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Profiling Bat Activity and Species Presence in Managed Longleaf Pine Landscapes

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ABSTRACT

Restoration of native flora or reintroduction of at-risk fauna includes management practices that while encouraging presence and proliferation of target species, may adversely affect non-focal species. An endemic ecosystem undergoing restoration within the southeastern U.S. is that of the longleaf pine (*Pinus palustris*). Bats inhabit key ecological niches in forest ecosystems, including the longleaf pine ecosystem, and can be indicators of ecosystem condition. This study investigated the effects of current forest management practices and landscape management history on bat species presence and activity levels within habitat undergoing longleaf pine restoration. We deployed bat detectors in two wildlife management areas within the Raccoon Creek Watershed of northwest Georgia, USA. These areas differed in landscape management history and intensity of longleaf pine restoration practices. Results indicated a significant difference in species activity between landscape management histories but no significant differences were detected in activity or species presence with respect to contemporary restoration practices. The species most active on the landscape were the big brown bat (*Eptesicus fuscus*) and eastern red bat (*Lasiurus borealis*). The data collected in this study will serve as a baseline for bat activity in the region and for evaluating the impacts of the restoration methods on the local bat community.

KEYWORDS: Longleaf pine, prescribed burning, bat activity, landscape restoration ecology, ecosystem health/condition

INTRODUCTION

Anthropogenic activity modifies landscapes and habitats and may be detrimental to native species. Disturbances originating from human activity influence resident wildlife in many ways. The construction of transit systems can change the movement and migration patterns, urbanization can alter mating or foraging behaviors by changing availability of resources, and global travel and commerce can introduce invasive organisms to ecosystems that affect susceptible native species. The construction of transit systems can change movement and migration patterns, such as in Wyoming, where the intersection of roadways with the migration routes of mule deer have changed migration patterns (Sawyer et al. 2012). Urbanization, or the onset of infrastructure on a landscape that often causes fragmentation of habitats, can alter mating or foraging behaviors by changing availability of resources. For example, oil and gas infrastructure have displaced grouse populations from suitable habitat and decreased survival rates in both Eurasia and North America (Hovick et al. 2014). Wildlife population densities have declined with proximity to human infrastructure as well (Benitez-Lopez et al. 2010). Global travel or commerce often introduces invasive organisms to habitats and thus impact susceptible native species. There is a recent worldwide trend of fungal epidemics caused by invasive organisms, such as chytridiomycosis in amphibians and white-nose syndrome in bats – these opportunistic pathogens have decimated populations of susceptible species, changing ecosystem dynamics (Foley et al. 2011). These anthropogenic disturbances to ecosystems, landscape, and habitats all originate from land-use or land-cover changes.

Land-use and land-cover change implemented by human activity, like infrastructure construction or even agriculture, affect habitat availability and have been modeled as leading factors in biodiversity change (Sala et al. 2000). Biodiversity is important to ecosystem function, and loss of biodiversity can reduce the efficiency with which ecosystems can capture and recycle essential biological resources and nutrients, which are services considered beneficial to humanity (Cardinale et al. 2012). In recent decades, the effects habitat modification at the landscape scale can have on biodiversity, and in turn on ecosystem function and services, has been recognized (Cardinale et al. 2012). Widespread initiatives in environmental conservation and habitat restoration have been implemented to mitigate negative effects of anthropogenic alteration to landscape or habitat. Restoration methods, though, can involve a degree of anthropogenic alteration to landscapes that now have established habitat or resident wildlife differing from the target habitat. These methods may include practices that can remove or drastically alter habitat, such as prescribed burning. Whether such anthropogenic alterations, although conducted as a form of restoration, may be adversely affecting non-focal species or ecosystems is a question that persists when these methods are put into practice. Identifying population characteristics – such as species presence, diversity, or activity levels – for non-focal species is crucial to understanding a more general wildlife response to changing landscapes.

One habitat within the southeastern United States undergoing restoration that could potentially impact non-focal, resident wildlife is the longleaf pine habitat. Longleaf pine woodlands are among the most biodiverse communities in temperate North America, and provide habitat for many endemic biota and specialist species (Mitchell et al. 2006). Longleaf pines are fire-dependent for proliferation, and thus have seen significant population decline since the introduction of anthropogenic fire suppression during the colonial settlement period (Parks 2013). As a result of this and anthropogenic land use practices such as logging and agriculture, current longleaf pine ecosystem coverage is only 3-5% of what it was before colonial settlement; longleaf-pine dominated landscapes have given way to less biodiverse, loblolly-pine dominated landscapes because of the absence of fire regimes (Mitchell et al. 2006, Mitchell & Duncan 2009). In an effort to preserve the biodiversity associated with longleaf pine habitat, regional wildlife management agencies are now focused on restoring this habitat by reintroducing fire regimes and long leaf pine through prescribed burning and forest thinning.

There are now several longleaf pine restoration efforts taking place in state- and federally-managed land throughout the southeast. Management studies have revealed the most effective restoration methods include a combination of periodic prescribed burns, overstory thinning, and herbicide control (Parks 2013). These methods are applied across the landscape on a periodic basis in order to ensure successful restoration. Since longleaf pine habitats are expected to encourage biodiversity within a landscape, measurements of overall biodiversity in restored stands – for instance, the annual cataloging of wildlife species presence – is an accepted index of successful restoration (Parks 2013, Mitchell & Duncan 2009, Mitchell et al. 2015). Cataloging the presence, richness, or activity patterns of endemic or sensitive species specifically may provide insight as to whether the applied restoration methods are effective at the cost of detrimental impacts to activity of other, non-focal wildlife. While collecting presence or activity data for all species within the longleaf pine landscape would be a thorough assessment of restoration impacts, this may be a challenge considering the resources necessary for continuous data collection. Instead, collecting data on representative organisms may provide a robust model for wildlife reactions to these anthropogenic management activities.

Bats are long-lived, low-fecundity organisms that provide important pollination services and insectivorous control to ecosystems, and are sensitive to environmental stressors (Jones et al. 2009, Foley et al. 2011). Bats also often occupy high trophic levels and have a wide distribution; if they react poorly to anthropogenic landscape changes or disturbances, it is likely that other wildlife will as well (Park 2015, Jones et al. 2009). Bats also indirectly affect other organisms in the same habitat through their ecological roles; due to these factors bats are thought to serve as good models for monitoring overall ecosystem health (Loeb et al. 2015, Webala et al. 2011). Assessing the effects longleaf pine restoration methods have on bats by profiling bat species presence and activity levels may provide an informed perspective on how these methods may affect other non-focal wildlife. Observing bat species response to such anthropogenic alterations to the landscape may also introduce a sustainable strategy for selecting effective restoration practices that will not adversely impact non-focal wildlife.

BACKGROUND INFORMATION AND LITERATURE REVIEW

The Longleaf Pine Habitat.— The biodiversity and endemicity encouraged by longleaf pine (*Pinus palustris*) is due to the characteristic habitat longleaf pine stands form on the landscape. Longleaf pines form distinctive, open-canopy habitats dominated by a low density of the pines with little to no midstory and a diverse herbaceous or grass understory growth that provides habitat to diverse species of insects, reptiles, amphibians, and small mammals. Several specialist species, such as the gopher tortoise and red-cockaded woodpecker, depend on the longleaf pine or the habitat it forms to persist on the landscape (Outcalt 2000, Van Lear et al. 2005). The habitat also provides refuge for more generalist species, some of which use the resources provided by the more specialist species. For example, the red-cockaded woodpecker excavates cavity roosts in mature longleaf pines that are used secondarily by several species, such as nuthatches or screech owls (Earley 2004). The gopher tortoise is also known for boosting the diversity of species found in longleaf pine habitats due to the burrows the tortoise will build – these are in turn used by hundreds of other species for shelter (Earley 2004).

There are five main types of longleaf pine habitat across the southeastern United States: the montane, the sandhill, the rolling hills, the flatwoods, and the savannah habitat (Outcalt 2000). These habitats are classified based on distinct landscape characteristics – for instance, the savannah habitat is known for its open-canopy grasslands and the flatwoods are known for proximity to wetland depressions and shrub bogs, while the sandhills are known for the dunes on which the pines and vegetation grow (Outcalt 2000, Earley 2004). As a testament to how distinct these habitat types can be, there are several sub-classifications used as well (Earley 2004). Habitats frequently seen in coastal regions are the sandhill and savannah, with the rolling hill habitats occurring further inland throughout the Gulf Coastal Plain (Earley 2004). The montane habitat, occurring throughout the low-laying mountains of northwest Georgia and northeast Alabama, is less pervasive and characterized by ridge-top pure or mixed stands with diverse herbaceous understories of which composition is dependent on the region (Maceina et al. 2000, Cipollini et al. 2012). Historically, the majority of longleaf pine habitat was either savannah, rolling hill, or sandhill types found within the coastal regions of the Carolinas, Georgia, and Florida; longleaf pine was able to dominate the sandy or clay-like soils of these regions, where other pine species could not persist (Outcalt 2000, Earley 2004). Today, there are only a few substantial populations of longleaf stands left of the savannah and sandhill habitat variety, with a smattering of other habitat types across the southeastern U.S. – but these are few and far in between (Earley 2004).

What gave the longleaf pine its historic ubiquity in the southeastern U.S. was the pine's adaptation to the wildfires that frequently ravaged the landscape pre-European settlement (Outcalt 2000, Earley 2004). When a frequent fire regime is in place, the longleaf pine can survive and persist on the landscape, along with several herbaceous species that take residence under its open canopy, while competitor species cannot (Outcalt 2000). With the arrival of European settlers and a colonial America, though, longleaf pine habitats began to disappear (Outcalt 2000, Earley 2004, Van Lear et al. 2005). Longleaf pine was harvested for timber or other forest products post-colonial settlement and into the twentieth century (Outcalt 2000, Parks 2013). Pre-settlement, natural wildfires burned every 2 to 8 years throughout the longleaf range – but with the arrival of the colonial timber industry, these wildfires were anthropogenically suppressed (Outcalt 2000, Van Lear et al. 2005). Thus, more competitive and fire-independent pine species such as the loblolly and shortleaf pine, as well as other hardwood species, replaced the longleaf pine once it was harvested (Outcalt 2000, Parks 2013). When the once open-canopy of the longleaf forests disappeared due to the absence of fire regimes and growth of these competitors, diverse herbaceous understories unique to the longleaf system also disappeared (Mitchell & Duncan 2009, Cipollini 2012). With canopy closure and the resultant decrease in understory diversity and cover, plant and animal biodiversity found within these regions often decreased as well (Brunjes et al. 2003, Parks 2013).

Longleaf pine restoration has become a priority for many wildlife management agencies, and several studies have explored silviculture practices that regenerate longleaf pine habitats of varying maturity. Typically, a combination of low-density planting, prescribed burning, overstory thinning, and selective herbicide application are used in rotations to establish and maintain longleaf pine stands (Kush et al. 2004, Mitchell et al. 2006, Mitchell et al. 2015, Parks 2013). Longleaf pine restoration using these methods does appear to increase immediate flora and fauna biodiversity, but various combinations of these methods have displayed differences in persistence of that biodiversity (Parks 2013, Mitchell et al. 2006). For example, in restored longleaf stands treated only with prescribed burns and thinning, gains in herbaceous diversity and abundance diminished over time; but in restored longleaf stands treated with prescribed burns, thinning, and herbicides, herbaceous diversity and abundance persisted (Brunjes et al. 2003, Parks 2013). Each restoration method controls for specific aspects of the intended habitat: the prescribed burns encourage germination of longleaf pine and control the growth of fire-independent woody vegetation; the overstory thinning reduces pine and other hardwood density to open canopy cover; and herbicides control for other woody vegetation such as vines or shrubs (Parks 2013). By varying the application of these methods, characteristics of restored habitat such as understory vegetation or canopy cover also display spatial and temporal variation. Managed pine forests generally provide heterogeneity of successional habitats that result in observed increasing biodiversity and a shift in species composition to open-pine adapted species (Greene et al. 2016). In landscapes undergoing longleaf pine restoration, the addition of varying transitional habitat – from dense, closed canopy conditions to open canopy conditions – through use of varying restoration methods may further these observed results as well as reintroduce longleaf specialist species (Brunjes et al. 2003; Greene et al. 2016).

Restoration of a dynamic system such as longleaf pine habitat therefore necessitates dynamic restoration and landscape management tactics. Successful restoration of longleaf pine habitat involves a dynamic approach of varying the methods used between different sites, or even at the same site at different times, in order to adapt to the system's needs and achieve the desired persistent diversity. Restoration prescriptions are often site-specific; variables such as previous land-use or climate affect initial landscape conditions and thus affect restoration results (Hu et al. 2016). A milestone of longleaf pine restoration is the presence of herbaceous understory – but the vegetation composition may vary by site depending on factors such as soil moisture or texture, which can in turn vary restoration outcomes for sites within the same region

(Hu et al. 2016). Site variation is not the only aspect that can cause differentiation in restoration results. Variation in restoration methods, or treatment, may also vary restoration outcome. A meta-analysis study of biodiversity response to managed pine forests in the southeastern U.S. revealed that while total biodiversity declined with increasing intensity of management treatments, the timing and type of treatments elicited differing responses from varying taxa. For example, while mid-rotation prescribed fire and/or herbicide treatments elicited positive or neutral diversity and abundance responses from plants, birds, and other focal species, there were negative responses from non-focal invertebrate, amphibian, and reptile species (Greene et al. 2016). The meta-analysis concluded that less intensive stand establishment practices had short-term benefits to many species, but that mid-rotation application of fire, herbicide, and/or thinning practices resulted in species-specific responses – and because the literature is over-saturated with bird and plant response studies, more data on other taxa such as small mammals, herpetofauna, and invertebrates is needed (Greene et al. 2016). Establishment of a more general restoration model for longleaf pine will require a comprehensive understanding of the variation present within all these system responses (Hu et al. 2016).

Amidst the larger picture of longleaf pine restoration in the southeastern U.S., there have been few studies to address restoration in specific habitat other than sandhill or savannah. Within the state of Georgia all four habitat types occur, making it a key state for longleaf pine restoration and study. Montane habitat is prevalent in the northwestern region of the state and is undergoing directed restoration management, but there is very little published literature on restoration of montane habitat. (Cipollini et al. 2012). The majority of information on longleaf pine forests is from coastal plain systems, both sandhill and savannah habitats, given the wider distribution of these habitat types (Cipollini et al. 2012). Most studies, even those based in montane habitat, also only revolve around vegetation structure, avian species assemblage, or the more publicized endangered species in these habitats – more research is needed in regards to the management response of other, non-focal species in longleaf pine systems (Cipollini et al. 2012, Maceina et al. 2000, Van Lear et al. 2005). Understanding the effects longleaf pine restoration have on an array of taxa and non-specialist wildlife is essential to establishing successful restoration techniques that do not restore habitat at the expense of non-focal species. Studying a non-focal organism with wide dispersion throughout the habitat, that may respond to a variety of restoration methods, and that could reflect the responses of other organisms within the system, is a necessary starting point. Bats, as an organism with a wide dispersion on the landscape, the potential for graded responses to habitat alteration or degradation, and a sensitivity to environmental stressors, are an appropriate small mammal model that may be used for such research (Jones et al. 2009, Park 2014).

Bats of the Southeastern U.S.— Bats form a unique taxon (Order: Chiroptera) as the only true flying mammal, and represent 20% of all classified mammal species worldwide (Altringham 2011). There are 45 species of bats (Suborder: Microchiroptera) resident to the continental United States (Altringham 2011, Miller et al. 2003, Foley et al. 2011). In the southeastern U.S., approximately 16 of those species can be found throughout the southeastern states and within the historic range of longleaf pine. These are all insectivorous, echolocating species that have similar dispersion, roosting, and foraging behaviors. The species are also long-lived, with some individuals documented as living up to 20 years, and only have one to two pups per year (Trani et al. 2007). Any impacts to species populations in the region will persist, making those species sensitive to environmental stressors (Jones et al. 2009, Park 2014). To be useful in indicating the effects longleaf pine restoration may have on non-focal species, a model organism or species must be present throughout the habitat and have the potential to respond to the various restoration methods used. As an organism within the longleaf pine system, bats display a wide dispersion across the habitat, would be sensitive to changes within the ecosystem, and exhibit a range of behaviors dependent on landscape structure. When observed at a species level, there are subtle differences in roosting and foraging behavior characteristics. Thus, a shift in species presence or activity composition may indicate a response to specific restoration practices that could affect other wildlife with similar niches or analogous ecological functions.

For example, while the species found throughout the longleaf pine's historic range use echolocation to navigate the environment and hunt invertebrate prey at night, there is a general divide between species in roosting and foraging behaviors. Forest- or tree-roosting species include the eastern red bat (*Lasiurus borealis*) and the evening bat (*Nycticeius humeralis*); these species will more often roost, and likely also hibernate, throughout the forest landscape in tree branches and cavities, under tree bark, or even under leaf litter (Trani et al. 2007, Fabianek et al. 2015). In the southeast, the Brazilian free-tailed bat (*Tadarida brasiliensis*) is a migratory species known for almost exclusively roosting in tree cavities (Trani et al. 2007). Then there are cave-dwelling species, or species that usually hibernate in caves, mines, or rock crevices, that typically include Myotis species, such as the little brown bat (*Myotis lucifugus*), and the tricolored bat (*Perimyotis subflavus*). There are also more generalist species, such as the big brown bat (*Eptesicus fuscus*) or the silver-haired bat (*Lasionycterius noctivigans*), that have been found roosting throughout the forest and hibernating in caves, but are also more commonly found in artificial roosts (e.g. buildings, bridges, tunnels, mines) than other species (Trani et al. 2007, Keeley & Tuttle 1999). Knowledge gaps on species-specific roosting behaviors, such as roost fidelity and variability in diurnal roost preferences, still exist for many of these species

(Miller et al. 2003, Foley et al. 2011). However, it is generally known that while these species may use the habitat differently, they value habitat resources such as snags (i.e. standing dead trees) or commutability to water sources (Fabianek et al. 2015).

Availability of water sources plays a part in foraging activity differences between species (Fabianek et al. 2015). Species display variation in habitat used for foraging, likely a function of body size and characteristics such as wing loading and aspect ratios (Trani et al. 2007, Fabianek et al. 2015). Larger species like the hoary bat (*Lasiurus cinereus*) are known to commute larger distances and forage in open environments such as fields or above the canopy, and so are not necessarily tied to water source accessibility for foraging habitat or roost selection (Trani et al. 2007). Other species generally select roosts or forage closer to pond, riparian, or standing-water habitats where prey and water availability is greater, and display different foraging behaviors (Trani et al. 2007, Fabienek et al. 2015). Species of medium sizes, such as the big brown bat or silver-haired bat, will forage on forest edges or closer to the canopy than larger species; smaller species, such as the eastern red bat or the Myotis species, often forage in more cluttered environments or within the forest canopy because they are more maneuverable (Trani et al. 2007, Armitage & Ober 2012). Clutter is the density of obstacles in a flyway or foraging area, and so less maneuverable species will avoid cluttered environments such as forest mid- or understory (Loeb et al. 2015).

These differences in roosting and foraging behaviors by species introduce two advantages to using bats as a model for how longleaf pine restoration may affect resident, non-focal wildlife. First, the differences result in the wide dispersion of bats throughout the longleaf pine habitat: there are bats roosting and foraging throughout the forest. Second, the differences provide a way to catalogue tiered responses to the landscape alteration involved in longleaf pine restoration.

Differing restoration methods will vary the change in habitat characteristics that these bat species value. Prescribed burning increases snag incidence and woody debris that may be used for roosting, but can reduce prey abundance and diversity or eliminate leaf litter and other understory used for cover. Bats that hibernate in leaf litter or trees have been observed vacating the habitat during winter prescribed burning; it is unknown whether these bats return to those roosts (Trani et al. 2007). Bats in the region have also been documented to have species-dictated dietary preferences in flying, nocturnal invertebrates: some species prefer soft-bodied prey, while others will not discriminate (Clare et al. 2011, Mossman et al. 2012). Altering habitat characteristics such as roost and prey availability may therefore alter the species composition on the landscape. Overstory thinning is a restoration practice that reduces forest clutter, opening the canopy or introducing forest edge and thus allowing less maneuverable species to forage where they previously would not (Armitage & Ober 2012). Again, such habitat alteration could change accessibility to the landscape and thus the species composition of activity on the landscape.

Undertaking the identification of bat activity, and to the species-level, on the landscape may seem unsustainable, even if appropriate, for modelling wildlife species response to longleaf pine restoration. However, the third advantage to using bats as a model involves the research method by which bat activity can be observed. Bioacoustics is a relatively new, when compared to more traditional ecological methods such as mark-recapture, but effective research method that has been refined for bats via passive acoustic monitoring of echolocation calls (Britzke et al. 2013). The majority of bat ecology research within North America now focuses on the study of bats with acoustic surveys due to the non-invasiveness and cost-effectiveness of the method; bat echolocation calls have become an accepted index of bat activity and species presence on the landscape (Loeb et al. 2015).

Acoustic Surveying of Bats.— Acoustic surveying is a passive monitoring technology used to catalogue bat activity and species presence or abundance. Echolocation calls are activity- and species-specific, providing a method to identify species presence and activity, estimate abundance or population sizes, and assess habitat use (Britzke et al. 2011, Russo & Voigt 2015). Bat calls are emitted at ultrasonic frequencies; an echolocation call is made up of ultrasonic "pulses" that can be at a constant frequency (CF) or frequency-modulated (FM), a changing frequency over time (Altringham 2011). The bat species that can be found in the historic range of longleaf pine use a composite of CF and FM pulses for their echolocation calls (Altringham 2011, Loeb et al. 2015). There are several types of echolocation calls: search phase calls are used to navigate environments; feed buzzes are used when capturing prey; and social calls are used for communication between individuals (Altringham 2011, Britzke & Murray 2013). Search-phase calls are species-specific and have consistent structure across a call sequence, and thus are used for species identification; feed buzzes and social calls, on the other hand, typically display more variation based on the individual bat, have not been as extensively studied, and thus are not used for species identification (Altringham 2011, Britzke & Murray 2013).

Acoustic monitoring generates data that is an index for bat activity and is a favorable method for researchers of bat ecology, due to its cost-effectiveness and passive approach that yields high amounts of data (Stahlschimdt & Bruhl 2012, Russo & Voigt 2015). Bioacoustic recorders called bat detectors are used to record the echolocation calls bats emit, and then digitally transcribe the ultrasonic data into sonograms. The patterns displayed on these sonograms that correspond to bat calls are then assigned to specific species, depending on species-specific variables such as pulse interspatial length and mean frequency of the call. There are libraries of species-specific calls, which researchers use to manually classify acoustic data based on referenced temporal and spectral variables (Russo & Voigt 2015). Biases regarding the high variability of echolocation, however, exist not only between species but between individuals of the same species as well; echolocation is a movement-functional vocalization, and therefore may change depending on habitat or activity (Britzke et al. 2011, Russo & Voigt 2015). The aforementioned libraries, which are continually expanded based on new and reviewed research, are one method to address these biases – the libraries provide an array of search phase calls by species from a variety of individuals in a variety of circumstances (Britzke et al. 2011).

Another, more recent method is the integration of artificial neural networks with bioacoustics in the form of automated-identification software programs, which learn from these libraries and ongoing research (Britzke et al. 2011, Loeb et al. 2015). While some researchers warn against the exclusive use of automated-ID software, the argument remains that as computer science technology such as artificial neural networks become more integrated into bioacoustics research it will improve – and so its use should not be precluded, but executed conservatively (Russo & Voigt 2015, Britzke et al. 2011, Loeb et al. 2015). This perspective of conservative use of automated-ID software has been adopted by most of the bat research community, and is currently reflected in the methods of acoustic monitoring studies concerning bat activity levels and species presence in managed forest landscape.

Acoustically Monitoring Bat Populations in Longleaf Pine Habitats.— Studies concerning bat activity level differences between logged, agriculture, and forested landscapes have been performed, but are scattered across bat species, countries, and decades. There have been several studies focused specifically on the effects of timber harvest or logging on bat communities, but relatively few have addressed bat species response to landscape management practices involving prescribed fire (Armitage & Ober 2012). Studies on bat species in managed pine habitats in the southeastern United States have mainly focused on roost selection, rather than foraging, commuting, or other activity, and only for a specific species (Miles et al. 2006, Hein et al. 2009, Armitage & Ober 2012). None to date have addressed bat activity levels or species presence as a function of restoration methods in montane longleaf pine habitat. Management practices such as prescribed fire, thinning, or herbicide application alter vegetation structure and therefore alter habitat aspects like invertebrate community dynamics and canopy structure. This directly affects habitat suitability for bat species; variation in insect biomass or forest clutter affects prey abundance and forest maneuverability for bat species differently, and so may cause shifts in species presence or activity (Loeb & Waldrop 2008, Armitage & Ober 2012). In longleaf pine landscapes undergoing restoration, these aspects can differ by treatment type and timing. Documenting bat species presence and activity levels provides information on which habitats correlate to more diverse presence and higher activity, indicating how successful treatment methods may be for increasing or maintaining diversity.

Of the studies that have used acoustic monitoring to document bat species presence and activity levels on managed landscape, most are focused on the effects of agriculture, logging, timber harvest, or hardwood forest restoration (Loeb & Waldrop 2008, Cox et al. 2015, Silvis et al. 2015). There have been only a handful of studies involving prescribed fire use and bat activity in either managed hardwood or pine forests in the southeastern U.S. (Loeb & Waldrop 2008, Silvis et al. 2015, Cox et al. 2016). Currently, there is only one published study involving longleaf pine restoration, which was conducted in the sandhill habitat of Florida (Armitage & Ober 2012). These studies, regardless of habitat, collected data on vegetation structure, prey availability or abundance, and bat activity via acoustic surveys within managed forest landscape undergoing either prescribed burning, overstory thinning, or a combination of management methods. Results did suggest a positive correlation between most bat species activity and management that removed clutter from the environment; the presence of clutter, as opposed to other characteristics such as roost or prey availability, appears to significantly impact bat activity (Loeb & Waldrop 2008, Armitage & Ober 2012, Silvis et al. 2015, Cox et al. 2016). In the longleaf pine restoration study, the researchers concluded that the frequency of fire involved in the restoration indirectly determined important structural characteristics of the habitat and thus influenced species habitat preference of bats foraging in the forest (Armitage & Ober 2012). Larger species limited foraging activity to frequent-fire, open-canopy or above canopy sites, while smaller, more maneuverable species displayed no difference in foraging activity (Armitage & Ober 2012). None of the studies commented on whether bat species response to the management practices might reflect other wildlife species responses. However, a review article did include the longleaf sandhill study in an evaluation of how longleaf pine restoration affects vertebrates; this article found that moderate fire regimes (>3-5 year frequency) increased species abundance, and also commented on the lack of small mammal data (Darracq et al. 2016).

Within the state of Georgia, all four longleaf pine habitats persist and are being restored on the landscape; the bat species that can be found within the historic range of longleaf pine are the same species that have been documented in Georgia. A study examining the effects longleaf pine restoration has on bat activity executed in Georgia is an ideal starting point for further statewide or regional studies on the effects longleaf pine restoration has on bats or other non-focal wildlife species. With an established white-nose syndrome (WNS) presence in Georgia, there has also been a call from government agencies such as the U.S. Fish & Wildlife Service and the Georgia Department of Natural Resources for more surveys to determine bat activity, species presence, and population movement within the state (K. Morris & P. Pattavina, Georgia Department of Natural Resources & U.S. Fish and Wildlife, personal communication).

The Georgia Department of Natural Resources is currently working on an expansive longleaf pine restoration project in the northwestern region of Georgia (B. Womack, Georgia Department of Natural Resources, personal communication). This region is dominated by natural timber, or timber not planted for harvest or other anthropogenic use, with extensive mixed hardwood and pine forests; most notably, there are remnant patches of montane longleaf pine habitat approximately an hour northwest of metro-Atlanta. By restoring this remnant montane longleaf pine habitat, wildlife management agencies hope to reintroduce and maintain the biodiversity historically associated with longleaf pine landscapes (B. Womack, personal communication). Documenting and characterizing bat activity in this region may introduce a method by which to evaluate the effects anthropogenic alteration to the landscape, in the form of longleaf pine restoration, may have on non-focal wildlife species. In addition, bat activity and population profiles alone are of interest to the research community and wildlife management agencies in Georgia, due limited regional baseline data on bat activity and the white-nose syndrome (WNS) epidemic.

RESEARCH OBJECTIVES

Successful conservation of longleaf pine habitat involves not only the restoration of longleaf pine on the landscape but also restoration of the associated biota and an increase, or at least no decrease, in biodiversity. The restoration of longleaf pine to the landscape requires intensive, cyclic prescribed burning that while restoring the habitat may be adversely affecting non-focal wildlife species and thus established, resident diversity of the landscape. To answer the question of whether longleaf pine restoration methods significantly affect bat activity levels and species presence, and thus may be affecting other non-focal wildlife, the following study measured bat activity levels as a function of restoration methods within a managed longleaf pine montane habitat. The study also provided a basic profile of species presence and species composition of activity in southeastern longleaf pine habitats undergoing restoration. Further goals of this study included gathering baseline data for bat populations in the region and establishing a working collaboration with the Georgia Department of Natural Resources (GA DNR) and the U.S. Fish & Wildlife Service (USFWS).

Species that have been detected in the region before include the tricolored bat (*Perimyotis subflavus*), the eastern red bat (*Lasiurus borealis*), the big brown bat (*Eptesicus fuscus*), the evening bat (*Nycticeius humeralis*), and the seminole bat (*Lasiurus seminolus*) (K. Morris, personal communication). Detection of, or lack thereof, the federally-listed northern long-eared bat (*Myotis septentrionalis*) in the region as well as other at-risk species is desired and applicable information for government agencies, and will inform future bat ecology studies in the area. Several more common species are also of interest to both researchers and wildlife management agencies, with the white-nose syndrome (WNS) epidemic now reaching into north and west Georgia. The little brown bat (*Myotis lucifugus*) has suffered severe mortality rates in north

Georgia with the arrival of the epidemic, and detection rates of this species – which was a common species of Georgia – may reflect this decline. The results of this study may differ from past studies not only due to the novel location of the project, but also due to the post-WNS timing of the project. An additional advantage to acoustic survey studies is the availability of the raw acoustic data after the study is completed – if safely stored, the data can be revisited and reanalyzed for a more thorough comparison of post-WNS detection rates to further declining or future recovery rates. Such availability is beneficial not only for future projects, but also for collaborating agencies such as the GDNR and USFWS.

The research objectives of this study were as follows: 1) Remote monitoring of bat activity and species presence in landscape undergoing longleaf pine restoration in order to determine whether restoration practices may be adversely affecting non-focal species; 2) Assess forest structural and prey availability variation between landscape undergoing restoration and landscape not undergoing restoration to ensure these variables are not a main influence on response variable variation rather than restoration practices; and 3) Establish baseline data for continued monitoring of these variables, because longleaf pine restoration is a dynamic and continuing process that may influence responses in the future. Bat activity, species presence, and diversity have not been characterized within the study area, aside from a few mist-netting or acoustic surveys in the surrounding areas (K. Morris, personal communication). This research is the first to document potential variation in bat species presence or activity levels related to restored longleaf landscape in this region and the first widespread acoustic monitoring survey for the focal wildlife management areas. Discovering whether acoustic surveying can determine if restoration efforts at the study sites are non-disruptive to bat species is applicable to other regions of this specific habitat type as well.

There is evidence from a limited number of past studies that agricultural, logging, or prescribed-burn landscape alteration affects bat activity. Several studies have concluded that bat activity increases in forest landscapes where anthropogenic land use, management, and/or restoration practices result in reduced forest clutter and more open canopy forest structures (Webala et al. 2011, Armitage & Ober 2012, Silvis et al. 2015, Cox et al. 2016, Loeb et al. 2016). These studies agree on vegetation structure varying greatly between natural timber stands and those undergoing prescribed burn or thinning treatments, but are conflicting on prey abundance results. Some studies have found total insect biomass or abundance does not appear to be affected by anthropogenic habitat alteration such as logging or prescribed fire (Webala et al. 2011, Cox et al. 2016). Prescribed fire in longleaf pine sandhill habitat, on the other hand, does appear to significantly decrease insect biomass and abundance when fire periodicity was frequent (Armitage & Ober 2012). While bat activity levels appear to be positively correlated with open canopy and reduced forest clutter, species presence and composition vary based on treatments, habitat types, and overall geographical ranges. Larger, less maneuverable species were more often present in landscapes with more open canopies, while small-bodied, more maneuverable species either displayed no variation in presence between landscapes or were more often present in more closed canopy landscapes (Silvis et al. 2015, Loeb et al. 2016, Armitage & Ober 2012).

We hypothesized that restoration practices and landscape management history affect bat activity levels and species presence. We predicted activity levels and species presence or activity composition were positively correlated with landscapes undergoing longleaf pine restoration, and differing patterns would be observed for differing landscape management history. Treated landscapes were expected to have more open canopy structures with understory growth, similar to established longleaf pine forest, and thus would be expected to demonstrate the associated increased diversity – which should correlate to higher levels of bat activity and species presence. Relative activity levels and species presence were expected to differ based on temporal application of prescribed fire and thinning practices, or when the restoration treatment began, because canopy cover, forest clutter, and prey abundance should differ between treatment tracts at different points in their cycles. Occurrence of snags or other refuge habitats may decrease directly after application of fire or thinning practices unless management practices consciously plan for occurrence (Zarnoch et al. 2014). The control stands were expected to display lower levels of activity due to higher frequency of closed and mid-story canopy, which would result in the more cluttered environment than treated stands.

Other than acoustically monitoring the landscape, recording habitat resource differences between landscape undergoing restoration and landscape not undergoing restoration may indicate which habitats are preferable for bat activity or certain bat species. Differences in habitat resources dependent on vegetation structure or prey availability may correlate with bat species presence or activity measurements. Recording potential differences will therefore provide inference for factors that may influence bat species presence and activity. It would be expected that restored longleaf pine landscape would provide greater variation in roost and prey availability than other managed areas, though only prey availability and canopy cover were recorded in this study as indices for greater resource availability. Correlation between availability of these resources and bat activity may influence management practices; however, a correlation has not been found in past studies. A significant relationship may encourage a closer look at whether management practices are affecting bat activity by affecting resource distribution. No significant relationship in this study could suggest that there is no significant difference in available resources between landscapes, or that current management practices are undisruptive to bat activity.

STUDY AREA

The study region consisted of two wildlife management areas undergoing longleaf pine restoration in northwest Georgia. The wildlife management areas are located within the Raccoon Creek Watershed, a region of the endemically-biodiverse Etowah River Watershed, and are home to one of the largest remnant montane longleaf pine habitats in northwest Georgia (***Fig.1***). The Sheffield Wildlife Management Area, located in the northern portion of the watershed, consists of 4,800 acres of natural timber, mixed hardwood-pine forests on state-owned land; the Paulding Forest Wildlife Management Area, located more southerly, consists of 28,233 acres of planted timber, mixed hardwood-pine forests on a combination of state-owned, county-owned, and leased land (B. Womack, personal communication, 2016). The focal study area contained state-owned, intensively managed longleaf restoration landscapes that undergo rotational combinations of forest thinning and prescribed burns on a 3-year cycle, as well as other wildlife management landscape not currently undergoing longleaf pine restoration.

There were several landscape tracts differing in temporal and methodical application of longleaf pine restoration methods throughout the two wildlife management areas. Sheffield represented restoration from a more "naturalized" landscape, or less altered for anthropogenic use, while Paulding Forest represented restoration from landscape altered for anthropogenic use (timber harvest). The Sheffield WMA contains landscape with historic natural timber, and longleaf pine restoration methods include 3-year, cyclic prescribed burning. The Paulding Forest WMA contains landscape that has been recently used for logging and timber harvest, and longleaf pine restoration methods include periodic over story thinning along with 3-year, cyclic prescribed burning and low-density planting of longleaf pine. For both WMAs, prescribed burning efforts for longleaf pine restoration began the winter of 2012-2013 (B. Womack, personal communication, 2016). Some tracts that were burned in the winter of 2012-2013 were also burned again the winter of 2015-2016, in accordance with the 3-year burning cycle; other tracts have yet to complete the first 3-year cycle.

A total of six sampling sites, three treated sites and three control sites, were surveyed within each WMA (***Fig. 2***). There were twelve sites sampled overall during the study. “Treated” sampling sites were located on landscape undergoing longleaf pine restoration; “treatment” consisted first and foremost of prescribed burning, but could have also included overstory thinning and low-density longleaf planting dependent on WMA location. Within each WMA, areas defined as a “plot” or “tract” consisted of landscape under the same, specific management scheme and contained by roads, firebreaks, and/or other natural boundaries (e.g. stream branches, creeks, dried creek beds). Plots on differing fire regimes, or burn cycles, were sampled for this study. However, fire regime was not included as a variable in our analysis. Cycle initiation for the sampled plots were all within 3 years of each other, and so the landscape was not considered overtly different in terms of structural or resource characteristics. “Control” sampling sites, on the other hand, contained landscape not undergoing longleaf pine restoration and thus may have exhibited distinct differences, in terms of structural or resource characteristics, from the treated sites. The sampled control plots were still actively managed by wildlife and forest management agencies, but were not managed with the specific restoration practices used for longleaf pine restoration.

Bat species typically found within the study region are cavity- or bark-roosting; past studies have revealed that habitat characteristics such as canopy closure, snag density, distance to resources (i.e. water and insect availability), and tree diameter are important for habitat use by these bat species (Fabianek et al. 2015). Thus, control and treated landscape within the study area was initially surveyed for suitable habitat with at least one of the following criteria: snag presence, canopy openings, and commuting distance to stream branches or standing water. After suitable habitat was found within treated and control landscape, sampling sites were selected from within the surveyed areas in each WMA. Sampling site selection mostly depended on accessibility and spatial distribution – all sampling sites were located in differing fire regime and control plots, as well as at least 60 meters from plot boundaries, firebreaks, and/or roads. The selected sampling sites were sampled two different times at two different sampling locations within the same plot. After an initial sampling location was selected, the subsequent sampling took place at least 60 meters away from the initial location to provide replicate sampling for that site and account for habitat variation within the sampled landscape. The two sampling locations within each sampling site remained within the same treatment cycle.

METHODS

Bat Activity and Species Presence

Acoustic monitoring.— Passive, stationary acoustic monitoring was performed throughout the summer and early-fall months, when conditions are optimal for bat activity (Loeb et al. 2015). Sampling began in July and concluded in September 2016, when suitable weather conditions such as nocturnal temperatures above 10°C, ended for the season. Four Wildlife Acoustics® SM3BAT bat detectors were deployed for at least four consecutive nights at each sampling location. Detector microphones were secured to trees at least 3 m from the ground, and the default programming for sunset to sunrise recording was used. A pair of sampling locations within each wildlife management area – a control and a treated site – were sampled simultaneously for each deployment. A sampling period was completed approximately every four weeks for a total of three sampling periods over the course of the study. Two sites within each WMA were surveyed per sampling period, with two locations surveyed at each site. Bat activity is known to vary with weather and climate changes, and is negatively correlated with conditions such as rain or low temperatures (Erikson & West 2002, Britzke & Murray 2013). Therefore, sampling was performed on a randomized, rotating basis throughout the summer once the first sampling period was completed in order to randomize conditions that may have affected the collected data.

Data processing and analysis.— Wildlife Acoustics® Kaleidoscope Pro 4.0.0 was used for batch processing of raw data and auto-identification of bat species. The software removed noise and low quality files through scrubbing, and tagged bat passes with a species auto-ID label. Computer algorithms that automatically build classifiers from a large library of pre-labeled full-spectrum and zero-crossing recording files performed species identification of call sequences (Agranat 2012). We analyzed post-scrubbed files as separate bat passes, with a bat pass defined as a call sequence of ≥2 pulses without an interruption of >5 seconds. Bat activity was quantified as the mean number of nightly passes recorded by each detector within a certain treatment tract each night, as done in previous studies. A bat pass is typically defined as a sequence of ≥1 identifiable search phase echolocation pulses (Loeb et al. 2008, Armitage & Ober 2012). Search phase echolocation calls are vocalizations made to explore the environment, and are consistent in structure throughout a sequence and by species – thus, call libraries used for species identification consist of search phase calls by species (Britzke & Murray 2013). Species presence was determined after manual confirmation of auto-ID labels using a reference call library. Labels with a pulse species identification match ratio threshold of ≤0.70 were only vetted for species known to have similar classifiers (which therefore had a higher probability of being mislabeled by the auto-ID software). Labels with a lower match threshold were manually vetted before being used in the data analysis. Groupings of species with similar search phase call frequencies and patterns are often used by other researchers, such as grouping all *Myotis* species together, to further reduce mislabeling error (***Table 1***). The species groupings made in this study are based off the Kaleidoscope classifier performance report released by Wildlife Acoustics® and previous studies that used species groupings (Cox et al. 2016). Two species that have been detected in the region but were not included in the auto-ID software classifier include the seminole bat (*Lasiurus seminolus*) and the eastern small-footed bat (*Myotis leibii*). These species have similar call structure and patterns to species within the species groups in which they have been placed (***Table 1***), and we assumed any detection of these species would fall within those species groups.

We used the R statistical program version 3.3.2 (R Development Core Team 2016) to conduct all data analyses, with packages lme4 and MASS used for mixed effects modelling. Repeated-measures ANOVA analysis was performed via construction of a generalized mixed effects model to test for significant differences ($\alpha = 0.05$) in bat activity levels between restoration treatment and land management history. A Chi-Square analysis was performed to test for relatedness between species presence and restoration treatment or land management history. A mixed effects model approach was used to determine if bat activity levels were a function of restoration. We used treatment, location, sampling round, and other collected covariates, such as canopy density and prey abundance, as fixed effects. We used sampling site as a random effect in the model (***Fig. 5 & 6***). Visual inspection of the data's residual plots did not reveal any obvious deviations from homoscedasticity, but did demonstrate deviation from normality in the form of a negative binomial distribution. Transforming data did not result in a normal distribution. Thus, the generalized mixed effects model approach was used instead of a linear mixed effects model. We built candidate models with the assumption that all the covariates, alone or in combination, could affect bat activity levels and examined all possible interactions. Model fit was determined by Akaike information criterion (AIC) tests of models with the effect in question against the models without the effect in question and a null model. The ΔAIC was calculated as the difference between the minimum AIC score and the AIC score of the model being tested. We considered models with $\Delta\text{AIC} \leq 20$ as candidates for the best fit model and ranked those models; the model with the lowest AIC score was determined to be the model that best fit the data (Burham and Anderson 2010, Cox et al. 2016).

Canopy Density and Prey Abundance Sampling

In addition to acoustic monitoring of the selected sampling sites, variation in habitat resources was also recorded through documentation of canopy cover and available prey abundance/composition. Clutter has been evidenced to influence bat activity, and therefore recording the type and amount of foliage or canopy cover in a landscape serves to characterize degree of forest clutter (Loeb et al. 2015, Cox et al. 2016). A convex spherical densitometer was used to quantify canopy cover. Mean canopy cover was recorded for each sampling site using two 10 m radial transects expanding from detector locations. A Two-Way ANOVA analysis, including further pairwise significance testing ($\alpha \leq 0.017$), was used to determine if mean canopy cover differed between wildlife management areas and treatment types.

Available diet composition, or prey availability, in the studied areas was quantified through the deployment of BioEquip® Universal Black Light Traps at survey sample sites and subsequent sorting of invertebrate samples obtained. Insect traps were located within a 60-meter radius of the detector locations at each site, but were deployed on different nights than the bat detectors to avoid possible baiting of bat activity (Webala et al. 2011). Due to the nature of the black light traps, specimen were euthanized with a mixture propylene glycol, ethylene glycol, and water. We preserved the collected samples from each site in 70% ethanol and sorted the specimen by Order. A Chi-Square analysis was used to determine if mean Order abundance differed between wildlife management areas and treatment type.

RESULTS

Bat Activity and Species Presence

Activity Levels.— We sampled bat activity for a total of 66 nights and recorded a total of 27,098 bat passes over the sampling period. Activity levels did not differ significantly between wildlife management areas (Paulding WMA = 113.20 mean passes/night, Sheffield WMA = 113.65 mean passes/night), but treatment did have a significant effect dependent on wildlife management area. The Paulding Forest WMA displayed no significant difference between control and burned stands sampled, while the Sheffield WMA displayed a significant difference ($P \leq 0.038$) between control (136.08 mean passes/night) and burned (91.42 mean passes/night) stands sampled, with control stands exhibiting slightly higher activity levels (***Fig. 3 & 7***). Bat activity levels were significantly different between the sampling rounds ($P \leq 0.001$), illustrating the expected seasonal shift in activity (***Fig. 4 & 8***).

Three models were the best predictors of bat activity levels and included the variables treatment, location, and sampling round. The model with an interaction term between treatment, location, and sampling round best fit the data, and demonstrated the significant effect treatment had dependent on wildlife management area (***Fig. 7 & 8***). This model best predicted activity levels out of the three candidate models with the lowest AIC score and ΔAIC (***Table 2***). The other two candidate models, a purely additive model and a model with only treatment and location in the interaction term, displayed similar AIC scores; in these models, there was no significant relationship between treatment and location, and neither treatment nor location alone had a significant effect on bat activity levels. Sampling round had a significant effect in all three candidate models, but this was an expected result given the seasonal shift in activity (***Fig. 7 & 8***). Candidate models including additional covariates, such as canopy density and prey abundance, produced models that failed to converge and thus were not included in further analysis.

Species Presence.— A total of twelve species were detected by auto-ID software, with the most common detections being the big brown bat (*Eptesicus fuscus*) and the eastern red bat (*Lasiurus borealis*). Approximately 30% (n = 8,093) of the total recorded bat passes were confidently identified to the level of species groups. The EPFU/LANO species group constituted 47% (n = 3,842) of identified calls, LABO/NYHU constituted 32% (n = 2,563), and PESU constituted 16% (n = 1,312). Bat species in the Myotis genus, Mexican free-tailed bats (*Tadarida brasiliensis*), and hoary bats (*Lasiurus cinereus*) were also detected consistently across locations and sampling rounds, though at much lower rates than the other species. No significant relationship was detected between treatment and relative species presence, or species composition of activity (***Fig. 9***). However, there was a significant difference in species activity composition between the wildlife management areas ($P \leq 0.001$, ***Fig. 10***). The Sheffield WMA displayed an activity composition with EPFU/LANO species group constituting 32% (*n* = 1,074) of identified calls, LABO/NYHU constituting 37% (*n* = 1,227), PESU constituting 24% (*n* = 776), and together TABR, LACI, and Myotis constituting 7% (*n* = 69, *n* = 29, and *n* = 137 respectively). The Paulding Forest WMA displayed an activity composition with EPFU/LANO species group constituting 58% (*n* = 2,768) of identified calls, LABO/NYHU constituting 28% (*n* = 1,336), PESU constituting 11% (*n* = 536), and together TABR, LACI, and Myotis constituting 3% (*n* = 29, *n* = 12, and *n* = 100 respectively).

Canopy Density and Prey Abundance

Canopy density did not differ significantly between the sampled wildlife management areas, but wildlife management area location did influence canopy density difference between control and burned sampling sites. Mean canopy density in control and burned stands displayed significant differences ($P < 0.001$) dependent on the wildlife management area. Control stands exhibited a higher canopy density (67.56%) than burned stands (51.29%). In Paulding Forest, there was no significant difference, while in Sheffield there was a significant difference (burn at 47.30%, control at 73.93%; $P < 0.001$). The difference between canopy densities in control versus burned stands within Sheffield was significant enough that when the canopy densities of each treatment type were averaged across the WMAs, a significant difference between control and burned stands overall was detected.

We collected samples of flying nocturnal insects for a total of three nights in September, sampling a control and burned site in each wildlife management area each night. Prey abundance was estimated by insect Order; nineteen Orders were collected throughout the sampling sites. The three most abundant Orders collected were Coleoptera, Lepidoptera, and Diptera, with relative abundances of 24%, 18%, and 16% respectively (*n* = 1,609). The Orders Homoptera

(14%), Hymenoptera (7%), and Isoptera (4%) were also collected at all sampling sites in larger numbers compared to the other Orders. The abundance of the other Orders collected were comparatively low (≤ 3%), and thus will not be discussed in this study.

Statistical analysis of insect Order distribution between treatment type and wildlife management areas returned significant differences in relative Order abundance for both variables ($P < 0.001$). In sampled burned stands, Coleoptera constituted 27% of relative prey abundance, Diptera constituted 20%, and Lepidoptera constituted 17% (n = 800). Homoptera abundance demonstrated an increase to 21% of relative prey abundance in burned stands compared to controls stands, while Hymenoptera and Isoptera abundances demonstrated a decrease to 3% and 1% respectively. In sampled control stands, the Order distribution of relative prey abundance changed as follows: Coleoptera constituted 21%, Lepidoptera constituted 18%, and Diptera constituted 13% of the collected specimen (n = 809). Homoptera demonstrated a decrease in relative abundance at 7% in control stands compared to treated stands, while Hymenoptera and Isoptera abundances both increased to 10% and 8% respectively.

Between wildlife management areas, similar changes in distribution were detected. The Sheffield WMA demonstrated a relative prey abundance where Coleoptera constituted 25%, Lepidoptera constituted 13%, and Diptera constituted 18% of collected specimen (n = 677). Homoptera constituted 12% of the relative prey abundance, Hymenoptera constituted 8%, and Isoptera demonstrated a noticeable 10% of relative prey abundance. The Paulding Forest WMA exhibited Coleoptera constituting 23%, Lepidoptera constituting 21%, and Diptera constituting 15% of relative prey abundance (n = 932). Homoptera constituted 15% and Hymenoptera constituted 6% of relative prey abundance, but Isoptera constituted less than 1%. Overall, more insect specimen were collected from the Paulding Forest WMA than the Sheffield WMA. The relative prey abundance between treatment types within each wildlife management area were not compared due to limited sampling; the analyzed samples were from only four sites sampled at the end of the study period. The four sites were replicates of the WMAs (two sites were from Sheffield WMA, two were from Paulding WMA sites) and treatment type (two sites were from control plots, two were from burned plots).

DISCUSSION

Our results indicate that longleaf pine restoration methods do not significantly affect bat activity levels or relative species presence within the sampled region. Bat activity levels did not significantly increase or decrease in response to prescribed burning; levels were consistent and robust across the sampled areas, even considering the effect of season. Of the three candidate statistical models produced, two supported an independent relationship between restoration treatment and bat activity levels. Relative species composition of those measured activity levels also did not significantly differ between control stands and burned stands. These results were unexpected given that canopy density did appear to change significantly between control and burn stands; past studies have recorded a positive correlation between low canopy density and bat activity, but our study did not demonstrate this correlation. Overall, it appears the cyclic burning and overstory thinning methods employed for longleaf restoration in this region have no immediate positive or negative effects on bat activity levels and species presence.

Interpretation of the results for each wildlife management area may suggest a more complex relationship. While there is no significant difference in bat activity levels across the sampled region, restoration treatment may be affecting bat activity levels and relative species presence differently between the two sampled wildlife management areas. As outlined previously, the WMAs have differing landscape management histories. Paulding Forest WMA has been more recently and extensively logged in the past and has a more homogenous, loblolly-dominated forested landscape. Sheffield WMA has extant longleaf pine stands and has not been logged in the past half-century, leading to a less disturbed, mature mixed hardwood and pine forested landscape. The statistical model that demonstrated best fit to the data suggested a significant interaction between treatment and location. According to this model, the effect that treatment has on bat activity levels varies with landscape management history.

The landscape with more recent logging history displayed similar activity levels in both control and burned stands, while the more mature landscape with extant longleaf pine stands displayed slightly higher activity in control stands when compared to burned stands. Although the difference in activity levels was only marginally significant, there was also a significant difference in relative species composition between wildlife management areas. This suggests as well that landscape management history, instead of restoration treatment alone, could be influencing the response variables. The differences in landscape management could be playing a larger role in how restoration may affect bat activity than is discernable with the current data set. No indices of landscape management history, other than location, were used in data collection. The only variable collected in this study that may have represented any differences between the management histories was canopy density, and no significant differences were found between the two wildlife management areas. The more mature, less disturbed landscape did display a significantly higher canopy density in control stands compared to burned stands, but this did not correlate to higher bat activity in the burned stands. Thus, possible factors behind the variance in treatment effect between the wildlife management areas are unclear.

We predicted that longleaf pine restoration treatment would correlate to higher levels of bat activity levels and species presence. Other studies involving the effect of prescribed fire and overstory thinning on bat activity have recorded a positive correlation (Loeb & Waldrop 2008, Armitage & Ober 2012, Cox et al. 2016, Silvis et al. 2016). It was hypothesized that this is due to the opening of canopy cover, and therefore removal of clutter, caused by these methods. While overall these studies agree that prescribed burning and overstory thinning appear to be beneficial to bat activity, several studies described differing specific results. Cox et al. (2016) found higher activity levels in burned and thinned stands in the upland hardwood forests of Tennessee. Loeb and Waldrop (2008) found no difference in activity between control stands and stands that were both burned and thinned in pine forests of South Carolina; the highest activity levels documented were instead in thinned-only stands. Many of these studies also conducted extensive sampling of activity at different canopy heights; this sampling revealed equal activity above the canopy for both treated and control stands (Loeb & Waldrop 2008, Armitage & Ober 2012). It was only below the canopy that activity changed dependent on treatment – and even then, the difference in activity varied among species groups. In a longleaf pine sandhill study Armitage and Ober (2012) found that species considered small-bodied and highly maneuverable, such as Myotis species, were equally active across all canopy levels, whereas species considered poorly maneuverable, such as big brown bats, were more active in stands where prescribed fire was more recently applied.

Our results at first appear to conflict with the narrative within the published literature. We hypothesized restoration methods and landscape management history would affect bat activity levels and species presence, but the data did not fully support this hypothesis. The results of our study indicate that landscape management history may play a role in how restoration affects bat activity levels and the species composition of that activity, but restoration treatment alone had no effect. Prescribed burning appeared to significantly reduce canopy cover and clutter in one wildlife management area, but not the other. However, there are aspects of the discussed previous studies that are still reflected in our results. Both thinning and burning methods were used indiscriminately the wildlife management areas we sampled, and more thinning was employed in the area had been more recently logged (B. Womack, personal communication). This was the WMA that exhibited no difference between control and burned stands, which is consistent with Loeb and Waldrop's (2008) findings in southeastern pine forests. More thinning and burning should equate to greater removal of clutter and opening of canopy. There was no difference in canopy density between the control and burned stands in this WMA, which lends support to the hypothesis that bat activity levels are correlated to open canopy – if canopy densities are similar between two areas, activity levels should remain consistent.

There is also the matter of bat species groups exhibiting a change in relative presence or activity distribution based on landscape management history. As past studies observed, there was a difference in activity composition/distribution between species groups considered small-bodied and highly maneuverable – the Myotis, PESU, and LABO/NYHU groupings – and species groups considered large-bodied and less maneuverable – the EPFU/LANO grouping (Armitage & Ober 2012, Silvis et al. 2016). There was a greater activity distribution of the more maneuverable species in the more mature, naturalized WMA with extant longleaf pine stands, while the less maneuverable species had a greater distribution in the WMA more recently logged and undergoing more extensive (i.e. more thinning) restoration. This change in species activity composition could be due to some intricacies involved in changing canopy cover as well. In the more mature, less disturbed WMA, a significant difference was found in canopy density between control and burned stands. Control stands had higher canopy density, but also displayed slightly higher bat activity levels. It is possible that this slightly higher activity may be due to some niche partitioning. Perhaps if the less maneuverable species are more active or present in burn stands and less so in control stands, this allows for the more maneuverable species to be more active in the control stands. Of course, all recorded bat passes would have to be identified to species or species group levels and analyzed to support or refute this speculation.

Relative prey abundance was also analyzed as a covariate that could be affecting activity levels or species presence. Unlike bat activity levels and species activity composition, there was a significant difference in insect Order distribution for both treatment type and landscape management history. The insect Order Coleoptera (beetles) remained the most abundant regardless of treatment or wildlife management area, but the relative distributions of the other most abundant Orders significantly changed dependent on these variables. Burned stands showed an increase in Coleoptera relative abundance when compared to control stands, demonstrating that other Orders may be more affected by prescribed burning than Coleoptera. Control stands exhibited an overall more evenly distributed order abundance than burned stands. Past studies have provided evidence that several insect orders, such as Lepidoptera or Hymenoptera, do exhibit sensitivity to prescribed burning (Armitage & Ober 2012, Cox et al. 2016).).

In control stands, most Orders that could be considered predominately flying insects – Lepidoptera (moths, butterflies), Diptera (flies, gnats), Isoptera (winged termites), and Hymenoptera (bees, wasps, winged ants) – increased in relative abundance. It is hypothesized that most of this study's focal bat species are more likely to ingest these "soft-bodied" insect orders as prey, although the more common of the focal species will ingest Coleoptera and Homoptera as well (Feldhamer et al. 2009, Clare et al. 2011, Moosman et al. 2012). The documented changes in insect Order distribution could therefore account for the difference in activity levels between burned and control stands in the more mature, naturalized WMA with extant longleaf stands. However, this possible explanation of higher bat activity correlating to higher relative abundance of these Orders was not adequately paralleled within the overall data set. There was no significant difference in activity levels between treatment types.

The more mature WMA did exhibit higher relative abundance of the aforementioned prey Orders when compared to less mature, more recently logged WMA. Again, this could explain the difference in bat species activity composition observed between the wildlife management areas, with the more mature landscape demonstrating higher relative activity composition of species hypothesized to eat more “soft-bodied” orders. The less mature landscape is more intensively managed for longleaf pine restoration, and burned stands demonstrated a higher relative abundance of Coleoptera and Homoptera – two Orders that the more common focal bat species ingest. The less mature landscape demonstrated a higher relative species activity composition of the more common bat species. To confirm these explanations, though, it would be necessary to include prey abundance as a covariate within our statistical models – this was not possible with the study’s current lack of statistical power, but has been accomplished in similar past studies. These studies did show that relative prey abundance played a role in bat species activity differences (Armitage & Ober 2012, Cox et al. 2016).

There were several disparities between our study and the published literature that could be driving the differences in results. It is important to note most of the reviewed studies were based in pine forest or mixed hardwood forest landscape; only one sampled a longleaf pine habitat, and it was a sandhill habitat rather than montane. Bat activity baselines may vary across these habitats, and our study did record considerably more activity overall than most of the reviewed studies. We also were not logistically able to sample as extensively as the published literature due to time and resource restraints. Several studies sampled at various heights of canopy or both below and above the canopy. The detectors used in this study sampled a 60-m spherical radius minimum surrounding the unit, and so may have captured some above canopy activity – but there was no way to differentiate activity by canopy levels. The published literature also involves sampling periods from consecutive years and sampling throughout the active season, whereas our study only included one active season. Future sampling in different years and throughout the active seasons will introduce year-to-year and seasonal variation that is not yet included in our models. Further sampling will also provide more data; one limitation of this study was that the number of observations (n = 66 nights) was too low to provide enough statistical power to include covariates such as canopy density, prey abundance, and weather in our models.

Another limitation of our study was introduced in the experimental design and may also be affecting the statistical power of our models. We sampled at two locations within each sampling site to introduce replication. However, the two locations were sampled for consecutive time periods, rather than the detectors returning for sample replication after sampling a different site. This replication design is not necessarily standard for repeated measures, because the variation between sampling locations may differ when measured consecutively versus at separate points in time, and thus may be affecting the way the generalized linear mixed effects model statistical function is interpreting the data. This possibility, however, is a topic beyond the scope of this study. It is likely this discrepancy is not significantly affecting these results, and another sampling round of the same sampling sites with standard repeated measures protocol is being conducted in the summer of 2017. These results will be included in future publications, and the addition of these results should provide enough data to examine more covariates as well. Subsequent sampling will also occur in future active seasons.

During subsequent sampling, it will be important to find ways to quantify specific variables. In this study, although landscape management history appears to play a role in bat activity, we had no way to measure or quantify this variable other than location (i.e. wildlife management area). Previous studies have measured variables such as live overstory basal area, midstory stem density, vegetation species, diameter at breast height, and coniferous/deciduous density to characterize clutter and forest structure (Cox et al. 2016, Armitage & Ober 2012, Loeb & Waldrop 2008). Measuring these or similar variables, such as longleaf pine or other pine densities within transects of the detector locations, may be an appropriate way to quantify the forest structural variation between the wildlife management areas and in turn the landscape management history. Due to time and personnel constraints, these measurements were not collected in this study. We would, however, encourage such indices to be recorded for future studies to further explore the effect landscape management history may be having on bat activity in this region.

Some limitations of this study that cannot be corrected in future data collection involve the inherent assumptions made for acoustic monitoring of bat activity. The most important assumption made in acoustic studies is that the number of echolocation calls is an accurate representation of activity levels (Loeb & Waldrop 2008). In this study, we reduced variation in probability of detection by ensuring detectors were calibrated, using the same programming and settings, and sampling replicate stands. Past studies have established that forest structure and clutter have little influence on detection probability (Cox et al. 2016). Our sampling sites were within the same region, and so we believe this to be the case for our study as well. So, in accordance with the published literature, the number of bat passes recorded should have been an accurate representation of activity levels. Another important assumption that parallels the number of bat passes accurately representing activity relates to the interpretation of results: the amount of activity recorded does not necessarily equate to organism abundance. An individual bat may make several passes by a detector in one night; one bat pass does not correlate to a single bat. However, we argue that important patterns on habitat or landscape use and suitability may be inferred from acoustical study by analyzing data in context. Bat passes do accurately represent bat activity levels. By interpreting activity levels in relation to randomly sampled, varied habitats and relative species presence of these activity levels, conclusions can be made on the type of landscape or habitat that may be suitable to specific species groups as well as to bat species overall.

Wildlife management objectives include conserving environments and restoring native biota, but can introduce elements of anthropogenic alteration to the landscape that may affect the activity of non-focal wildlife. Bats inhabit key ecological niches in several ecosystems and exhibit sensitivity to environmental changes. In habitats where bat species are present, they are often considered indicators of ecosystem health or condition. By documenting and characterizing bat activity in wildlife management areas, effectiveness of restoration methods can be evaluated. Our study indicated that longleaf pine restoration has not caused significant disruption to bat activity, and so other wildlife populations may also not be adversely affected. Whether this describes successful restoration practices may be a subjective matter, and more data on other organisms may be needed to fully detail the effectiveness of this restoration in regards to effects on non-focal species. In conclusion, although montane longleaf pine restoration introduces elements of anthropogenic alterations to the landscape, sensitive and non-focal wildlife such as bat species did not exhibit negative responses to restoration methods. These restoration practices introduced minimal ecological disturbance, which alone can be viewed as a type of restoration success.

MANAGEMENT IMPLICATIONS

Longleaf pine restoration methods do not appear to have any immediate or negative effects on bat activity levels and relative species presence. Our study suggests that contemporary practices, such as prescribed cyclic burning and overstory thinning, may proceed without concern for mitigation of negative impacts on the bat community. The changes in community activity and structure that did occur indicate that landscape management history may be more important in determining wildlife response to longleaf pine restoration. Landscape with more established longleaf pine stands, higher canopy density, and less frequent prescribed burning demonstrated slightly higher levels of activity and the relative activity of less dominant species groups also increased. The landscape that demonstrated these qualities was located within the more mature wildlife area management area, and is characteristic of landscape that restoration is geared towards reintroducing to the region. This indicates that restoration efforts, while not displaying overt signals of effectiveness such as increased bat activity in stands undergoing active restoration, should continue. Active restoration does not adversely impact bat activity, and once restored the landscape may exhibit higher activity levels and species presence – it could simply be a matter of the longleaf pine habitat becoming re-established.

Further research should focus on quantifying variables that measure the differences between the landscape that did display higher activity and the landscape that did not. These variables may elucidate the exact relationship between bat activity levels and landscape management history, and will be necessary to explore whether these activity levels may depend more on variables such as the presence of longleaf pine than prescribed burning. Of course, further data collection on the bat community throughout subsequent seasons will further characterize this restoration response as well. Data should also be collected on other organisms within this longleaf pine ecosystem, such as plant, avian or amphibian communities, to confirm if the largely neutral response to the restoration exhibited by bat species is a parallel response. Accomplishing these objectives will provide further evidence as to whether the restoration methods used in this region are effective or at least non-disruptive for non-focal wildlife. This study primarily introduced a baseline for which to build on, and so more research is needed. However, the study does support an overarching theme in this field: the complexities of forest restoration produce varying effects on the organisms participating in the ecosystem, dependent on landscape structure and habitat type. Documentation of this variation is needed to comprehend the significant effects in context, and apply that comprehension towards management of wildlife populations and ecosystem health.

INTEGRATION OF THESIS RESEARCH

This study integrated several techniques from an array of biological disciplines. How land management impacts bat activity and species composition is foundationally an ecological question, but it also relies on the investigation of animal morphology and behavior. Additionally, aspects of remote sensing and detection probability were needed to investigate this question. This required an understanding of the basics of the physics of sound for proper soundwave detection, the factors that can affect sound detection, the differences in soundwave use for echolocation between bat species, and the computer science behind the digital transformation sound for use in bat presence and species identification. Ecological field techniques were used to collect the data needed for the study. In addition to bat echolocation data collection, insect collections and identification to Order, estimation of cover at field sites, identification of major forest tree components, and recognition of potential habitat favorable to bats were also executed. This project also required integration of ecological data with real-world management goals. The project necessitated knowledge of the longleaf pine ecosystem, its history and how local forest management agencies are currently managing sites to restore longleaf pine habitat. Overall, techniques from ecology, animal biology, morphology, behavior, physics, computer science, and biostatistics were integral to the completion of this research.

Acknowledgements

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APPENDIX A – LIST OF FIGURES & TABLES

APPENDIX B – FIGURES & TABLES

Figure 1.

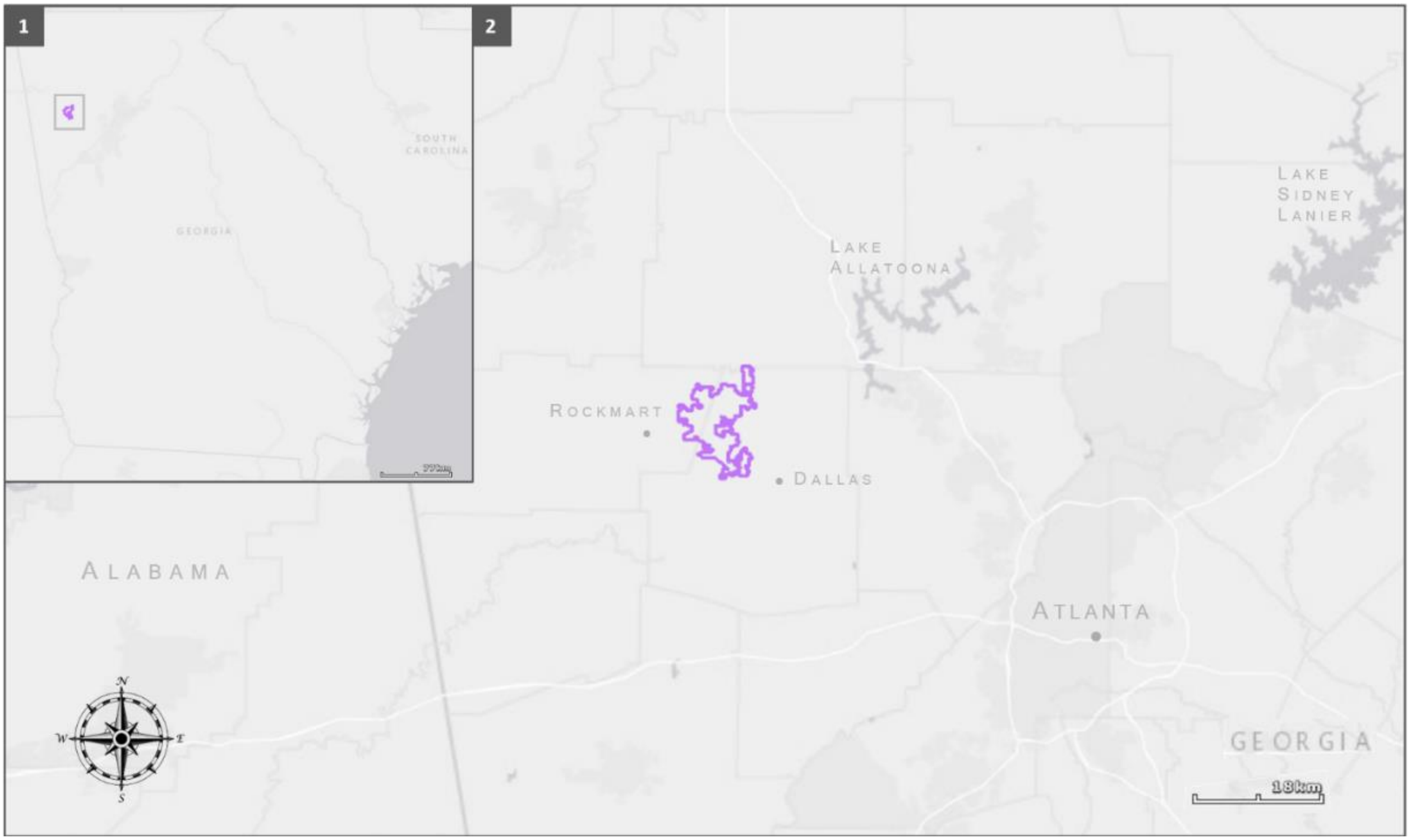

Figure 2.

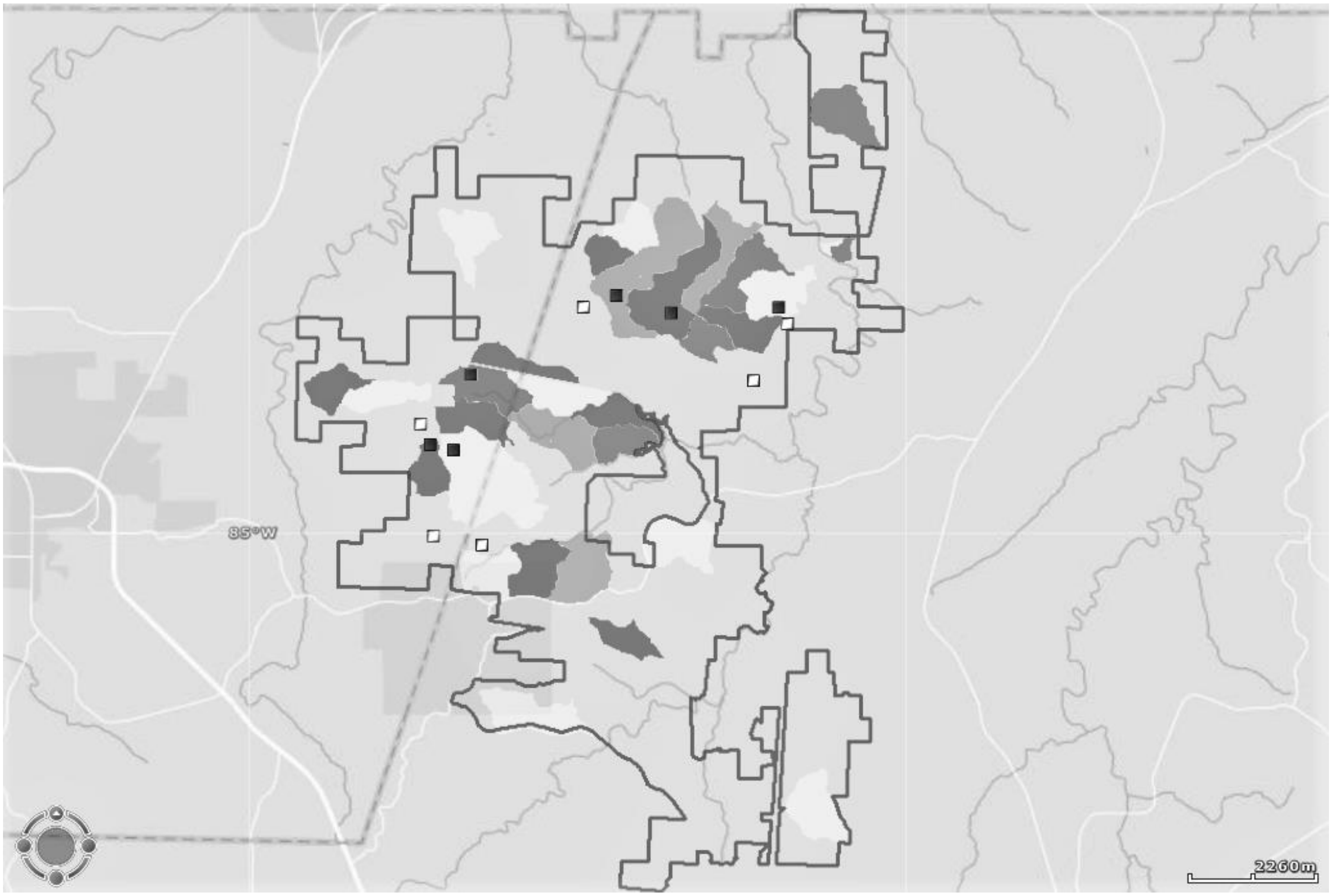

Figure 3.

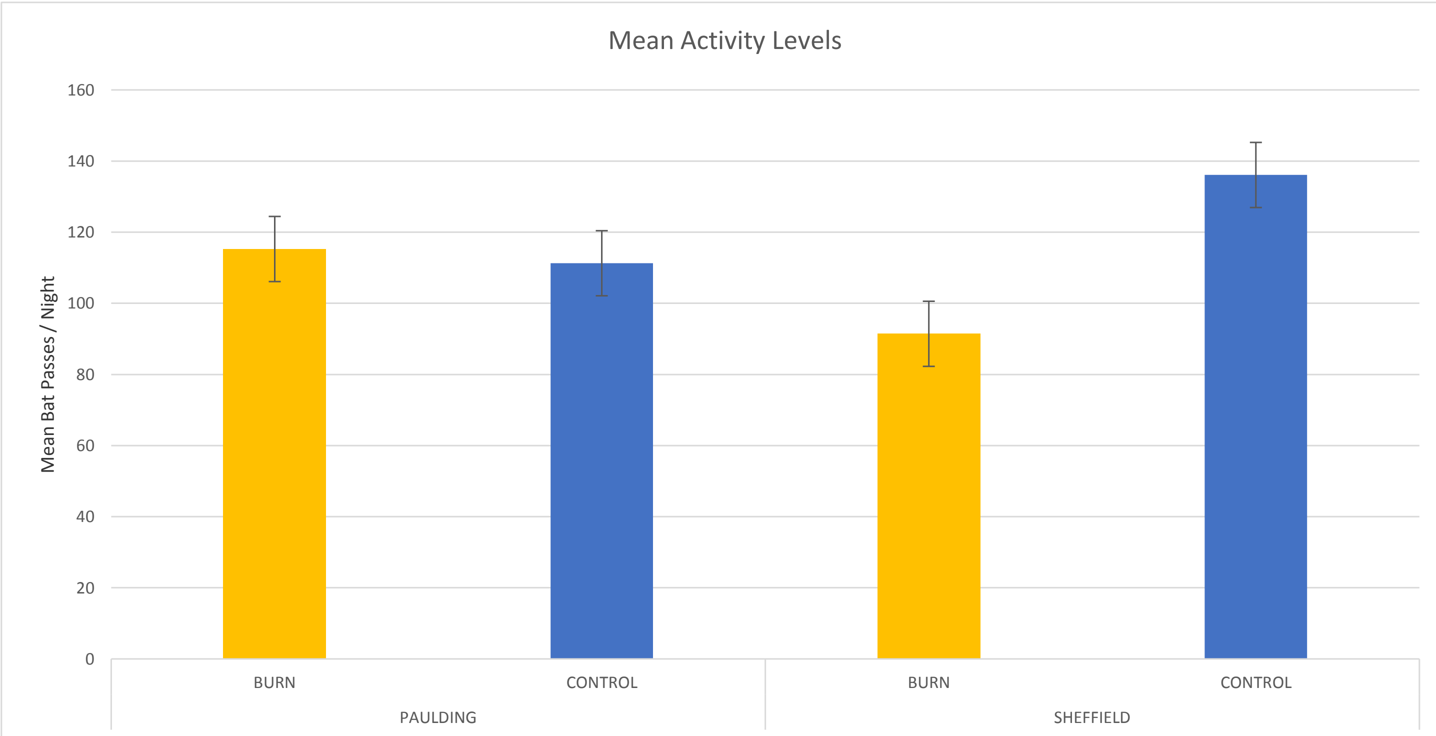
Mean Activity Levels
Mean Bat Passes / Night
160
140
120
100
80
60
40
20
0
BURN
CONTROL
BURN
CONTROL
PAULDING
SHEFFIELD

Figure 4.

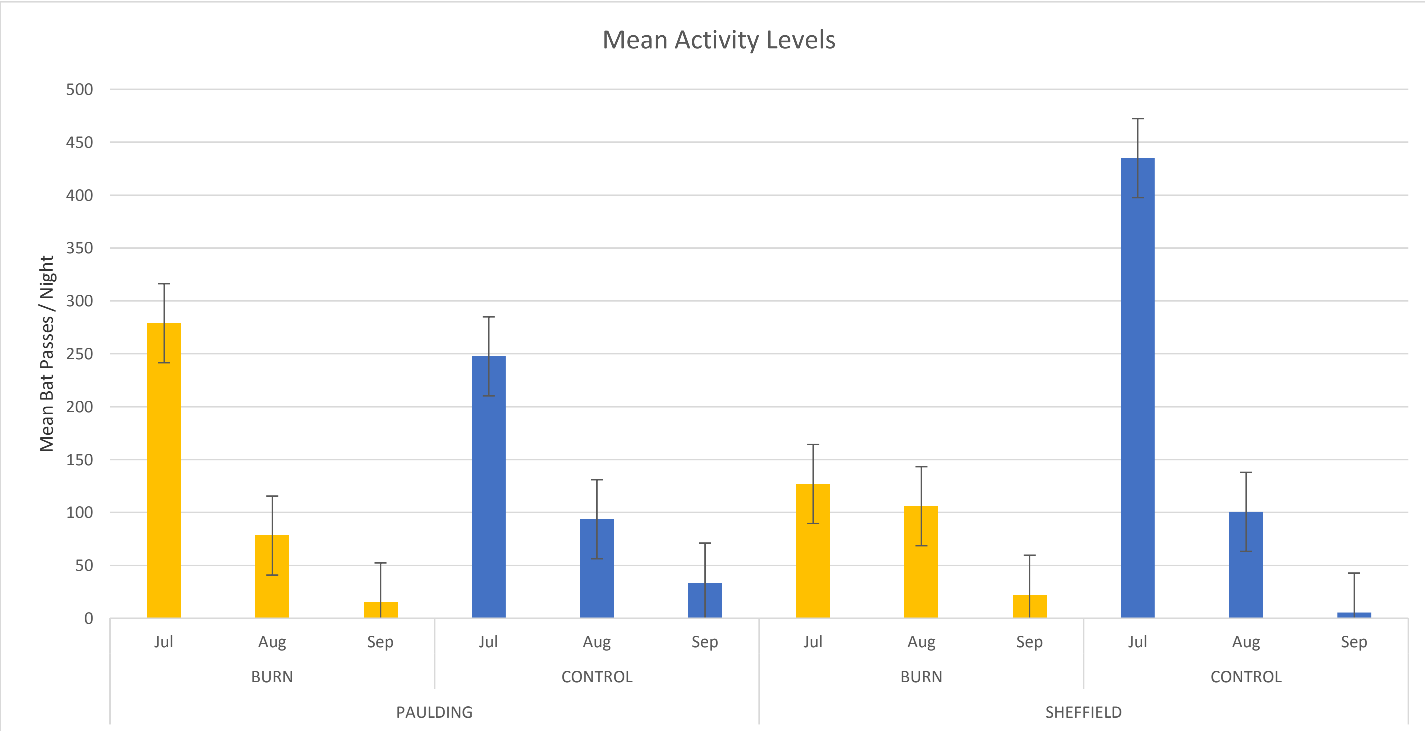
Mean Activity Levels
Mean Bat Passes / Night
500
450
400
350
300
250
200
150
100
50
0
Jul
Aug
Sep
Jul
Aug
Sep
Jul
Aug
Sep
Jul
Aug
Sep
BURN
CONTROL
BURN
CONTROL
PAULDING
SHEFFIELD

Figure 5.

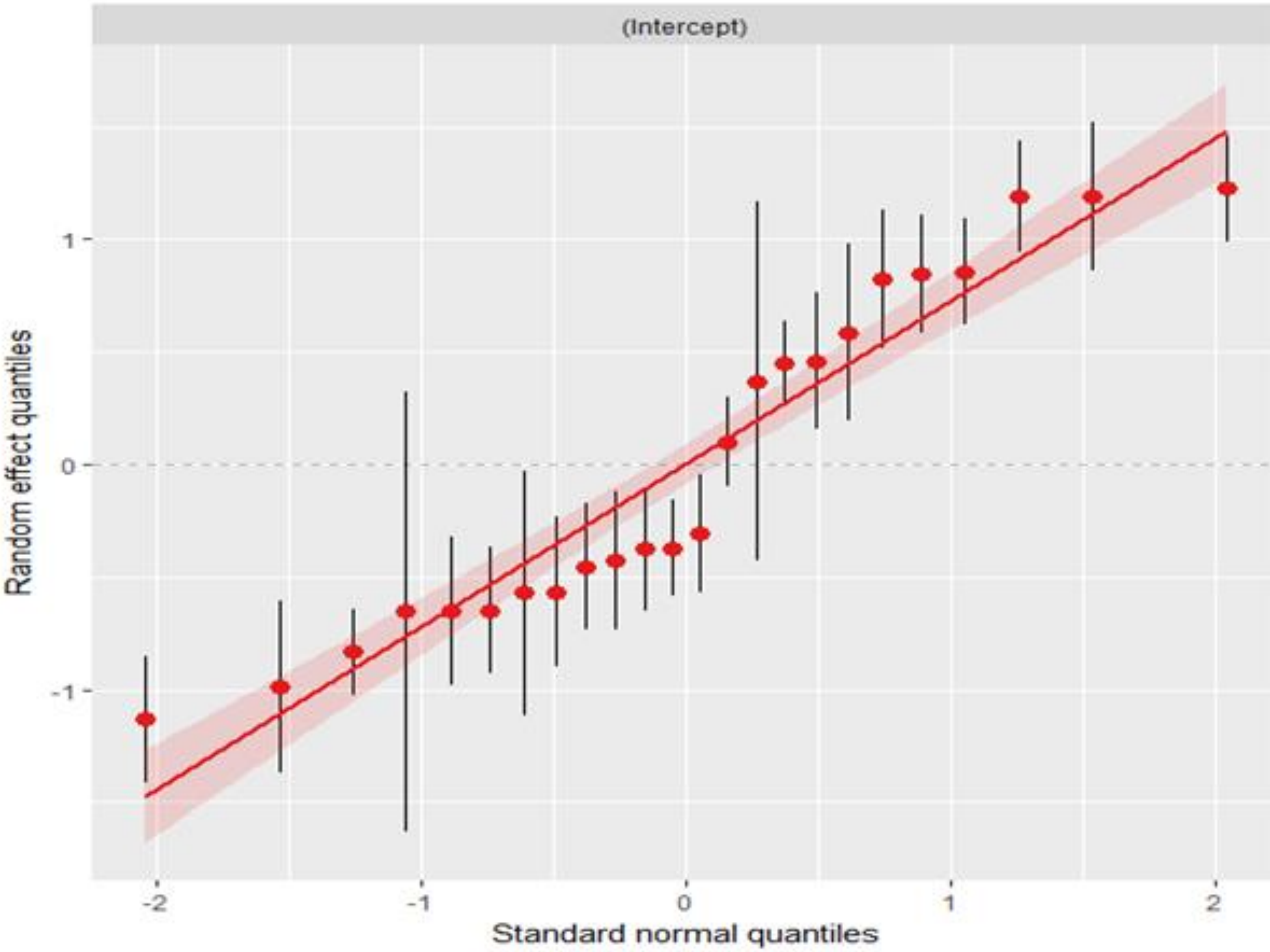
(Intercept)
1
0
-1
Random effect quantiles
-2
-1
0
1
2
Standard normal quantiles

Figure 6.

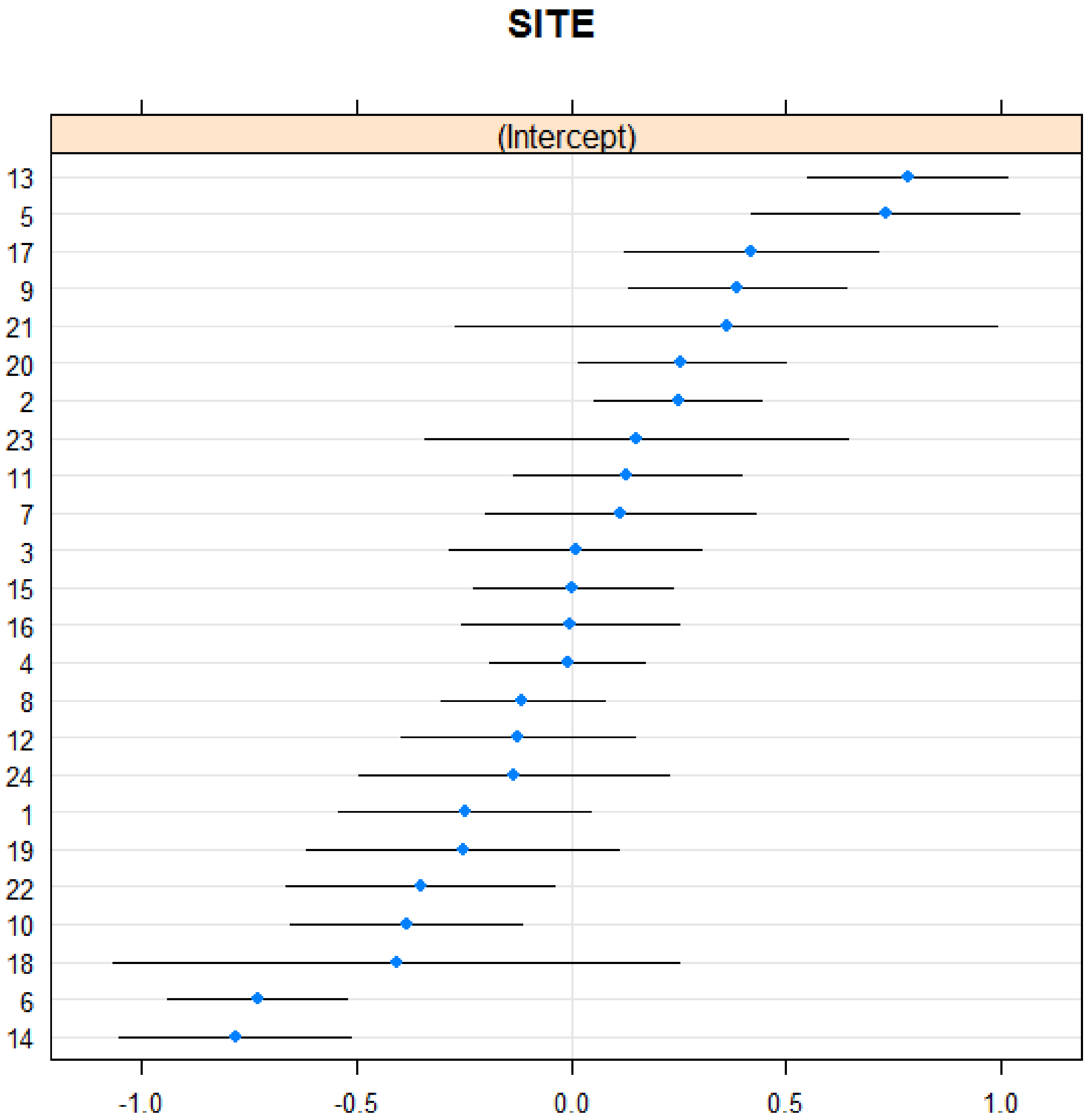
SITE
(Intercept)
13
5
17
9
21
20
2
23
11
7
3
15
16
4
8
12
24
1
19
22
10
18
6
14
-1.0
-0.5
0.0
0.5
1.0

Figure 7.

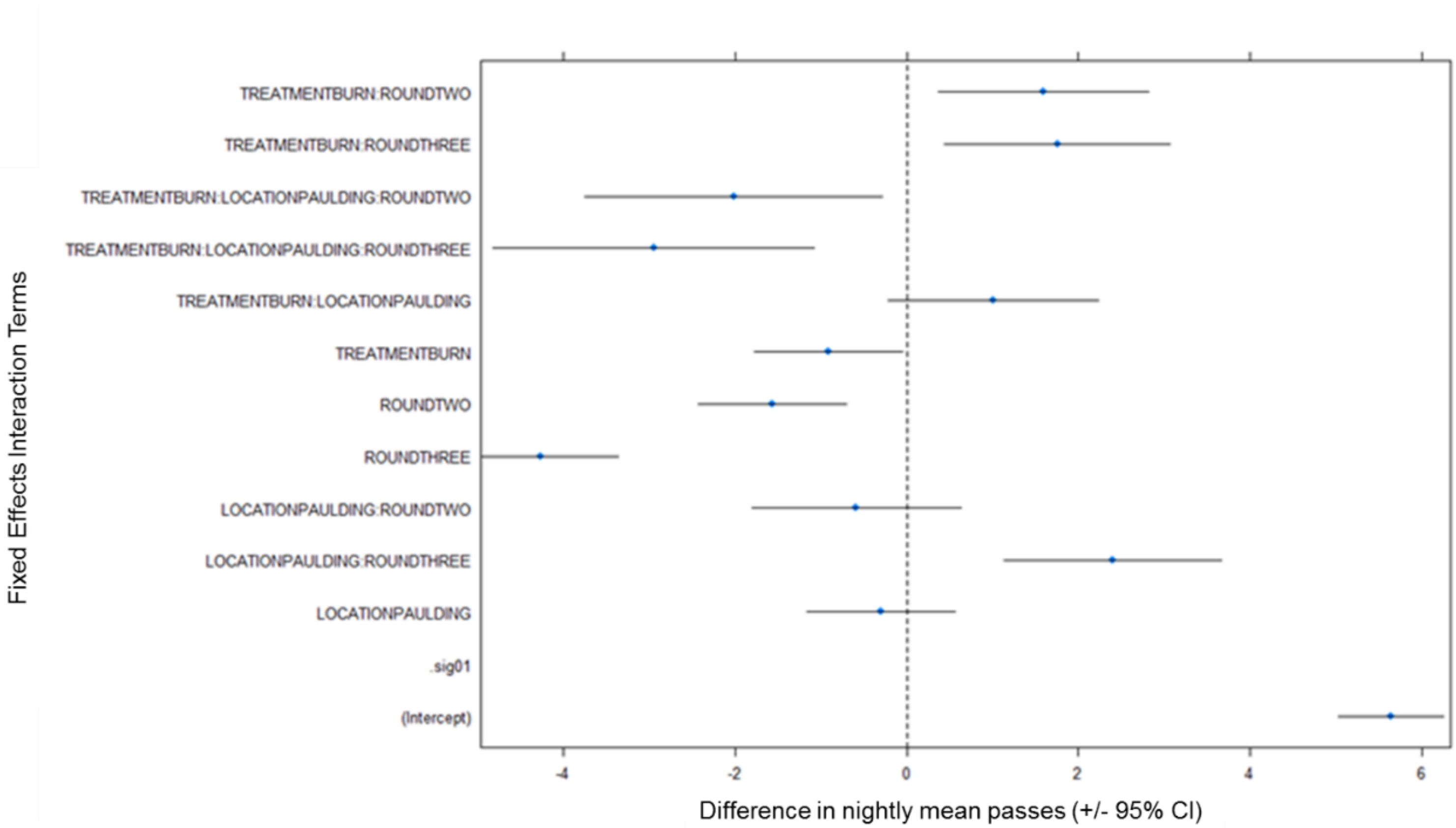
TREATMENTBURN:ROUNDTWO
TREATMENTBURN:ROUNDTHREE
TREATMENTBURN:LOCATIONPAULDING:ROUNDTWO
TREATMENTBURN:LOCATIONPAULDING:ROUNDTHREE
TREATMENTBURN:LOCATIONPAULDING
TREATMENTBURN
ROUNDTWO
ROUNDTHREE
LOCATIONPAULDING:ROUNDTWO
LOCATIONPAULDING:ROUNDTHREE
LOCATIONPAULDING
.sig01
(Intercept)
Fixed Effects Interaction Terms
-4
-2
0
2
4
6
Difference in nightly mean passes (+/- 95% CI)

Figure 8.

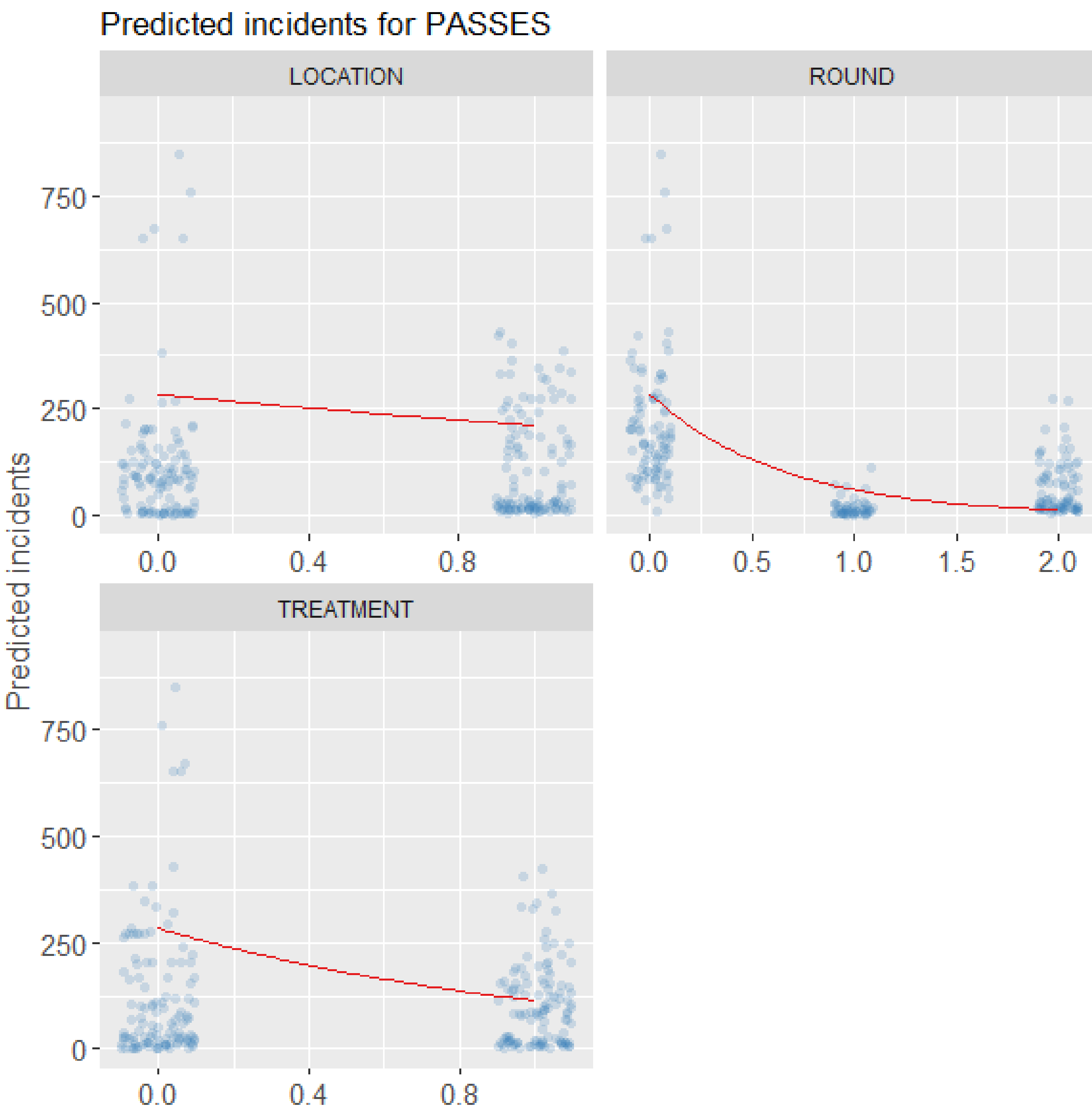
Predicted incidents for PASSES
LOCATION
ROUND
TREATMENT
Predicted incidents
750
500
250
0
0.0
0.4
0.8
0.5
1.0
1.5
2.0

Figure 9.

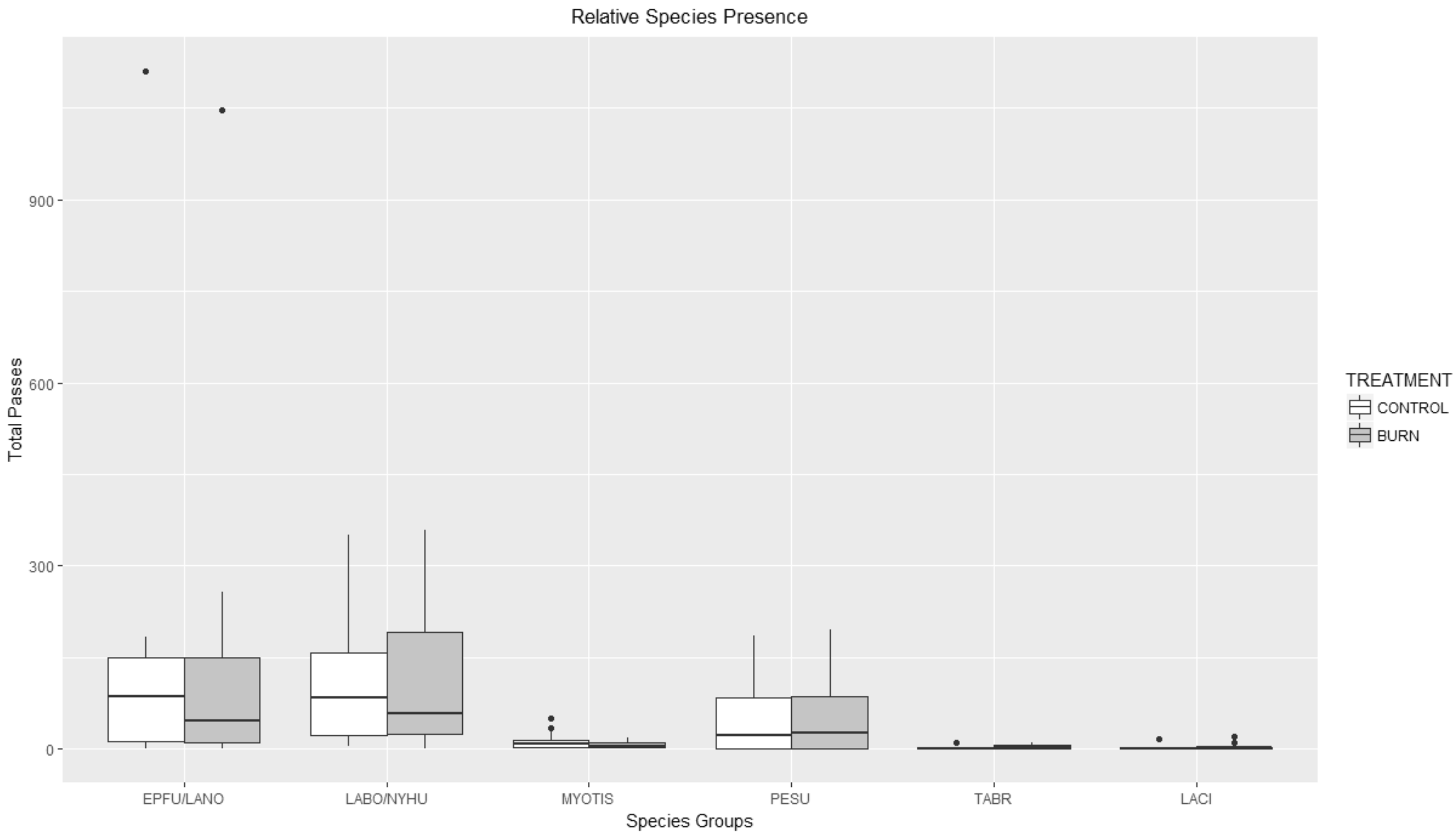
Relative Species Presence
Total Passes
900
600
300
0
EPFU/LANO
LABO/NYHU
MYOTIS
PESU
TABR
LACI
Species Groups
TREATMENT
CONTROL
BURN

Figure 10.

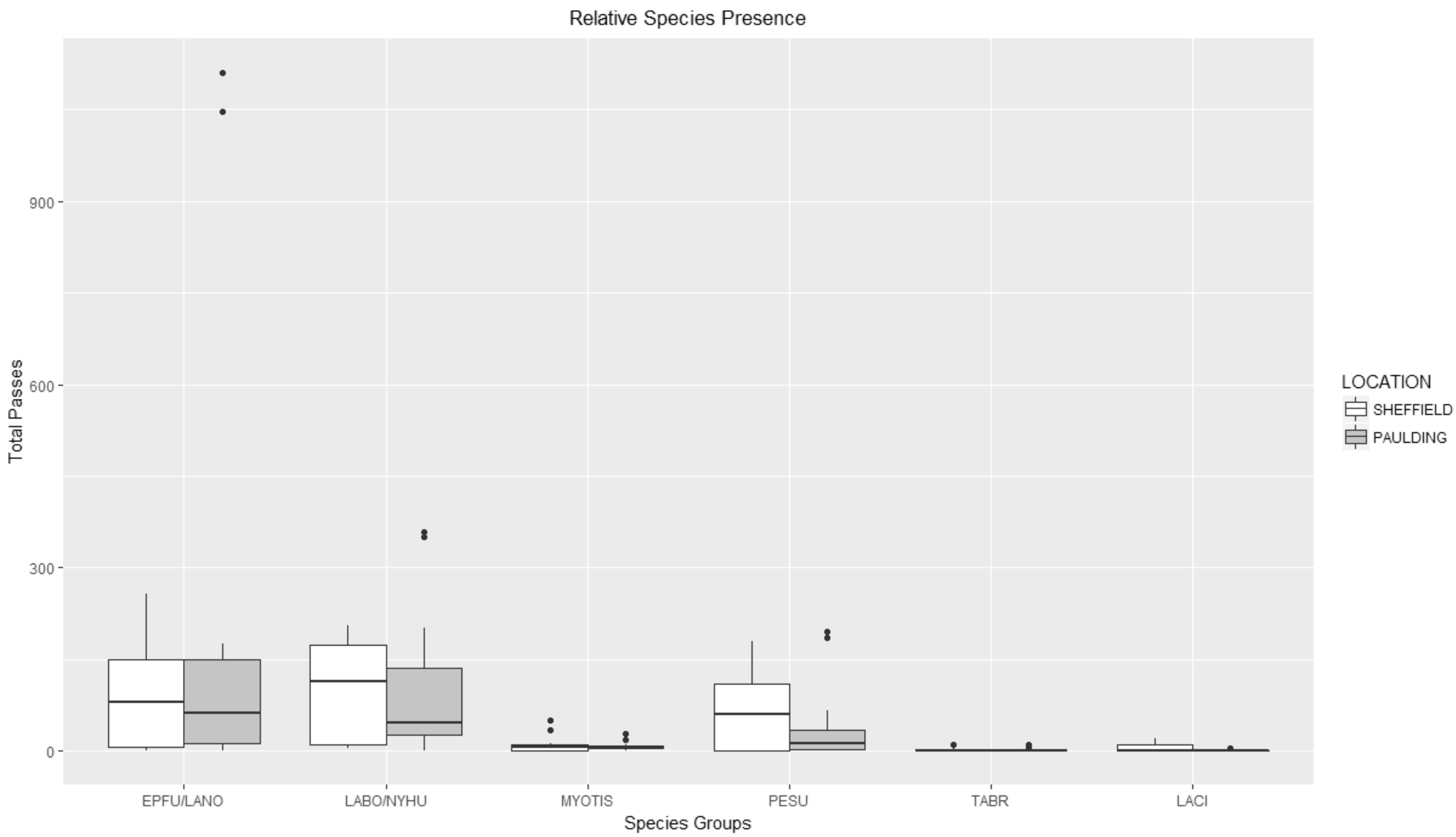
Relative Species Presence
Total Passes
900
600
300
0
EPFU/LANO
LABO/NYHU
MYOTIS
PESU
TABR
LACI
Species Groups
LOCATION
SHEFFIELD
PAULDING

Table 1.

Species group	Bat species	Call frequency (Hz)
Myotis	Little brown (*Myotis lucifigus*)	High
	Indiana (*M. sodalis*)	High
	Northern long-eared (*M. septintrionalis*)	High
	Gray (*M. grisescens*)	High
	Southeastern (*M. austroriparius*)	High
	Eastern small-footed (*M. leibii*)	High
LABO/	Eastern red (*Lasiurus borealis*)	High
NYHU	Evening (*Nycticeius humeralis*)	High
	Seminole (*Lasiurus seminolus*)	High
EPFU/	Big brown (*Eptesicus fuscus*)	Moderate
LANO	Silver-haired (*Lasionycterius noctivigans*)	Moderate
PESU	Tricolored (*Perimyotis subflavus*)	High
TABR	Mexican free-tailed (*Tadarida brasiliensis*)	Low
LACI	Hoary (*L. cinereus*)	Low

Table 2.

	Resid. Df	Resid. Dev	dAIC	weight
1 Treatment:Location:Round	225	221.128444925257	0	0.99
2 Treatment:Location + Round	231	218.181346860337	11.6	0
3 Treatment + Location + Round	232	218.286996564817	11	0

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