kHz) columns indicate the duration (seconds), and the peak frequency (kHz) at maximum amplitude of each USV syllable. Peak frequency (kHz) at maximum amplitude is the frequency of the syllable at the loudest point in the syllable.

Treatment	Motif	Syllable	Interval (s)	Duration (s)	Frequency (kHz)
P	SV	1	---	0.44	19.5
P	SV	1	---	0.32	19.5
		2	0.14	0.28	19.5
P	SV	1	---	0.25	19.5
		2	0.09	0.16	18.5
P	SV	1	---	0.23	19.5
		2	0.09	0.26	19.5
P	SV	1	---	0.06	29.2
		2	0.07	0.16	29.2
P	SV	1	---	0.20	18.5
		2	0.12	0.48	18.5
		3	0.13	0.32	16.6
P	SV	1	---	0.06	22.4
		2	0.09	0.08	22.4
		3	0.11	0.08	22.4
		4	0.07	0.32	23.4
		5	0.09	0.21	21.4
		6	0.28	0.09	22.4
PxS	SV	1	---	0.20	15.6
		2	0.08	0.26	13.6
PxS	SV	1	---	0.16	15.6
		2	0.24	0.25	14.6
		3	0.32	0.05	13.6
PxS	SV	1	---	0.05	13.6
		2	0.10	0.15	14.6
		3	0.08	0.26	13.6
		4	0.10	0.26	14.6
PxS	SV	1	---	0.06	43.9
		2	1.10	0.02	49.8

APPENDIX B

FIGURES

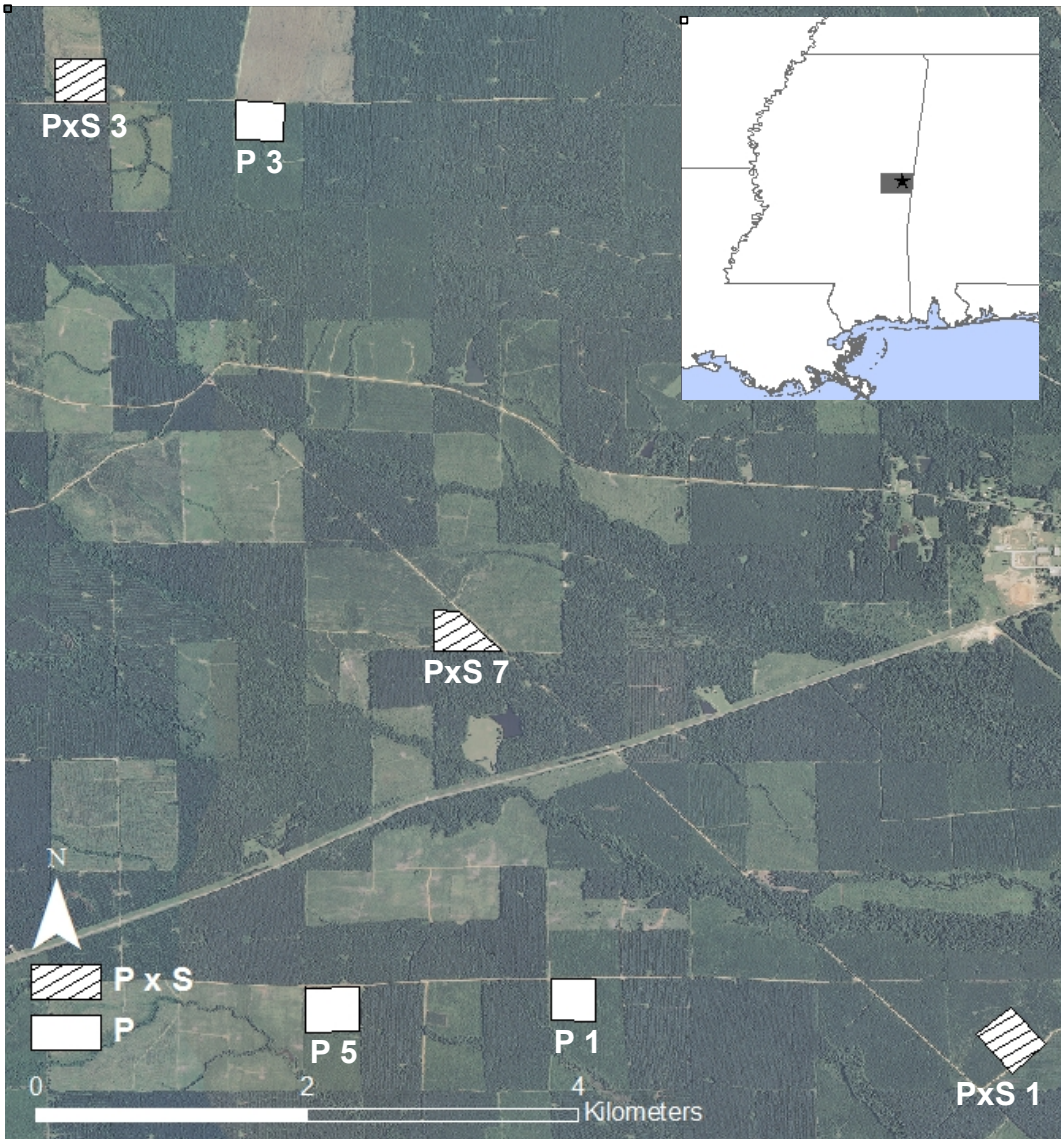


Figure 1. Map of the Kemper Co., MS study site in 2012. The map inset shows where Kemper Co. is located within the state of Mississippi and the star indicates the location of the study site within Kemper Co. Solid white squares are managed pine forests that are not intercropped with switchgrass (P) plots and white squares with black lines are managed pine forests intercropped with switchgrass (PxS).

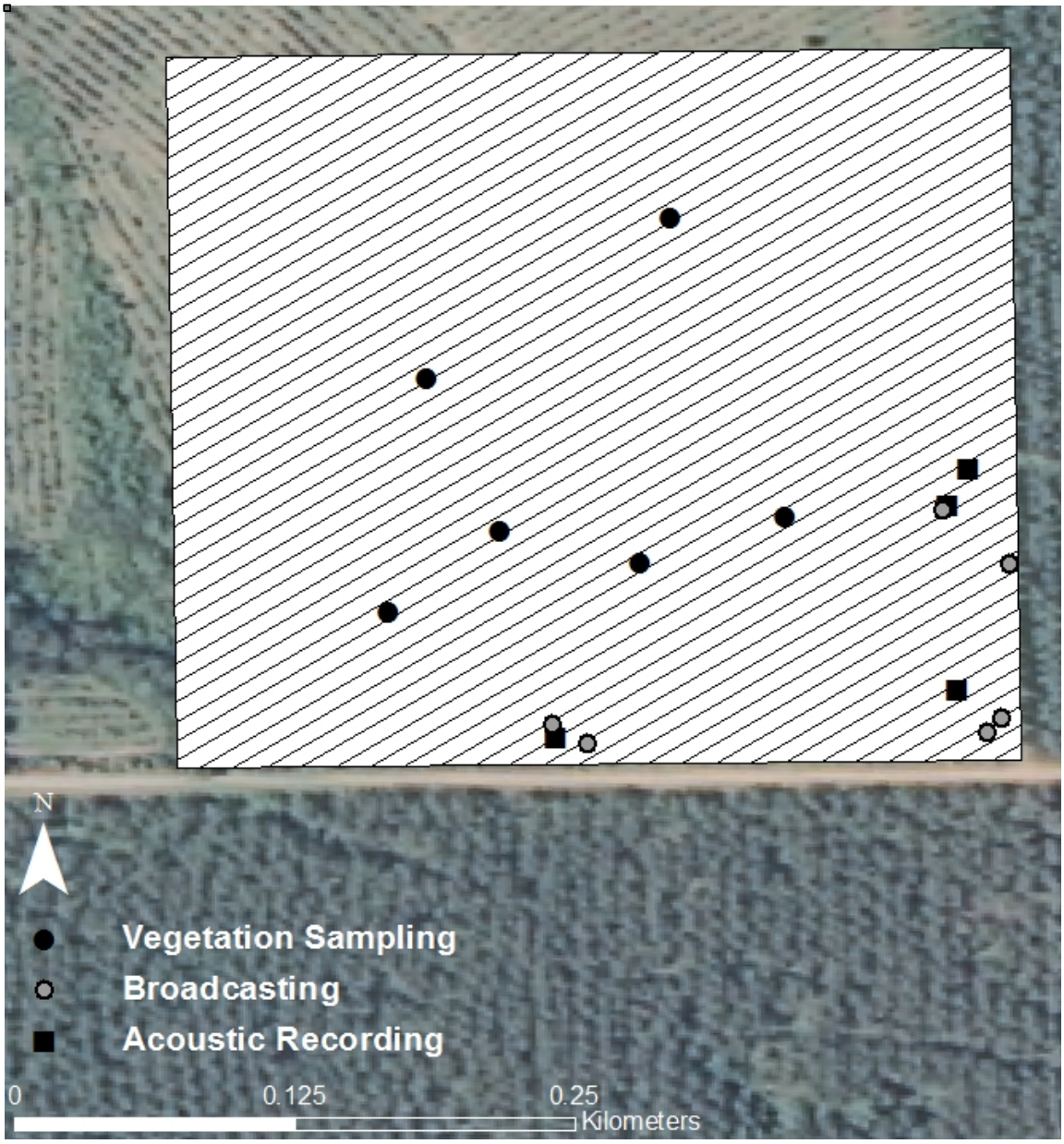
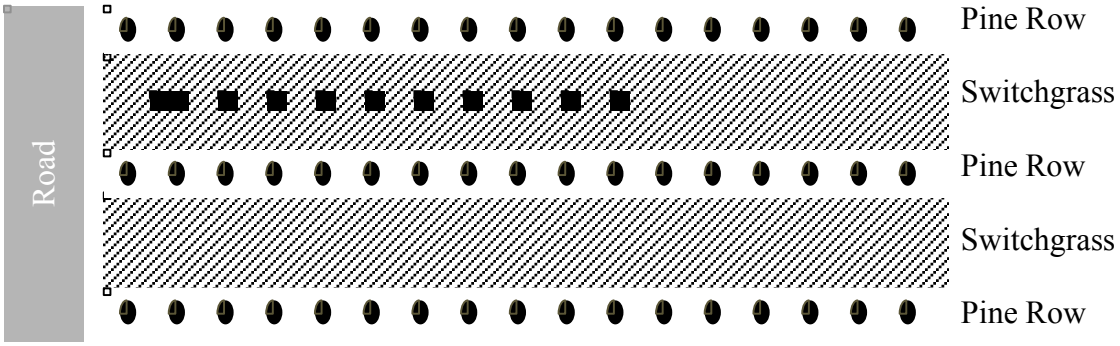
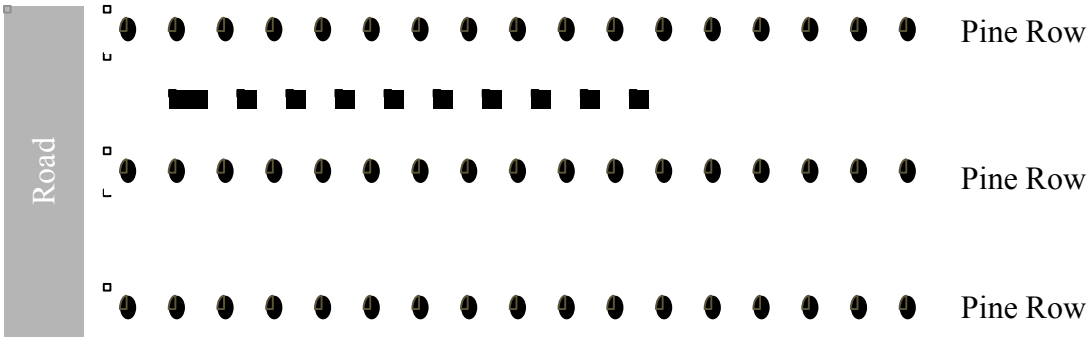


Figure 2. Close up view of the PxS 3 treatment plot showing an example of locations where vegetation sampling, broadcasting, and recording took place. Vegetation cover sampling sites were randomly generated points, whereas broadcasting and acoustic recording sites were systematic selected.

A. Managed pine forest intercropped with switchgrass (PxS treatment plot)



B. Managed pine forest that is not intercropped with switchgrass (P plot)



C. Gravel road "no vegetation" control (C road)

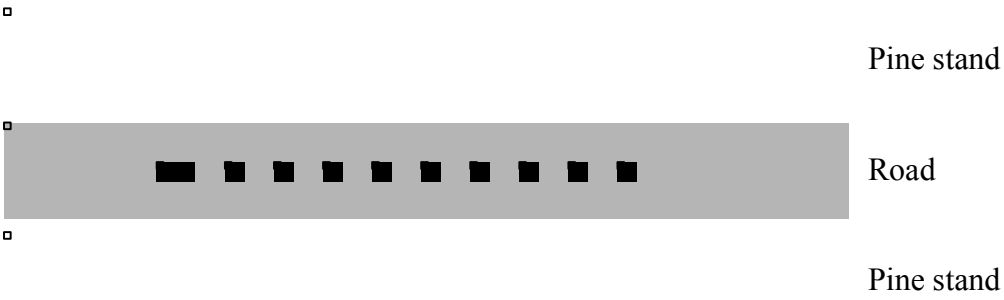


Figure 3. Schematic diagram showing the equipment set up for broadcasting experiments conducted in Kemper Co., MS. A and B) For the P plots and PxS treatment plots a transect of microphones was set up from the edge towards the interior of the forest to record sound that were broadcasted from a speaker located at the forest edge. C) For the C road the transect was set up on the center of the road. The AT-100 ultrasound speaker is represented by ▬, microphones are represented by ■, and pine trees (in A and B) are represented by ●.

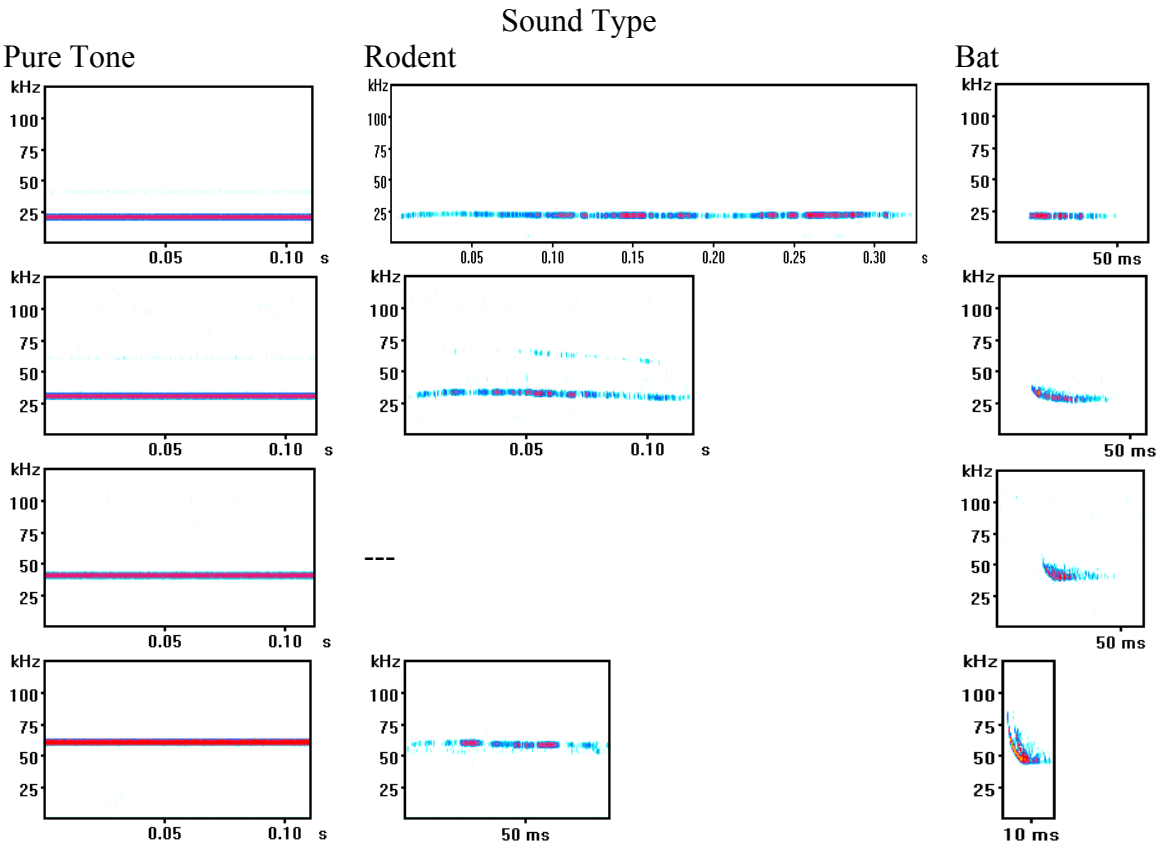


Figure 4. The spectrographs of pure tone, rodent and bat sound used in broadcasting experiments in Kemper Co., MS. In all spectrographs time (s or ms) is on the x-axis, and frequency (kHz) is on the y-axis. The first row has spectrographs of sound that were broadcasted at 20 kHz, second row at 30 kHz, third row at 40 kHz, and fourth row at 60 kHz. The first column has spectrographs of the pure tone sound, these sound were generated using G'Tools ultrasonic generation software that accompanyed the AT-100 ultrasound speaker. The second column has spectrographs of rodent vocalizations that were broadcasted, the 20 and 30 kHz vocalizations were recorded in California and the 60 kHz vocalization was recorded in Mississippi. The third column has bat echolocation calls, all of which were recorded in Mississippi.

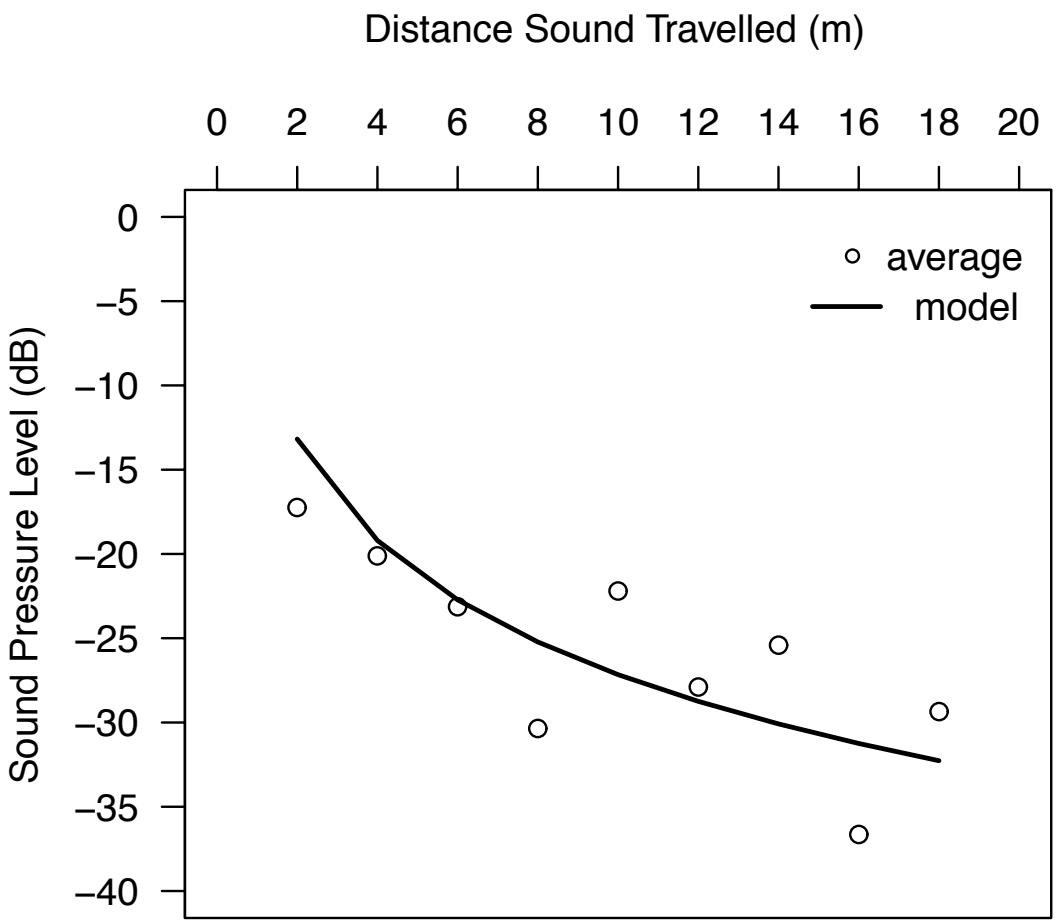


Figure 5. An example showing how I modeling the attenuation of sound to determine the absorption coefficient and reference value for a C treatment site. In this example I am showing averaged sound pressure level (dB) data plotted as a function of distance sound travelled (m) for 20 kHz pure tone sound broadcasted at 80 dB on the C road on night 9. The model line is the predicted sound pressure level based on minimizing the standard error between the actual mean sound pressure level and the predicted sound pressure level.

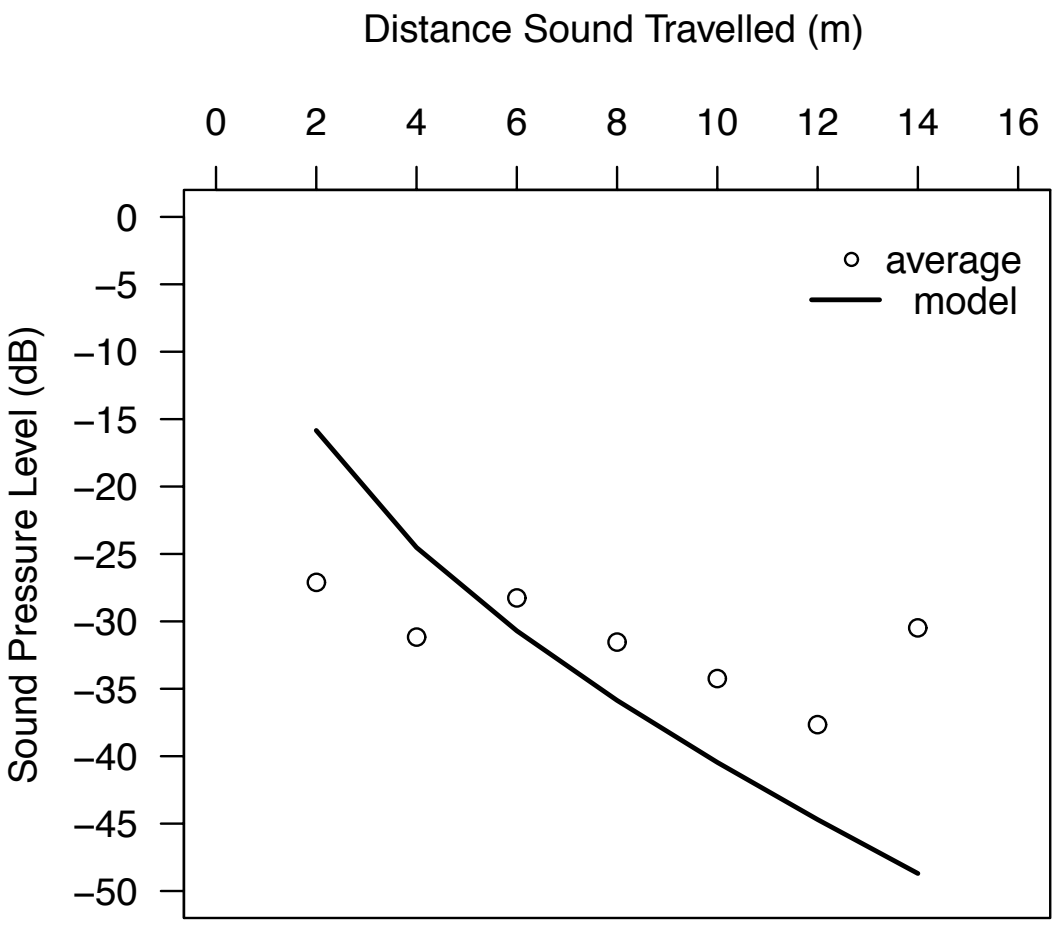


Figure 6. An example showing how I modeling the attenuation of sound to determine the absorption coefficient in a P treatment plot. In this example I am showing averaged sound pressure level (dB) data plotted as a function of distance sound travelled (m) for 20 kHz pure tone sound broadcasted at 80 dB on night 9. The model line is the predicted sound pressure level based on minimizing the standard error between the actual mean sound pressure level and the predicted sound pressure level.

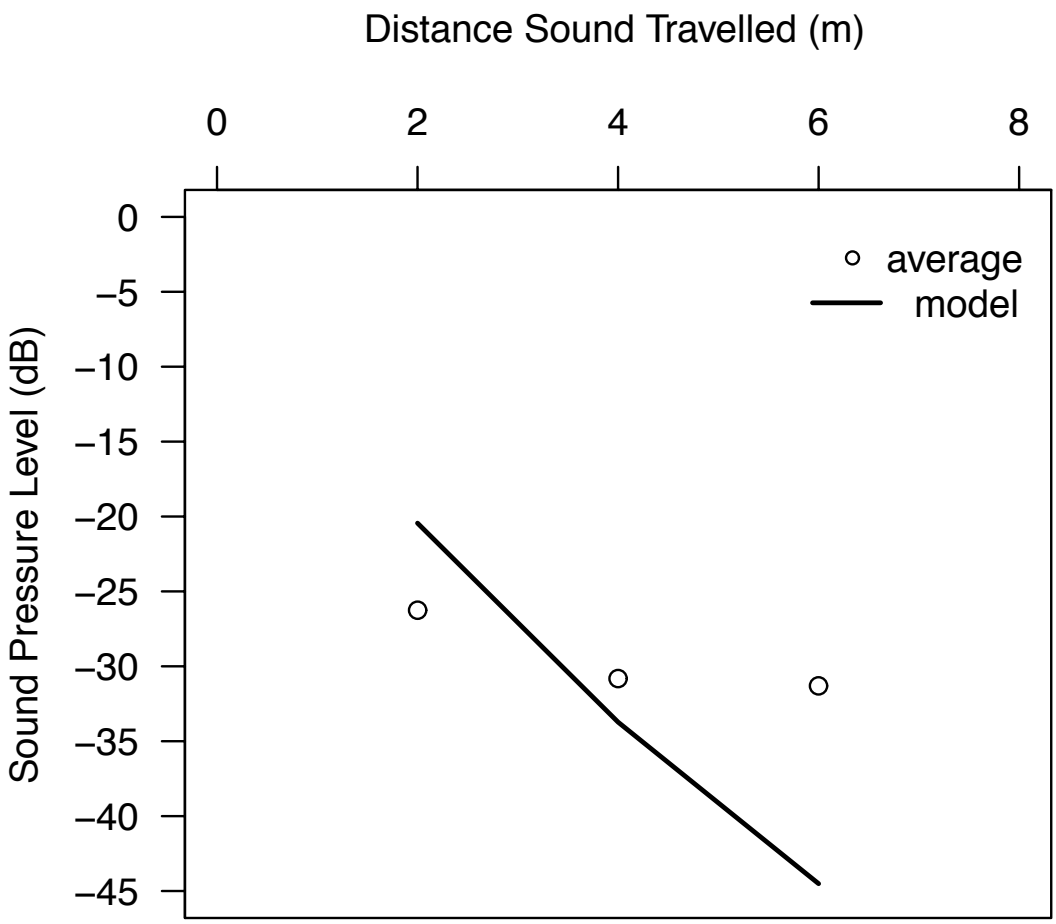


Figure 7. An example showing how I modeling the attenuation of sound to determine the absorption coefficient in a PxS treatment plot. In this example I am showing averaged sound pressure level (dB) data plotted as a function of distance sound travelled (m) for 20 kHz pure tone sound broadcasted at 80 dB on night 9. The model line is the predicted sound pressure level based on minimizing the standard error between the actual mean sound pressure level and the predicted sound pressure level.

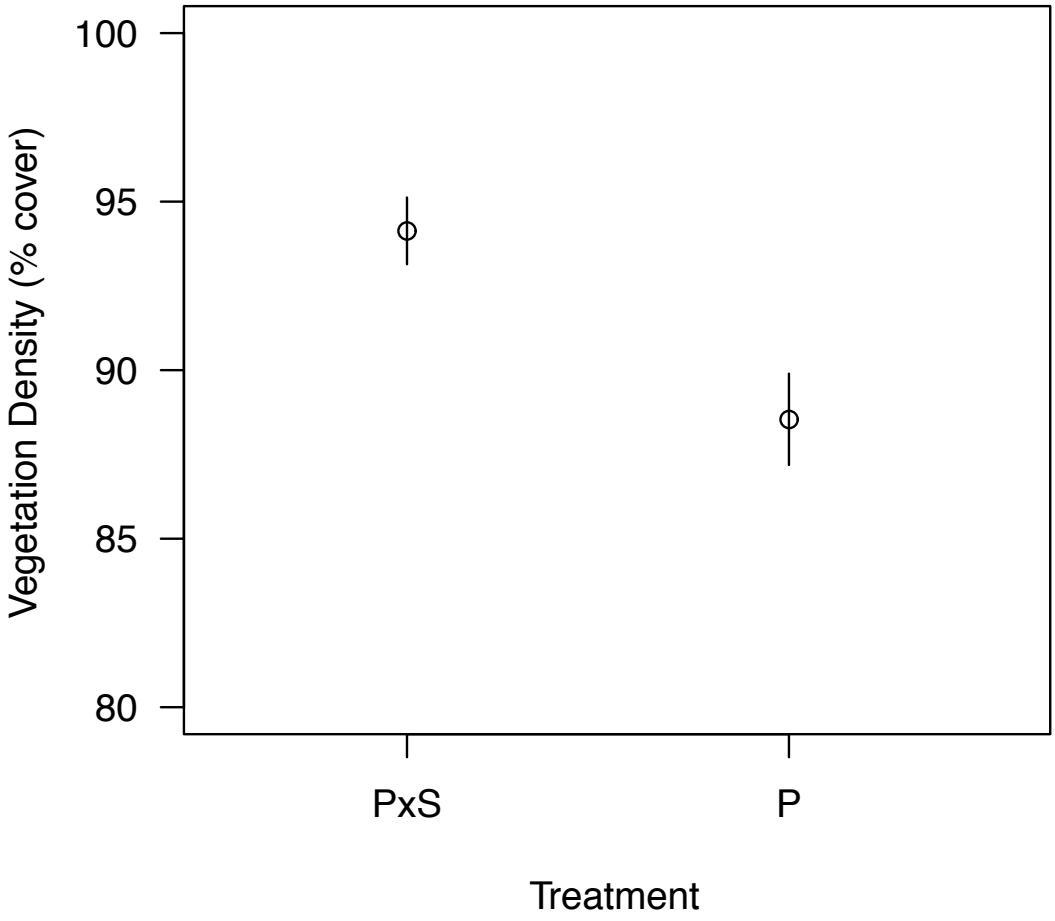


Figure 8. Mean understory vegetation density (% cover) ± 1 SE per treatment. Treatments were managed pine forests intercropped with switchgrass (PxS), and managed pine forests that are not intercropped with switchgrass (P). Data were collected in Kemper Co., MS, in July and August 2012.

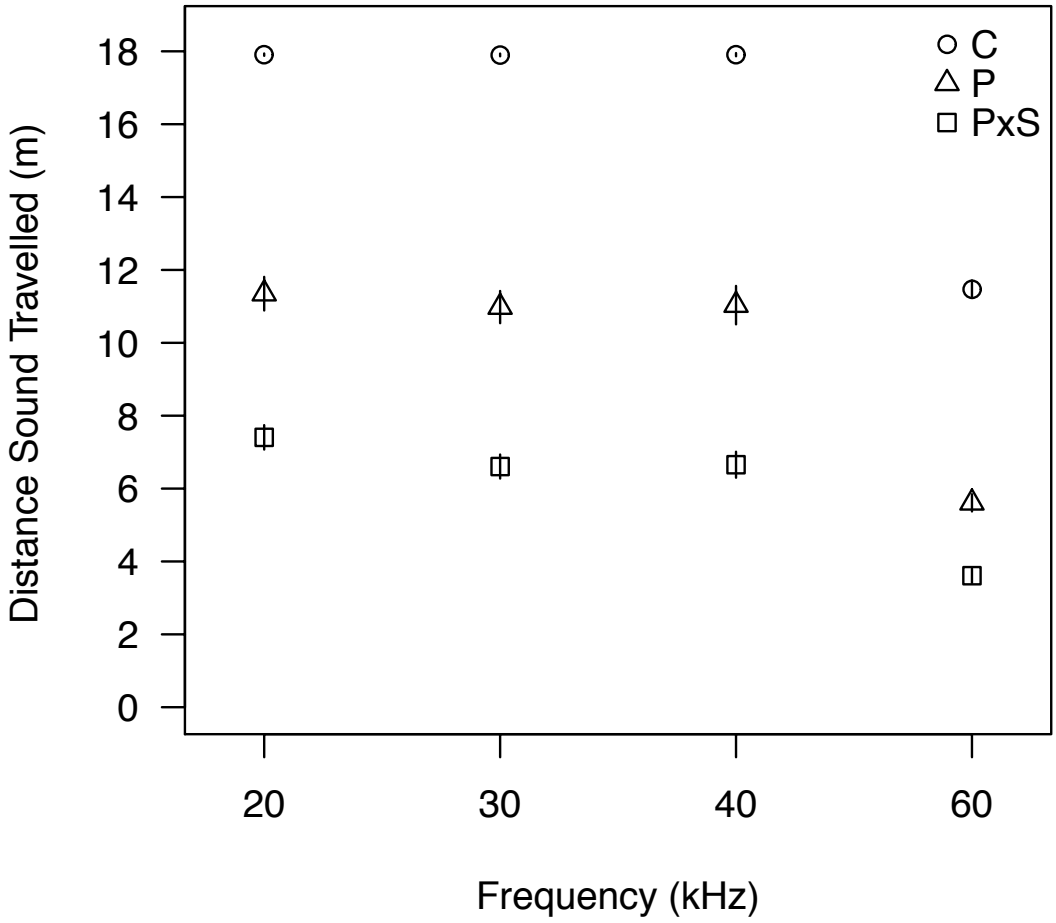


Figure 9. Mean distance sound travelled (m) ± 1 SE per treatment and frequency. Tukey HSD post-hoc tests were significantly different for all comparisons. Treatments were managed pine forests intercropped with switchgrass (PxS), managed pine forests that are not intercropped with switchgrass (P), and a gravel road no vegetation control (C). Data were collected in Kemper Co., MS, from June to August 2012.

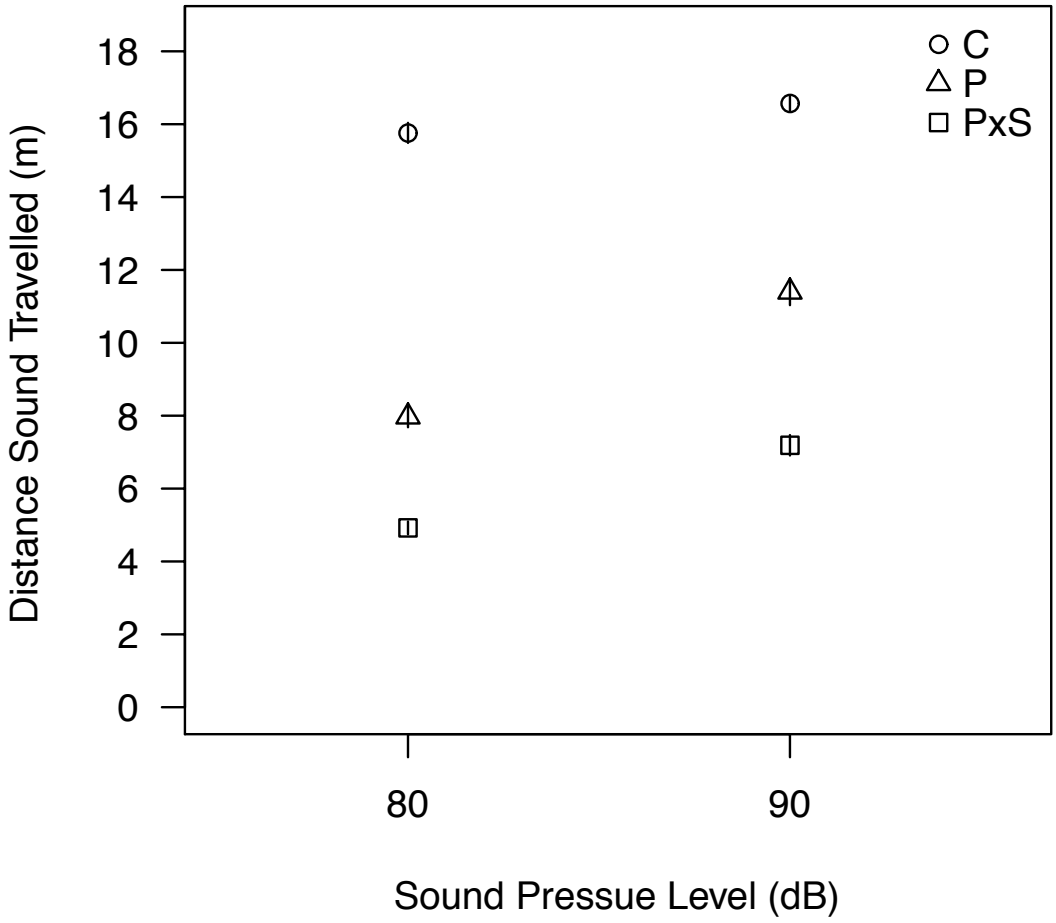


Figure 10. Mean distance sound travelled (m) ± 1 SE per treatment and sound pressure level. Tukey HSD post-hoc tests were significantly different for all comparisons. Treatments were managed pine forests intercropped with switchgrass (PxS), managed pine forests that are not intercropped with switchgrass (P), and a gravel road no vegetation control (C). Data were collected in Kemper Co., MS, from June to August 2012.

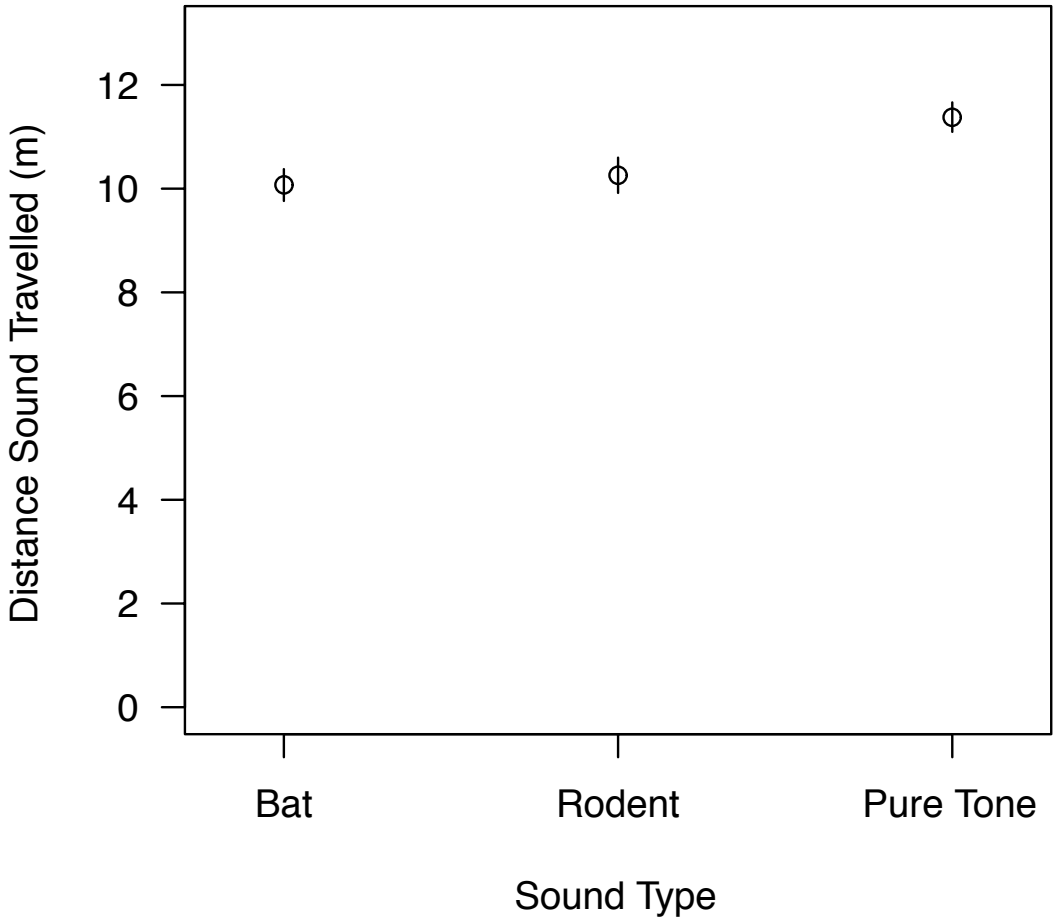


Figure 11. Mean distance sound travelled (m) ± 1 SE per sound type. Tukey HSD post-hoc tests were significantly different for all comparisons. Data were collected in Kemper Co., MS, from June to August 2012.

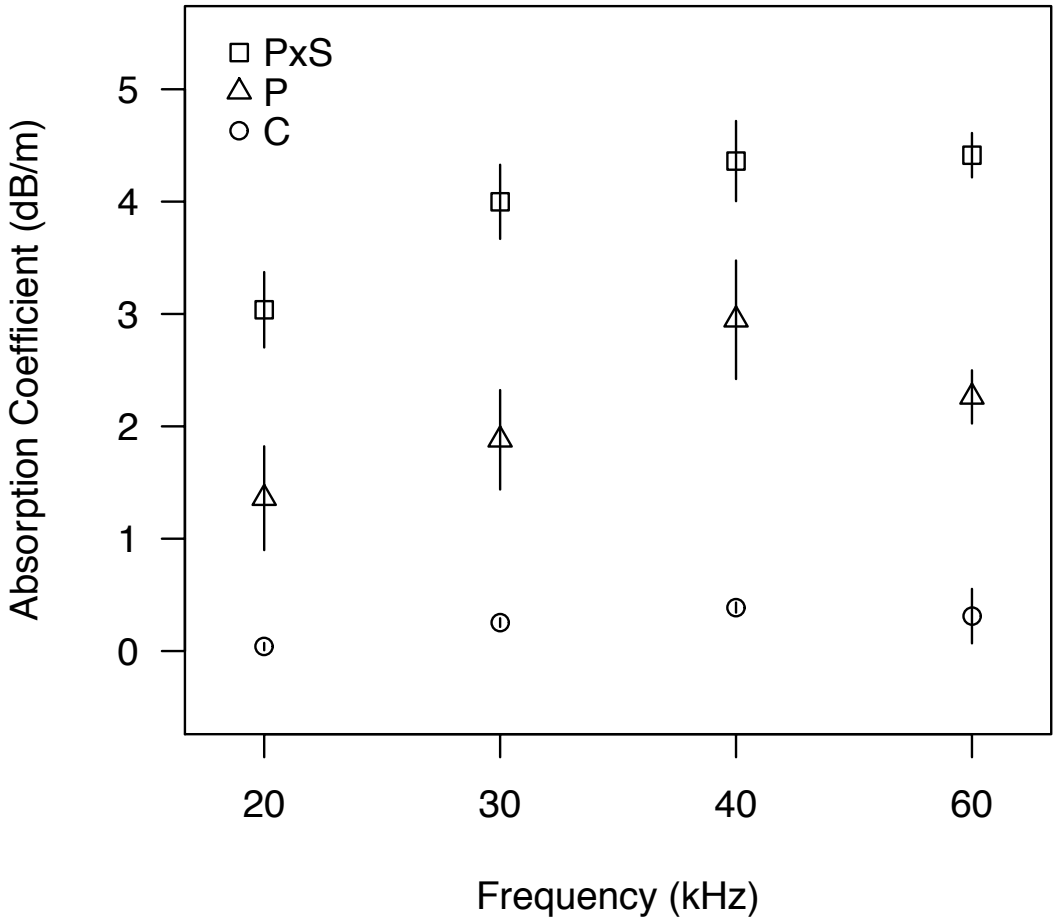


Figure 12. Mean absorption coefficient (dB/m) ± 1 SE per treatment and frequency. Treatments were managed pine forests intercropped with switchgrass (PxS), managed pine forests that are not intercropped with switchgrass (P), and a gravel road no vegetation control (C). Data were collected in Kemper Co., MS, from June to August 2012.

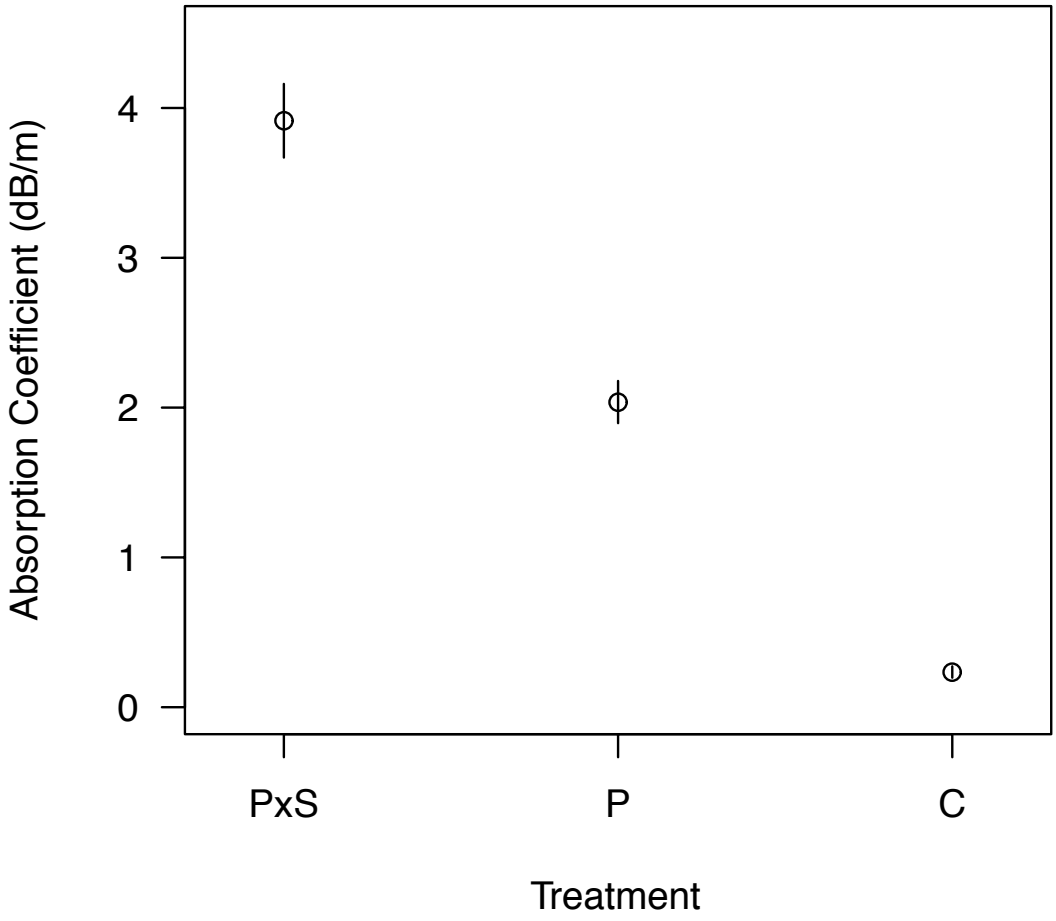


Figure 13. Mean absorption coefficient (dB/m) ± 1 SE per treatment. Tukey HSD post-hoc tests were significantly different for all comparisons. Treatments were managed pine forests intercropped with switchgrass (PxS), managed pine forests that are not intercropped with switchgrass (P), and a gravel road no vegetation control (C). Data were collected in Kemper Co., MS, from June to August 2012.

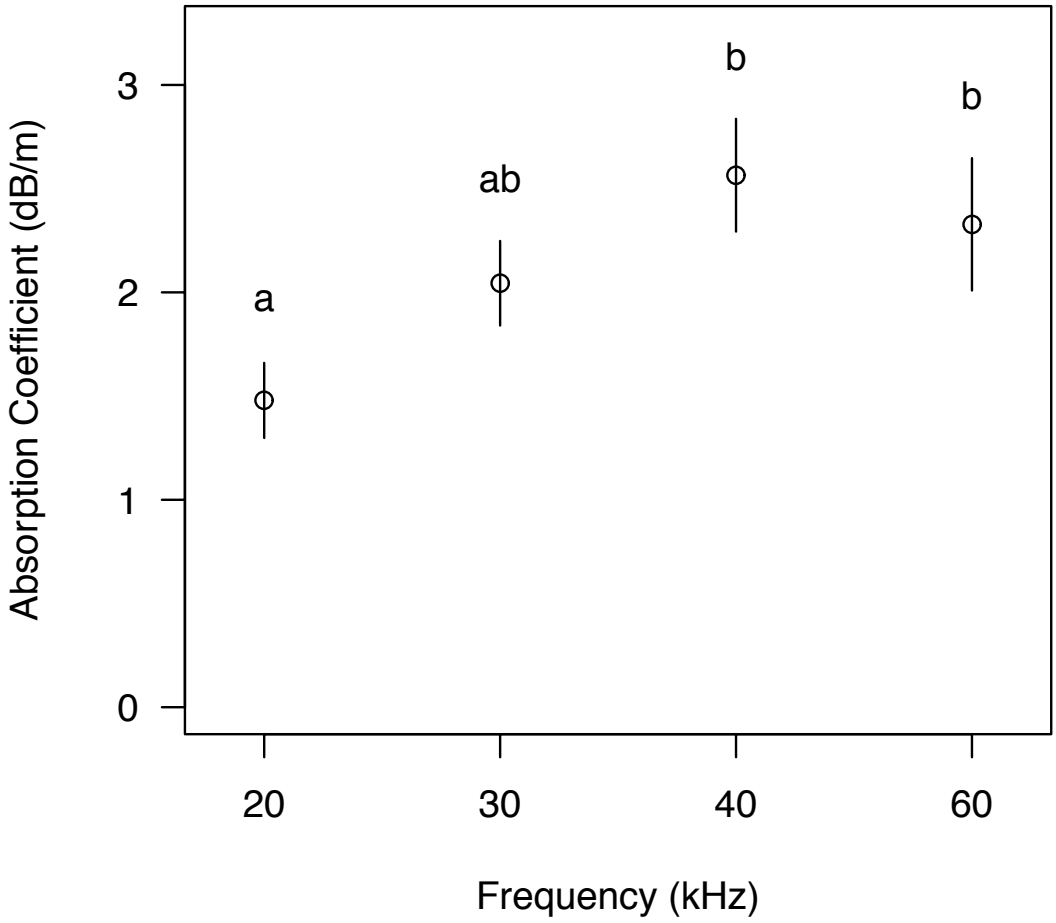


Figure 14. Mean absorption coefficient (dB/m) ± 1 SE per frequency. Letters within the figure represent Tukey HSD post-hoc test results, with 20 kHz sound having a smaller absorption coefficient than 40 and 60 kHz sound. Treatments were managed pine forests intercropped with switchgrass (PxS), managed pine forests that are not intercropped with switchgrass (P), and a gravel road no vegetation control (C). Data were collected in Kemper Co., MS, from June to August 2012.