Comparison of Gopher Tortoise and Nine-Banded Armadillo Associate Fauna

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ABSTRACT

Burrowing organisms are ecosystem engineers that augment the availability of resources for other species. Throughout the Coastal Plain of the southeastern United States the gopher tortoise (*Gopherus polyphemus*) is a keystone species in open canopy pine-forest ecosystems as its burrows are utilized by over 360 species. These species are responsible for numerous ecosystem processes that maintain ecosystem functionality and health. Across its current range, the gopher tortoise is in decline and has been listed as a vulnerable species by the International Union for the Conservation of Nature (IUCN). Declining tortoise abundance negatively impacts the populations of species that depend on tortoise burrows which will, in turn, have negative impacts on ecosystem function. The introduced nine-banded armadillo (*Dasypus novemcinctus*) is another burrowing species of similar size that is highly abundant and syntopically distributed with the gopher tortoise. Recent research has found high diversity of vertebrates utilizing armadillo burrows, implicating that armadillos support local biodiversity in a similar manner as gopher tortoises. I compared vertebrate visitation between armadillo and tortoise burrows in a mixed-pine hardwood forest at the Lake Louise Field Station in Lowndes County, Georgia using motion activated game cameras placed at equal numbers of burrows produced by each excavator species. I also tested for burrow and microhabitat effects on visitation by associate vertebrates and investigated patterns of metacommunity nestedness within the study area. A total of 40 vertebrate taxa were observed visiting burrows between October 2019 and December 2020. Species richness, biodiversity, and community composition were not significantly different between burrow types. However, total visitation was significantly greater at tortoise burrows as well as visitation frequency for 15 taxa. Burrow and microhabitat variables showed varying effects on burrow visitation for different categories of vertebrates. Most notably, vertebrate visitation frequency was positively affected by tortoise burrows, active burrows, and increased tree species richness while consistently negative effects were observed for increased canopy cover and high proportions of hardwood trees. Patterns of nestedness were not found to correspond with any applicable environmental variable. This research provides a unique framework for comparing utilization of habitat features, adds information to the growing body of work on the ecological effects of the nine-banded armadillo's range expansion, and pinpoints aspects of the habitat that relate to the importance of burrows for other species. My study also highlights and reinforces the ecological significance of the gopher tortoise and suggests that armadillo control efforts may need to be considered on a case-by-case basis.

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Introduction

Burrows provide refugia from stressful environmental conditions such as severe weather, thermal extremes, fire, and predation while also providing a safe location for essential life processes such as mating, resting, and growth (Friend 1993; Pike and Mitchell 2013; Laidre 2018). Burrowing organisms are considered ecosystem engineers due to their ability to modify habitats through soil mixing and creation of important habitat features (Jones et al. 1994). Many vertebrates and invertebrates use burrows that have been excavated by other animals (Kinlaw 1999). Burrow usage is an example of a direct positive interaction between ecosystem engineers (i.e., burrowing species) and the species that benefit from their habitat modification (Jones et al. 1994). Specifically, these interactions are classified as commensalism, where one or more species benefit from another without positively or negatively affecting the species providing the benefits (Van Beneden 1887). In arid regions, burrows in the landscape are especially important for many species in preventing desiccation, thus increasing local biodiversity that would otherwise not be supported given the circumstances of the environment (Kinlaw 1999; Read et al. 2008; Mukherjee et al. 2017).

In the southeastern United States, the gopher tortoise (*Gopherus polyphemus*), a medium-sized terrestrial reptile, inhabits the arid and semi-arid regions of the Coastal Plain (Fig. 1A) and constructs extensive burrow systems that are utilized, for various purposes, by other species (Auffenberg and Franz 1982; Jackson and Milstery 1989). Organisms that have been documented using tortoise burrows can be separated into two distinct categories: "obligate commensals", if a burrow is required for their survival, or "facultative associates" if the species is not fully dependent on burrows but utilizes them opportunistically (Dziadzio and Smith 2016). These species are often referred to as "commensals" or "associates" depending on the degree of the animal's dependance on burrows (Jackson and Milstery 1989). Many other burrowers also have associate species that utilize their burrows (Anker et al. 2005; Aya-Cuero et al. 2017; Tamaki et al. 2018), but of all terrestrial burrowing vertebrates that have documented associate species, the gopher tortoise's burrow supports the greatest diversity (Kinlaw 1999).

Burrows excavated by the gopher tortoise are utilized by over 350 species, more than 65 of which are vertebrates (Jackson and Milstrey 1989; Lips 1991; Alexy et al. 2003; Dziadzio and Smith 2016; White and Tuberville 2017), and due to the high quality refugia created by a tortoise burrow, the presence of gopher tortoises supports and maintains local biodiversity in habitats where tortoise colonies are established (Cantano and Stout 2015). Additionally, active burrows (i.e., burrows that are consistently occupied by a tortoise) may contain a continuous supply of dung which has been implicated in driving commensal use through cascading effects by providing a direct food source for coprophagous organisms who, in turn, are a food source for other species within the burrow (Young and Goff 1939; Lips 1991; Witz et al. 1991; Kent and Snell 1994; Dziadzio and Smith 2016). Facilitation of biodiversity is associated with areas of high environmental stress or predation risk (Hacker and Gaines 1997), and ecosystem engineers that manipulate habitats in a way that reduces environmental stress or predation risk for other species are deemed facilitator species that positively affect local biodiversity (Jones et al. 1997; Bruno et al 2003). Therefore, the gopher tortoise can be classified as a facilitator species because it positively influences the survival of other species and increases local biodiversity through its manipulation of the environment (Jones et al. 1994; Hacker and Gains 1997).

Gopher tortoises are associated with different habitat types, including longleaf pine-oak uplands, xeric hammocks, sand pine-oak ridges, and ruderal successional habitats (Auffenberg and Franz 1982). Historically, gopher tortoise populations were abundant throughout a vast and continuous longleaf pine (*Pinus paulustris*) wiregrass (*Aristrida stricta*) ecosystem; which has been reduced to an estimated 3% of its original range within the last century (Noss 1989; Noss et al. 1995; Kush 2016), leaving tortoise populations severely fragmented and their abundance reduced by up to 80% (Auffenberg and Franz 1982; Hermann et al. 2002; McCoy et al. 2006). Despite this drastic reduction in abundance, the gopher tortoise is only federally listed as a threatened species in the portion of its range west of the Mobile and Tombigbee Rivers in Alabama (Smith et al. 2006). However, the International Union for the Conservation of Nature (IUCN) recognizes the gopher tortoise as a vulnerable species, and it is protected under state regulations in all parts of its range (Ernst et al. 1994; Tortoise & Freshwater Turtle Specialist Group 1996).

Essential gopher tortoise habitat is subject to frequent fire regimes, which are necessary to maintain habitat suitability for tortoises, and the inclusion of prescribed fire has been demonstrated to increase vertebrate use of tortoise burrows (Knapp et al. 2018). Therefore, declines in gopher tortoise populations, along with fire suppression, can negatively impact populations of burrow-associated species (Kinlaw and Grasmueck 2012), potentially leading to an overall decrease in ecosystem function (Paine 1966; Catano and Stout 2015). For this reason, the gopher tortoise is considered a keystone species in the longleaf pine-wiregrass ecosystem (Eisenberg 1983; Catano and Stout 2015).

Throughout its current range, the gopher tortoise is now fully syntopic with another species of similar size that also excavates burrows, the nine-banded armadillo (*Dasypus novemcinctus*; hereafter "armadillo") (Taulman and Robbins 2014). The armadillo is a medium-sized mammal that is not native to the United States. There are no records of armadillos occurring within the United States before 1850 (Audubon and Bachman 1854); before the

1850’s, armadillos were only widely distributed throughout South and Central America, including Mexico. At that time, the armadillo’s distribution within the United States was restricted to the lower Rio Grande River Valley (Taber 1945). The spread of armadillos throughout the southern United States began in Texas after armadillos crossed the Rio Grande River from Mexico but later, captive animals originating from this source were intentionally and/or accidentally released in Florida (Bailey 1924; Humphrey 1974). During the twentieth century, armadillos expanded their range (Fig. 1B), encompassing the distribution of the gopher tortoise. Currently, the armadillo can be found throughout the southern United States, from New Mexico east to the Atlantic coast and as far north as Nebraska (Humphrey 1974, Loughry and McDonough 2013, and Taulman and Robbins 2014).

In certain parts of the United States, the armadillo has been classified as an invasive species because: 1) it was, in part, introduced by humans, 2) it causes economic harm through its burrowing behavior, 3) it predates nests of species that are of conservation concern, and 4) it poses a threat to human health (Staller et al. 2005; Holcomb and Carr 2013; Dziadzio et al. 2016; Ober et al. 2011; Pristo de Medeiros Oliveria et al. 2019). For these reasons, efforts to control armadillo populations have been placed in effect (Chamberlain 1980; Layne 1997). However, classification of armadillos as an invasive species is debated as their range expansion is thought to be the result of both natural and anthropogenic factors (Humphrey 1974; Loughry and McDonough 2013), and, since their arrival, people have speculated whether this species will have positive or negative interactions with local fauna in the introduced ecosystems.

Numerous gaps exist within armadillo research (Loughry et al. 2015) one of which is the topic of burrow commensalism. Vertebrate and invertebrate associates of armadillo burrows have been documented in the United States (Taber 1945; Clark 1951; Hunt 1959; Thomas 1974;

Butler 2020) and Belize (Platt et al. 2004), and although their burrow system differs from that of the gopher tortoise in physical [e.g. entrance shape, width, and length (Sawyer et al. 2012)] as well as microhabitat aspects, this research suggests that armadillo burrows serve as important habitat features for other organisms as well. The most extensive study pertaining to commensal use of armadillo burrows documented 46 vertebrate species interacting with burrows in a dune complex and maritime forest on Little St. Simon's Island, Georgia, U.S.A. (Butler 2020). However, this study represents only two habitat types on one barrier island where armadillos are the only medium-sized burrowing species present, and an exhaustive list of burrow-associated species (vertebrates and invertebrates) for the armadillo throughout its full range has not yet been produced. Therefore, additional studies on species utilization of armadillo burrows are needed in other habitat types as well as in other parts of its range to adequately assess the ecological importance of these burrows and the effects that the armadillo's range expansion may have on ecosystems where it has been introduced. For this reason, there exists a unique opportunity, not only to document novel observations of armadillo burrow associates in different habitat, but also to compare commensal visitation between armadillo and gopher tortoise burrows in areas where both burrowers co-occur.

Study Objectives

The main objective of this study was to compare measures of commensal burrow visitation and community composition of burrow-associated vertebrates between two syntopic burrowing organisms of similar size that occur in the southeastern United States: the gopher tortoise, being of well-known ecological importance (Eisenberg 1983), and the armadillo, classified in Georgia and Florida as an invasive species (FFWCC 2011; GISTF 2011). I compared and contrasted community composition (i.e., species richness and diversity index) and frequency of visitation by vertebrate fauna at gopher tortoise and armadillo burrows by implementing non-invasive, passive-monitoring techniques and evaluating microhabitat variables that could potentially influence burrow visitation and patterns of species nestedness.

Previous methods for investigating burrow dwelling-organisms of armadillo burrows have included active methods such as burrow excavation and using flashlights to search visible portions of burrows (Taber 1945; Clark 1951; Platt et al. 2004); the former being arguably too destructive and laborious, while the latter may not be a thorough enough approach to yield quantitative results. Passive monitoring of gopher tortoise burrows has been utilized in recent years (Alexy et al. 2003; Dziadzio and Smith 2016; White and Tuberville 2017; Knapp et al. 2018), but to date, only one study has used passive monitoring, via camera traps, to investigate vertebrate associates of armadillo burrows (Butler 2020).

Within the last two decades, camera trapping has become a commonly used observational method that has improved our understanding of ecological relationships and allowed researchers to collect data on the behavior of cryptic species that are sensitive to active observational methods (O'Connell et al. 2011). The disruptive nature of the invasive techniques used in previous studies (i.e., burrow excavation and visual observations) to investigate armadillo burrow associates may have resulted in taxonomic bias (Taber 1945; Platt et al. 2004). Because certain taxa may be more sensitive to disturbance and remain undetected when using active observational techniques, the use of camera traps allows improved detection of burrow visitation by vertebrates while minimally disturbing the burrow and surrounding habitat (Caravaggi et al. 2017). Camera traps have also been demonstrated to be a viable alternative to live trapping, allowing for reliable detection of animals without causing physiological stress and while still producing comparable density estimates (Villette et al. 2017). However, there are limitations to using camera traps. For example, collecting data on individual animals is often not possible unless target species possess unique markings (Kolowski and Forrester 2017) and similarities between closely related species hinder accurate identification.

My study incorporated a series of motion-activated camera traps deployed at the entrances of armadillo and tortoise burrows in a study area where gopher tortoises and armadillos co-occur. This method allowed me to test quantitatively for associate species' preference of burrow type and activity status, compare vertebrate assemblages between burrow types and burrows of differing activity statuses, identify shared associate species between burrow types, and assess the influence of various spatial and environmental factors on measures of commensal burrow visitation.

Research on the potential ecological effects of armadillo burrows in the United States has only recently become a topic of interest for ecologists (Butler 2020) and has not been thoroughly investigated. Nevertheless, research on armadillo species in South and Central America has demonstrated their ability to provide numerous ecosystem services (Platt et al. 2004; Aya-Cuero et al. 2017; Rodriquez et al. 2019; Di Blanco et al. 2020). Currently, no studies compare the commensal assemblages between gopher tortoise and armadillo burrows despite the fact that both co-occur throughout the Coastal Plain of the southeastern United States and can occupy the same habitats (Kinlaw 2006; Bhandari 2019). Many studies have documented associate vertebrates of gopher tortoise burrows (Jackson and Milstrey 1989; Lips 1991; Alexy et al. 2003; Smith et al. 2005; Dziadzio and Smith 2016; White and Tuberville 2017). Conversely, very few studies documenting vertebrate utilization of armadillo burrows have mentioned more than one animal associate (Taber 1945; Clark 1951; Platt et al. 2004; Butler 2020). While studies of vertebrate associates of gopher tortoise burrows have documented over 65 vertebrate species

(Jackson and Milstrey 1989; Dziadzio and Smith 2016; White and Tuberville 2017), only one study has reported more than 10 associate vertebrates of armadillo burrows (Butler 2020). The degree to which armadillo burrow commensalism has been understudied may indicate that more research is needed to identify additional vertebrate species utilization of burrows and to determine the ecological significance of these burrows within the armadillo's introduced range.

Comparative studies of burrow-associated species of gopher tortoise and armadillo could provide insight into ecological questions pertaining to the range expansion of the armadillo:

1) Will associate species of tortoise burrows be adequately supported by armadillo burrows in areas with reduced or extirpated tortoise populations? One study found that burrows produced by two different species were not interchangeable options for nesting burrowing owls (*Athene cunicularia*) in South America (Machicote et al. 2004), while another suggests that introduced European rabbits (*Oryctolagus cuniculus*) have, to an extent, replaced the ecological role of locally extinct burrowing mammals in arid regions of central Australia (Read et al. 2008).

2) Will associate species of armadillo and tortoise burrows colonize new areas following the range expansion of the armadillo? For example, burrowing shrimp reportedly facilitated range expansion of a commensal amphipod in tidal flat ecosystems (Tamaki et al. 2018). However, in range expansions that occur along climactic gradients, as is the case for the armadillo, environmental conditions may limit the dispersal of symbionts but not the host organism, causing replacement of symbiont assemblages (Rolshausen et al 2020). This could result in tortoise associates utilizing armadillo burrows in place of species that utilize armadillo burrows in lower latitudes and the possibility of undocumented assemblages of armadillo associates occurring in higher latitudes.

3) If vertebrate communities are dissimilar between gopher tortoise and armadillo burrows, what consequences would an abundance of armadillo burrows have on ecosystems where armadillos have been introduced? Abundance of armadillo burrows could lead to the development of novel networks within ecosystems where new species assemblages and/or altered community compositions may now be supported by burrows constructed by an introduced excavator, which could have unpredictable consequences as new combinations of species co-occur and potentially disrupt delicate ecosystem processes (Hobbs et al. 2006).

Hypotheses

During the preliminary stages of the current study, many of the same vertebrates were observed visiting both armadillo and gopher tortoise burrows, as well as a few that only visited one burrow type. While not all previously documented armadillo burrow associates were observed during the short duration of preliminary data collection, many species that have not been noted in the literature were identified, indicating that more species utilize these burrows than previously assumed. These results may also indicate that some commensals and associates of gopher tortoise burrows could utilize armadillo burrows for the same purposes, with the main implications of this work being that armadillos may aid in supporting local biodiversity in a similar manner as the gopher tortoise despite their classification as an invasive species. Specifically, our study compared associate species visitation between burrow types by using camera trap data to calculate the following response variables: 1) Vertebrate species richness, 2) Shannon-Weiner diversity index, and 3) frequency of vertebrate species visitation.

Burrow visitation between armadillo and gopher tortoise burrows was not expected to be equal for several reasons. Gopher tortoise burrows are similar to armadillo burrows in terms of tunnel height and width but are more spacious, as they are typically much longer and therefore greater in volume (Kinlaw and Grasmueck 2012; Sawyer et al. 2012). Tortoise burrows also may be more easily detectable by associate species, particularly birds, as their burrow aprons are larger and generally composed of light-colored sandy soil (White and Tuberville 2017), as well as being excavated in areas with less dense vegetation than armadillo burrows (Bhandari 2019). Lastly, the fact that gopher tortoises are native to the region and have a long standing co-evolutionary relationship with most associate species observed in this study may play a role in the frequency of vertebrate visitation of burrows.

Community composition was expected to be dissimilar between vertebrate assemblages visiting tortoise and armadillo burrows for many of the same reasons visitation frequency by associate species was expected to be unequal between burrow types: burrow size differences, potential differences in microhabitats of burrow locations between tortoises and armadillos (Bhandari 2019), large burrow aprons of tortoise burrows serving as a visual cue to associate species, and differences in co-evolutionary history between the local species pool and the two excavators.

Microhabitat characteristics were expected to influence vertebrate assemblages visiting burrows (Di Blanco et al 2020). Specifically, species richness and biodiversity were expected to be highest near habitat edges where there is a greater diversity of foundation species (i.e., trees, shrubs, and other vegetation) (Harris 1988), as habitat edges in this study were ecotonal habitats between pine and hardwood forests. Additionally, I expected variables relating to thermal stress (i.e., high light intensity, low vegetative density, and low canopy cover) to influence burrow visitation by temperature and moisture sensitive species (i.e., reptiles and amphibians). Specifically, burrows in areas with low shade and high light intensity are expected to have higher visitation by herpetofauna.

In ecology, nestedness is a concept relating to processes that determine community composition, generally when comparing high richness communities to low richness communities and is typically based on one or more environmental variables that relate to distance or habitat quality (Atmar and Patterson 1993; Almeida-Neto et al. 2008). A system is considered nested if there is an ordered decrease in species richness and abundance observed across sampling locations that corresponds to a variable relating to species dispersal potential or habitat suitability. The distance of a habitat from source areas, habitat patch size, and degree of isolation are examples of variables that influence nested patterns (Wright et al. 1998). Treating monitored burrows in the pine stand as insular units, I expected to detect nested patterns based on increasing distance from habitat edges as well as with decreasing values of burrowing intensity. Distance from pine stand edges was expected to produce a nested pattern across community assemblages due to the expectation that species richness would be highest near habitat edges, much in the way that the mainland is expected to have the highest species richness in island biogeography (McArthur and Wilson 1963) and would show an ordered decrease when moving toward the interior of the study site. Burrowing intensity was used in this study as a measure of isolation, with burrows in lower intensity areas considered more isolated than those in high intensity areas. The higher intensity areas should produce a nested pattern because dispersal of vertebrate associates between burrows would be more likely to occur in areas with greater burrow availability.

I examined the following hypotheses: H1) burrow visitation by associate species is not equal between tortoise and armadillo burrows; H2) community composition is not equal between tortoise and armadillo burrows; H3) burrow type, activity status, location, and microhabitat characteristics have an effect on burrow visitation by associate species; and H4) patterns of nestedness coincide with spatial attributes of burrows within the study area.

Methods

A. Study Site

Data were collected in a mixed-pine and hardwood stand (hereafter, “pine stand”) at the Lake Louise Field Station (LLFS) in Lowndes County, Georgia (Fig. 2). LLFS is a 76.9-hectare plot of land located in a rural area 15 kilometers south of Valdosta State University. The defining feature of the property is a 5.7-hectare lime-sink pond on the southwest part of the property known as “Lake Louise.” The lake is located immediately west of Interstate 75, the latter of which comprises the western border of LLFS. Several habitat types occur within LLFS including: an Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, and Baygall; a Gulf and Atlantic Coastal Plain Swamp System; and a Southern Atlantic Coastal Plain Wet Pine Savanna and Flatwoods (Riggs et al. 2010). The study area within LLFS was a 10.4-hectare section of forest located north of the lake and west of the main entrance off Touchton Road, consisting predominantly of slash pine (*Pinus elliottii*) and loblolly pine (*P. taeda*). Hardwood encroachment [by water oak (*Quercus nigra*) and, to a lesser degree, by southern live oak (*Q. virginiana*)] occurred along the margins of the stand, with some pockets of hardwoods in the interior. The northwest sector was generally more open and xeric, containing an understory with more grasses, sedges and forbes. Otherwise, the understory was highly variable, consisting of hardwood saplings and small shrubs, including *Vacinuum* spp., *Asimina augustafolia*, and *Myrica cerifera*. Hardwood forest surrounded the pine stand on all sides and was partitioned from the study area by a dirt road. Predominate hardwood species in the surrounding forest were southern live oak, water oak, southern red oak (*Q. falcata*), black cherry (*Prunus serotina*), pignut hickory (*Carya glabra*), and American sweetgum (*Liquidambar styraciflua*).

The study area was heavily modified during the twentieth century, being used for agriculture, turpentine production, and logging (Riggs et al. 2010). Most notably, aerial photos indicate that it was used as an agricultural field up until the 1940s and was subsequently scatter planted with slash and loblolly pine, with the exception of a portion of the northeastern sector that was not part of the field and contains a higher density of older growth oak and hickory compared to the rest of the pine stand. Prescribed burning, conducted at intervals of one to five years, is now used to maintain the pine stand. The stand was first burned in 1998 and subsequently in 2000, 2005, 2006, 2010, 2014, and 2019.

Evidence of armadillo activity existed throughout LLFS, as many burrows and foraging depressions were found in the hardwood forest surrounding the pine stand. However, the hardwood forest was not surveyed, and these burrows were not included in this study. Gopher tortoises were mostly restricted to the pine stand due to preference for loose sandy soils that are required for burrowing, and open-canopy habitat that facilitates thermoregulation and nest incubation (Auffenburg and Franz 1982; Diemer 1986). Both species excavate burrows and co-occur within the pine stand.

B. Survey

Following the prescribed burn of 2019, the pine stand was exhaustively surveyed for tortoise and armadillo burrows. Four surveys took place from April and May of 2019. During each survey, one to two teams of two observers, spaced several meters apart, walked the length of the stand, in overlapping belt transects, searching along a north-south bearing.

Three burrow types were present in the study area: armadillo, tortoise, and co-opted. Burrows were differentiated by the presence of an apron and shape of the burrow entrance. Tortoise burrows were identified by their characteristic half-moon shaped entrance (Fig. 3B) and age class (i.e., hatchling, juvenile/subadult, or adult) which was determined by entrance size (Doonan and Stout 1994). Armadillo burrows were identified as having a circular to ovular entrance (Fig. 3A) (McDonough et al. 2000; Sawyer et al. 2012). Age class was not taken into account as this species only constructs burrows once it is nearly adult size (McDonough et al. 2000). Co-opted burrows were those that were first excavated by a tortoise but had been taken over and maintained by an armadillo and were typically characterized by the presence of pine straw and other dried vegetation lining the burrow entrance and modifying it into a circular shape. However, due to the low abundance of co-opted burrows in the study area, they were excluded as a category for monitoring but were included as data points in burrowing intensity calculations described later.

I included burrow activity status as a categorical variable in certain analyses; four categories of activity status were recorded: active, inactive, abandoned, and uncertain. Activity statuses were determined for both burrow types using criteria from Cox et al. (1987). Active burrows were considered those with freshly disturbed soil at the burrow mouth. Inactive burrow entrances did not contain disturbed soil but retained their shape and the apron did not exhibit an overabundance of vegetation. Abandoned burrows had severely degraded or misshapen entrances with an excess of vegetation present on the apron or were partially collapsed. If activity status could not be agreed upon by both observers in the survey team, the burrow activity status was recorded as “uncertain”. Due to the high degree of changing activity statuses (i.e., active burrows becoming inactive and vice versa) observed during preliminary data collection, active and inactive burrows were grouped into a single category named “possibly occupied”. Therefore, in my analyses there are two categories for burrow activity status: possible occupied and abandoned. There were no instances of uncertainty when differentiating between abandoned and possibly occupied burrows.

All burrows were marked with a metal tag displaying a unique identification number at ground level on the right side of the entrance. Brightly colored ground flags displaying the burrow’s identification number, burrow type, and activity status were placed directly adjacent to the metal tag and fluorescent pink flagging tape was tied to the nearest eye-level vegetation. Burrow locations were georeferenced in Universal Transverse Mercator (UTM) coordinates with 200 fixes per burrow using a centimeter grade Trimble Geoexplorer 6000 Series (GeoXT) handheld GNSS unit. Coordinate data were post-processed using Trimble GPS Pathfinder Office software, and then exported in a database format containing the following information: burrow identification number, burrow type, activity status, UTM coordinates, and relevant comments [e.g., if armadillo burrows were feeding burrows (i.e., excavations made during foraging < 25cm in length) and age class of tortoise burrows if they were not adult size].

C. Camera Trap Configuration

Camera traps were used to monitor entrances of 10 tortoise and 10 armadillo burrows (N = 20) from October 2019 to December 2020. At each burrow entrance we placed a Bushnell NatureView HD Cam (Model# 119740) with a 16 or 32 gigabyte SD card. The NatureView HD

Cam was chosen for its unique external viewing feature that shows a first-person view through the camera's lens displayed on a handheld screen that is separate from the camera itself. This provided greater precision of lens orientation during camera trap deployment and data retrieval. Using the external viewer during camera placement, I was able to ensure that the burrow entrance was the focal point of the camera's field of view and that surrounding ground would be visible in all directions from the entrance to maximize observations of vertebrate visitation of burrows.

Camera mounts consisted of 40 to 45 cm sections of 2x4 (inch) mounting board with a 2.5 cm hole drilled near each end of the 4-inch side, 100 cm lengths of 1.2 cm diameter PVC pipe inserted into each pre-drilled hole, and 7.6 cm wood screws fastening the PVC to the mounting board (Fig. 4). The length of board used for the mount depended on the width of each monitored burrow. Most tortoise burrows required a camera mount with a 45 cm mounting board while most armadillo burrows, being narrower, only required a 40 cm board. Cameras were fastened to the underside of the mounting boards using a canvas belt threaded through two eyelets on the back of the camera housing. Belt eyelets were not equidistant between the top and bottom of the cameras but were slightly closer to the top causing the bottom end of the cameras to progressively sag over time, altering the camera's field of view. To mitigate this, a zip tie was used to loosely fasten the bottom end of the camera to the mounting board which stabilized cameras and prevented sagging for consistently accurate lens orientation throughout the monitoring period.

D. Sampling

To distribute camera traps evenly across the study area and promote spatially independent sampling, we developed a random burrow selection function which we applied in conjunction with a quadrat system using custom scripts in R (v. 4.0.4, R Core Team 2021). The quadrat system was created by reading in a shapefile of the pine stand boundary using the R package, ‘rgdal’ (Bivand et al. 2021), then overlaying a 3x4 quadrat grid using the “quadrats” function within the R package ‘spatstat’ (Baddeley et al. 2015). Quadrats 8 and 11 were combined along with quadrats 9 and 12 due to the small area of quadrats 11 and 12 (Fig. 5). Survey data were then divided into subsets of burrows based on the quadrat where they were found, and the random selection function was employed to select one armadillo burrow and one tortoise burrow for monitoring within each quadrat.

Activity status of selected burrows was alternated so that a possibly occupied and an abandoned burrow would be monitored within each quadrat. This sampling technique was to assess variation in commensal use between burrow types as well as examine variation in commensal use between activity statuses. In total there were four categories of burrow type and activity status combination with five replicates of each.

Because larger burrow entrances are correlated with longer burrow lengths (Hansen 1963), only adult tortoise burrows (entrance width > 23 cm; Alford 1980) were considered eligible for monitoring in order to obtain the greatest diversity and visitation frequency estimates. Similarly, for armadillos, the distinction between feeding burrows and shelter/nest burrows was made in the survey data and only shelter or nest burrows (length > 25cm; McDonough et al. 2000) were chosen for monitoring.

Camera trigger parameters were standardized across all cameras (Table 1). Cameras were set to operate 24 hours per day and image format was set to full screen. Hybrid mode was applied, which allowed cameras to record images and videos during each trigger. Image size was set to eight megapixels and video size was set to 1920x1080 pixels per frame with each trigger producing two still images and a 10-second video with a two second interval (i.e. wait time before next trigger can occur) between triggers. Trigger sensitivity was set to low to avoid an overabundance of false triggers leading to a depletion of SD card storage and battery life. However, even at low sensitivity, cameras were triggered by small insects. To reduce the number of blurred images, the night vision shutter was set to its maximum speed. LED control was set to low to minimize flashes reflecting from sandy soil, which was further reduced by covering the flash of each camera with yellow electrical tape. All images and videos were time stamped and display the unique identification name of the camera.

Camera traps were checked every two to four weeks. SD cards were exchanged if a camera had taken over 200 photos and videos, if the camera had malfunctioned since the previous check, or if the SD card had not been exchanged in two or more checks. All photos and videos were reviewed by eye. During photo review, vertebrate animals were identified to species, when possible, using field guides or confirmation from experts.

Due to the limited inclusion of surrounding ground around burrows in the camera's field of view (~ 15 cm), we considered any vertebrate present in an image or video to be utilizing the burrow in some way. Many photos could not be identified to species due to poor image quality or the identifying characteristic of the animal being out of frame. In these instances, images were only identified to class. We were also not able to identify mouse, skink, and shrew observations to species level for various reasons. Mouse observations were pooled because they were primarily active during night hours, thus identifying characteristics were obscured by low quality night-vision images. Possible mouse species that have been reported utilizing tortoise burrows and occur in South Georgia are the oldfield mouse (*Peromyscus polionotus*), cotton mouse (*Peromyscus gossypinus*), house mouse (*Mus musculus*), and golden mouse (*Ochrotomys nuttalli*) (Jackson and Milstrey 1989; Dziadzio and Smith 2016). Skink observations were also pooled due to the similarity in coloration of juvenile life stages of the three common species occurring in South Georgia; the broadheaded skink (*Plestiodon laticeps*), common five-lined skink (*Plestiodon fasciatus*), and the southeastern five-lined skink (*Plestiodon inexpectatus*) (University of Georgia 2021). Lastly, shrews were not identifiable from images because distinguishing characteristics (i.e., belly and tail coloration and dentition) were not visible in camera trap images. However, it is of note that all shrews observed in this study had short tails that appeared to be less than one inch in length. Therefore, possible shrew species were the southern short-tailed shrew (*Blarina carolinensis*) and the least shrew (*Cryptotis parva*) as they are the only short-tailed shrews occurring in the region (Reid 2006).

Camera trap photos and videos were sorted into directories formatted for compatibility with the R package “camtrapR” (Niedballa et al. 2016). Directories consisted of a network of nested file folders where each burrow was represented with a unique folder labeled with its respective burrow identification number. Within each burrow folder were subfolders for each species observed at that location. During the image sorting process, photos were placed into the correct species folder within the correct burrow folder to construct the directory. A database was generated from the directories using the ‘recordTable’ function in “camtrapR”.

D. Environmental Data

Microhabitat variables were included in our multivariate analyses to identify environmental factors that influence commensal use. Variables were chosen based on microhabitat characteristics that influenced burrow site selection from Bhandari (2019) and included: light intensity, distance from the nearest habitat edge, canopy cover, and percent visibility surrounding burrow entrances. Additional variables expected to influence commensal use of burrows included burrow type, easting, northing, burrowing intensity, vegetative density, richness of tree species, proportion of hardwood trees, relative abundance of excavator species (i.e., frequency of visitation by tortoises and armadillos), and initial activity status (activity status of burrow during the 2019 burrow survey).

Light intensity was measured using a lux meter. Lux was measured at ground-level over the burrow entrance and again at 2.5 meters from the entrance to the north, south, east, and west. Measurements were taken over a one-week period, after camera trapping was completed, on clear sunny days between 12PM and 2PM to ensure the highest possible light intensity would be recorded. The five lux measurements were averaged for each burrow before incorporation into our analyses. Canopy cover was visually estimated as a proportion at monitored burrows using a canopy densitometer. Five canopy cover estimates were taken at each burrow location; from directly above the burrow entrance, and again, from 2.5 meters to the north, south, east, and west of the burrow and averaged for analyses.

Burrow visibility was estimated using a 43 x 31 cm black and white checkerboard. The checkerboard was placed at the entrance at ground-level of each monitored burrow and visibility was calculated as the percent of visible black squares. Four visibility percentage estimates were taken at 5 m from north, south, east, and west of each burrow and averaged then converted to a proportion. Mean proportion estimates of visibility were used in analyses.

Burrowing co-intensity was calculated by creating a point pattern of burrow locations then using the ‘density’ function in “spatstat” (with the default method of bandwidth selection based on the study area geometry) to return a kernel-smoothed surface representing the co-intensity of burrowing at each burrow location (i.e., number of burrows per hectare) (Fig. 6). Burrowing co-intensity values at monitored burrows were extracted from this data set and used as a covariate in our analyses. Because our goal was to measure overall burrowing activity by both species in different areas, hatchling and juvenile gopher tortoise burrows were included in intensity calculations (Cox et al. 1987).

Distance from the nearest habitat edge was calculated using the ‘nncross’ function in “spatstat”. In our case the function was used to measure the distance between each burrow location in the point pattern and the line segment pattern that was derived from the shapefile representing the pine stand boundary. Distance from the nearest habitat edge was included as a covariate because the pine stand’s edges represent the boundary between pine forest and hardwood forest where we expected the highest values of commensal use to occur. We also expected a negative relationship between commensal use of burrows and greater distances from habitat edges.

Vegetative density measurements at burrow locations were derived from LiDAR data, downloaded as a LAS file from the National Oceanographic and Atmospheric Administration (NOAA) Office for Coastal Management. LAS file data were processed in ArcGIS 10.4.1, with the aid of the LAS Point Statistics as Raster utility and Spatial Analyst Toolbox. Vegetative density was measured as the proportion of above ground returns in 10x10 m pixels. The vegetative density raster was saved as TIFF file, imported into R via the “rgdal” package, and then into “spatstat” where vegetative density data were extracted to each camera position.

Values of tree species richness and proportion of hardwood species were generated using universal Kriging interpolation of lattice data collected at 186 points within the pine stand (Oliver and Webster 1990). Kriging interpolation is used to predict data values at unsampled locations by using data from adjacent sampled locations. Interpolated surface maps of tree richness and hardwood proportion were created using the ‘krige’ function within the R package “gstat” (Pebesma 2004). Kriging interpolated surface maps were converted to raster layers and values at burrow locations were extracted using the ‘extract’ function in the package “raster” (Hijmans 2020).

E. Statistical Analysis

Commensal use of burrows was used as the response variable to examine associations with selected environmental variables in our analyses. Commensal burrow use was quantified in four ways: 1) species richness, 2) visitation frequency (counts) 3) Shannon-Weiner diversity index, and 4) relative abundance index (RAI). Mean values are displayed in the results in parentheses followed the standard error.

Species richness was calculated by summing the number of species observed at a burrow entrance during the sampling period. Visitation frequency was calculated for each species by summing the number of independent visitation events per burrow. We considered a single visitation event as the presence of any vertebrate captured on camera at a burrow entrance. Due to the inability to distinguish individuals for most associate species, consecutive observations of conspecifics were condensed to a single event for subsequent triggers occurring within 10 minutes of the previous trigger. Visitation frequency data were used to calculate guild- and class-level visitation frequency as well as total commensal visitation for each monitored burrow. Shannon-Weiner diversity was calculated from visitation frequency data using the ‘diversity’ function in the R package “vegan” (Oksanen et al. 2020). Shannon-Weiner diversity was included as a response variable because it is a metric influenced by both richness and evenness of species’ abundance. Therefore, rare species will have less influence on the measure of diversity than they will on species richness. A relative abundance index (RAI) representing the number of burrow visits per 100 trap nights was calculated for each species by dividing the number of independent visitation events by the number of trap nights then multiplying by 100 (O’Brien et al. 2003). Species RAIs were calculated at two levels: on a burrow-by-burrow basis and by pooling observations for each burrow type.

Differences in Commensal Visitation Between Burrow Types

Due to species richness at armadillo burrows being non-normally distributed, richness between burrow types was compared using a Mann-Whitney U test. Shannon-Wiener diversity indices were normally distributed for both burrow types and a Welch’s two-sample t-test was used to compare mean diversity of visitation between armadillo and tortoise burrows. To test for differences in total commensal visitation between burrow types, as well as differences in commensal visitation at guild, class, and species levels, we tested for fit to a proportional model using the Chi-square goodness of fit test, where expected counts were based on the proportion of total trap nights for each burrow type. The null hypothesis was that frequency of commensal visitation would fit a proportional model when comparing between burrow types. For these analyses, all observations of burrow specific excavator species (i.e., tortoises at tortoise burrows and armadillos at armadillo burrows) were removed from the data set so that only observations of associate species remained. For guild-level comparisons each associate species was assigned to its respective guild (i.e., carnivore, granivore, herbivore, insectivore, or omnivore) and visitation events for each guild were summed. Guilds were determined using species information from animaldiversity.org (University of Michigan 2020). Taxonomic classes of associate species included mammals, birds, reptiles, and amphibians. Due to the low number of amphibian observations ($N = 4$), reptiles and amphibians were grouped into one category named “herpetofauna”. Species that could only be identified to class level were included in the data for total commensal use and class-level commensal use but were removed from data used to compare commensal use by guilds. Variation in sampling effort was accounted for by setting the proportion of total trap nights for each burrow type as the probability argument in the ‘chisq.test’ function in R.

Because expected counts were low for some guilds, *P*-values were calculated via Monte Carlo simulation (rather than the Chi-square distribution). The number of trap nights were randomly sampled from individual burrows 999 times to generate expected frequencies of visitation for each species per burrow type under a proportional model. Expected frequencies were then compared to observed frequencies to calculate X^2 scores and *P*-values. For species that had less than five observations at one or both burrow types we used two tailed binomial tests, setting the number of successes as the number of observations at tortoise burrows and setting the probability of success as the proportion of trap nights at tortoise burrows. Rare species (i.e., species with less than five total observations) were not included in this test.

Community Dissimilarity

In order to decipher whether armadillo and tortoise burrows have the potential to support similar communities of vertebrates we used distance-based measures of dissimilarity between the two burrow types (Bray and Curtis 1957). A data matrix of Bray-Curtis dissimilarity values was generated using the ‘metaMDS’ function from the “vegan” package in R. This function calculates pairwise dissimilarity values for each possible pair of monitored burrows in the study area by comparing the community composition between all burrows. For this test we used RAI data to standardize rates of species detections based on sampling effort.

Significance testing was done using a permutational analysis of variance (PERMANOVA) specific to distance matrices. We used the ‘adonis’ function in the “vegan” package with 999 permutations to test if mean dissimilarity between armadillo and tortoise associate species communities was significantly different from random. An assumption of this test is that there is homogeneity of multivariate dispersion, thus a test for inhomogeneity of multivariate dispersion was conducted using the ‘anova’ function in conjunction with ‘betadisper’ on the dissimilarity distance matrix before running the PERMANOVA.

Environmental Characteristics’ Influence on Commensal Visitation

I used correlational principal components analyses (PCA) to visualize relationships between predictor variables as well as response variables. I also generated a correlation matrix to measure the magnitude of Pearson’s product moment correlation coefficients between all predictor and response variables using the ‘cor’ function in R. Canonical correspondence analysis (CCA) was used to identify relationships between each burrow associate species and environmental variables and to determine how much variance in species data was explained by these variables (Ter Braak 1986). This was accomplished using the ‘cca’ function within the R package “vegan”.

To quantify the effect of changes in predictor variables on commensal visitation of burrows, we used both generalized linear models (GLMs) and linear models (LMs), depending on the type of response variable. Environmental variables included for our models were burrow type, Easting, Northing, distance from the nearest habitat edge (in meters), burrowing co-intensity, excavator species RAI (RAI of combined observations of armadillos and tortoises at each burrow), light intensity, proportion of canopy cover, proportion of visibility at 5 m, vegetative density, tree species richness, and proportion of hardwood trees. Response variables tested against environmental predictor variables in our models were species richness, Shannon-Wiener diversity, and total commensal visits. Additional GLMs included response variables at the guild and class level. Total number of visits from guilds and classes were tested independently against environmental predictor variables. Log trap nights were included as an offset term in all models that used count data as a response variable to account for variation in sampling effort.

Stepwise model selection was conducted using Akaike Information Criterion (AIC) (Akaike 1974). We accomplished this by first running GLMs and LMs that included the full set of environmental predictor variables using the ‘glm’ function in base R (R Core Team 2021). We then passed each GLM and LM to the ‘stepAIC’ function from the R package “MASS” (Venables & Ripley 2002). This function reduces the number of variables included in a model using stepwise forward and backward model selection and retaining only the predictor variables that are informative.

Meta-Community Nestedness

Nestedness analyses are applied to insular systems in island biogeographic studies where a system is considered perfectly nested if there is an ordered decrease in species richness from areas of high richness to areas of low richness with each sampling location containing only a subset of species that were present in the previous sampling location (Ulrich et al. 2009). These analyses are helpful in making predictions on the order of species extinction and recolonization, as well as identifying barriers to dispersal, across island archipelagos and habitat fragment networks (Atmar and Patterson 1993). In the current study, burrows were treated as insular units in a semi-xeric environment and nestedness was tested based on increasing distance from the pine stand edges (distance), decreasing burrowing intensity (degree of isolation), increasing vegetative density (habitat quality), and increasing proportion of hardwood trees (habitat quality).

Using site specific species RAI data, I tested for patterns of nestedness using a recently developed technique: nestedness metric based on overlap and decreasing fills (NODF) (Almeida-Neto et al. 2008). NODF measures the degree of overlap in species abundances as well as the decrease in species richness between sampling locations with data frames being ordered by a particular environmental variable. I performed four nestedness analyses with sampling locations ordered by: increasing distance from the nearest edge, decreasing burrowing intensity values, increasing degree of vegetative density, and increasing proportion of hardwood trees.

I used the 'nestednodf' function within the R package "vegan" to calculate nestedness values and the 'oecosimu' function to develop a null model for comparison and significance testing by specifying "swsh_samp" for the "method" argument and setting this function to generate 999 simulated random communities from the data set via permutation. The "alternative" argument within the ‘oecosimu’ function was set to “greater” which prompted this function to only test for a greater-than-expected pattern of nestedness when compared to a fully random pattern.

Results

A. Survey Data

A total of 234 burrows were recorded within the pine-stand during the post-burn burrow survey. The majority of burrows were armadillo (N = 145; 61.96%) with tortoise burrows being less numerous (N = 82; 35.04%). Only seven co-opted burrows (3%) were found.

Of the tortoise burrows, 57 (69.5%) were initially identified as possibly occupied with 37 active (45.1%) and 20 inactive (24.4%) (Fig. 7B). Seventeen abandoned tortoise burrows (20.7%) were identified during the survey and activity status was uncertain for the remaining eight (9.8%). Adult tortoise burrows (i.e., entrance width > 23 cm) comprised 65.9% of all tortoise burrows (N = 54), while 26.8% were juvenile/subadult burrows (N = 22), and 7.3% were hatchling burrows (N = 6).

For armadillo burrows, possibly occupied was also the most abundant activity status category with 108 (74.5%) burrows, where 26 (17.9%) were active and 82 (56.6%) were inactive (Fig. 7A). Twenty-five (17.2%) armadillo burrows were identified as abandoned and activity status was uncertain for 12 (8.3%). Of the seven burrows that were co-opted by armadillo from the gopher tortoise, three (42.9%) were possibly occupied with one active (14.3%) and two inactive (28.6%) and activity status was uncertain for the remaining four burrows (57.1%).

B. Camera Trap Data

Camera traps were operational for a total of 7064 trap nights over the 14-month sampling period. Sampling effort varied across stations due to camera malfunctions, battery depletion, and user error. Trap nights per station ranged from 174 to 405 days (353.2 ± 14.37).

Camera traps produced a total of 36604 images and 18302 videos representing 18302 camera triggers comprising 7281 independent burrow visitation events from 40 vertebrate species (Table 2). Of these visitation events, 6991 produced images and videos of vertebrates that could be identified beyond taxonomic class. Overall, 14 mammal, 14 bird, 9 reptile, and 3 amphibian species were observed interacting with burrows, comprising 64.5%, 14.4%, 21%, and 0.05% of total visitation events, respectively. Species from five guilds were observed: carnivores (1.4%), granivores (0.4%), herbivores (17.3%), insectivores (17.9%), and omnivores (62.8%). In addition, images and videos revealed 11 species that have not yet been documented utilizing armadillo burrows and four species that have not been documented utilizing tortoise burrows (Table 2).

Visitation was highest at tortoise burrows for both the burrow engineer and commensal visitation. However, there was greater variation in tortoise burrow visitation when compared to visitation at armadillo burrows. A total of 4638 visitation events occurred at tortoise burrows while 2643 occurred at armadillo burrows, with a respective 3678 and 2459 events being from associate fauna (i.e., vertebrate species other than the respective burrow excavator). Total visitation events per burrow (including visits from respective excavator species) ranged from 48 to 1372 across all burrows (363.8 ± 63.87), 48 to 585 for armadillo burrows (264.1 ± 47.24), and 59 to 1372 for tortoise burrows (463.5 ± 113.07) (Table 3). Associate visitation events ranged from 46 to 655 across all burrows (306.85 ± 37.87), 46 to 554 for armadillo burrows (245.9 ± 46.05), and 57 to 655 for tortoise burrows (67.8 ± 55.77) (Table 3).

Species richness and Shannon-Weiner diversity were highest for tortoise burrows and showed greater variation than armadillo burrows, the latter of which were more uniformly distributed in these metrics. Pooled species richness (across all burrows for each excavator) equaled 31 for armadillo burrows and 37 for tortoise burrows. For individual burrows, species richness ranged from 10 to 25 for both species, combined (15.9 ± 0.82), 12 to 17 for armadillo burrows (4.5 ± 0.67), and 10 to 25 for tortoise burrows (17.3 ± 1.41) (Fig. 10). Twenty-eight species were observed utilizing both burrow types, while three species were only observed at armadillo burrows and nine species were only observed at tortoise burrows (Table 2). Shannon-Weiner diversity ranged from $H = 1.2$ to $H = 2.24$ across all burrows (1.78 ± 0.06), $H = 1.49$ to $H = 2.09$ across armadillo burrows (1.77 ± 0.06), and $H = 1.2$ to $H = 2.24$ across tortoise burrows (1.79 ± 0.11).

The most frequently observed taxa across all burrows were mice (RAI = 36.65, 37.03%), gopher tortoise (RAI = 15.15, 15.3%), and hispid cotton rat (*Sigmodon hispidus;* RAI = 11.98, 12.1%). At armadillo burrows the most observed associate species were mice (RAI = 27.06, 41.6%), hispid cotton rat (RAI = 11.43, 17.5%), and Carolina wren (*Thryothorus ludovicianus*; RAI = 5.91, 9.1%) while the most observed associate species at tortoise burrows were mice (RAI = 47.74, 42.4%), armadillo (RAI = 12.73, 11.3%), and hispid cotton rat (RAI = 12.61, 11.2%). Armadillos were a frequent user of tortoise burrows and although tortoises were occasional users of armadillo burrows the frequency of visitation was low compared to most burrow associates.

Few species using burrows in our study site were of conservation concern. Most notably, the gopher tortoise, listed as vulnerable by the IUCN, was the most frequently observed species of conservation concern (N = 1070) and was observed interacting with both burrow types. Other species of conservation concern observed in this study were the northern bobwhite (*Colinus virginianus*; near threatened; N = 23) and the eastern box turtle (*Terrapene carolina*; vulnerable; N = 8) both of which were observed at both burrow types.

C. Multiple Individuals

Two or more individuals were present in images and videos from 85 burrow visitation events. Fifteen events of multiple individuals occurred at armadillo burrows while 70 occurred at tortoise burrows. Eighty-three events of multiple individuals were conspecific and contained two or more individuals of the following species: armadillo, bobcat, Carolina wren, hispid cotton rat, mouse spp., northern bobwhite, raccoon, skink spp., and tortoise. The most frequently observed conspecific event was two tortoises present at tortoise burrows (N = 25) which included images and videos of tortoises fighting (8/25) as well as mating attempts (13/25). The highest number of individuals present in a conspecific event was six northern bobwhites, which occurred at tortoise burrow #2119 potentially due to this burrow having much greater than average visitation by gopher tortoises, thus being well maintained, and being located in an area with low canopy cover and high light intensity. Conspecific events at armadillo burrows included two or more individuals of the following species: armadillo, bobcat, Carolina wren, hispid cotton rat, mouse spp., and skink spp. The most frequently observed conspecific event at armadillo burrows was two mice (N = 6) and the most individuals present simultaneously was three mice. Only two interspecific visitation events occurred during the monitoring period: a Carolina wren and tortoise present at tortoise burrow #2119 and an unidentified frog sp. and hispid cotton rat seen together at tortoise burrow #90.

D. Comparison of Species Richness, Diversity, and Visitation Frequency

Mean Comparisons

Mean species richness between armadillo and tortoise burrows (Fig. 8A) could not be compared with a parametric test due to armadillo burrow richness not being normally distributed, even after log transformation. Nonetheless, a Mann-Whitney U test revealed no significant difference in median species richness between burrow types (U = 29.5, $P = 0.1$). The null hypothesis of equal variance in diversity indices could not be rejected at a significance level of 5% based on the *F*-test (F = 0.28, df = 9, $P = 0.07$). Shannon-Weiner diversity (Fig. 8B) was not statistically different between burrow types (t = -0.13065, df = 18, $P = 0.8$). Additionally, variance in species richness and biodiversity was greater for tortoise burrows when compared to armadillo burrows which were more consistent in these metrics.

Comparisons of Burrow Visitation Frequency

There was strong evidence against a proportional model for total commensal visitation to each type of burrow ($X^2 = 453.46$, df = 1, $P = < 0.001$), with visitation frequency much higher than expected at tortoise burrows ($r_p = 15.59$) and lower than expected at armadillo burrows ($r_p = -14.5$) (Table 4). Class (Fig. 9A) and guild-level (Fig. 9B) comparisons of commensal visitation frequencies were all significantly higher than expected at tortoise burrows and lower than expected at armadillo burrows (Table 4), with the exception of herbivores ($X^2 = 10.2$, df = 1, $P =$

0.001) and herpetofauna (X^2 = 4.06, df = 1, P = 0.04), which both had higher than expected frequencies at armadillo burrows (r_p = 2.17 and r_p = 1.37, respectively) and lower than expected frequencies at tortoise burrows (r_p = -2.34 and r_p = -1.48, respectively). However, Chi-square Goodness-of-Fit results for herbivore and herpetofauna visitation can be attributed to one individual tortoise that took up residence in armadillo burrow #2382 and increased visitation frequencies for these categories by 108 observations between the 12th and 29th of June 2020. These data were considered outliers and when tortoise observations from armadillo burrow #2382 from this time period were removed from herbivore and herpetofauna counts at armadillo burrow #2382, visitation frequency for herbivores (X^2 = 16.99, df = 1, P < 0.001) and herpetofauna (X^2 = 5.79, df = 1, P = 0.01) was higher than expected at tortoise burrows (r_p = 3.02 and r_p = 1.76, respectively) and lower than expected at armadillo burrows (r_p = -2.81 and r_p = -1.64, respectively).

For class-level visitation frequencies (Table 4), the deviation between expected and observed frequencies was highest for mammals (X^2 = 424.94, df = 1, P = < 0.001) and birds (X^2 = 105.01, df = 1, P = < 0.001), both of which were observed at higher than expected frequencies at tortoise burrows (r_p = 15.09 and r_p = 7.5, respectively) when compared to armadillo burrows (r_p = -14.04 and r_p = -6.98, respectively).

For guild-level frequencies (Table 4), the deviation between expected and observed frequencies was highest for omnivores (X^2 = 419.2, df = 1, P < 0.001) and insectivores (X^2 = 88.708, df = 1, P < 0.001) with both guilds having higher than expected frequencies at tortoise (r_p = 14.99 and r_p = 6.89, respectively) versus armadillo (r_p = -13.94 and r_p = -6.41, respectively) burrows.

For individual species, comparisons of visitation between burrow types revealed significantly higher than expected visitation frequency ($P < 0.05$) at tortoise burrows for 15 species (Table 5). Eleven species were not observed at higher-than-expected frequencies ($P > 0.05$) at either burrow type, and the remaining 14 species were too rare ($N < 5$) for inclusion in these tests.

E. Community Dissimilarity

Non-metric multidimensional scaling (NMDS) via ‘metaMDS’ implemented a square root transformation on the Bray-Curtis dissimilarity matrix of burrow community composition. Twenty runs were produced, and a solution was reached after the 20th run with a high stress value of 0.22. To assess the assumption of homogeneity of multivariate dispersion required for PERMANOVA, we employed the ‘anova’ and ‘betadisper’ functions together on our Bray-Curtis dissimilarity matrix; a multivariate analog to Levene’s test for equal variance. The null hypothesis of equal variance of dissimilarity between burrow types could not be rejected ($P = 0.4$) and our data was considered appropriate for NMDS. Spider plot centroids representing mean dissimilarity scores obtained from community RAI data showed minimal separation. This result shows that there was little dissimilarity between armadillo and tortoise burrow community assemblages. The *P*-value obtained from PERMANOVA was near significant at 0.08 and substantial overlap between point clouds representing armadillo and tortoise burrow communities was observed in our plot (Fig. 11).

Tortoise burrow communities showed greater variance in species composition than armadillo burrow communities. The degree of spread observed in spider plot point clouds was wider for tortoise burrow communities when compared to armadillo burrow communities, meaning tortoise burrows supported a wider array of vertebrate assemblages.

F. Environmental Factors' Effects on Commensal Visitation

In the canonical correspondence analysis (CCA) biplot, burrow visitation for many species was shown to be associated with one or more environmental variables (Fig. 12A). A second biplot shows the variation among monitored burrow locations with respect to environmental variables (Fig. 12B). Total inertia for the CCA model was 0.83 and constrained inertia was 0.74. This result suggests that 74% of variance in species data had the potential to be explained by the included environmental variables and of that percentage, our model accounted for 83% of explainable variance in species occurrences. The CCA axes 1 and 2 had eigenvalues of 0.41 and 0.11, respectively, showing that 52% of variance in species occurrences was explained by the first two CCA axes. Several environmental variables contributed significantly to the variance in species data, including initial activity status ($P = 0.01$), easting ($P = 0.002$), northing ($P = 0.01$), distance from the nearest edge ($P = 0.002$), average light intensity ($P = 0.02$), canopy cover ($P = 0.02$), and relative abundance of excavator species ($P = 0.003$).

Strong correlations were discovered between predictor and response variables in a correlation matrix displaying all relationships between variables in the study (Fig. 13). Most notably, a strong positive correlation was detected between excavator species RAI and bird visitation ($r = 0.82$, df = 18, $P < 0.001$). Associations among predictor variables and response variables were investigated using correlational principal components analyses (PCA). In the PCA for predictor variables (Fig. 14A) the first two principal components (PCs) accounted for 41% of the variation and the scree plot (Fig. 14B) does not display a steep decline after PC1&2. No correlations with *r* values greater than 0.8 were found between predictor variables. In the PCA for response variables (Fig. 15A) PC1&2 accounted for 68% of the variance and the scree plot displays a steep decline after PC2 (Fig. 15B). For response variables strong correlations existed between insectivore visitation and bird visitation ($r = 0.97$, df = 18, $P < 0.001$), omnivore visitation and mammal visitation ($r = 0.99$, df = 18, $P < 0.001$), omnivore visitation and total commensal visitation ($r = 0.97$, df = 18, $P < 0.001$), and mammal visitation and total commensal visitation ($r = 0.97$, df = 18, $P < 0.001$). These results indicate significant overlap between species contributions to each category of response variable; most insectivore observations were of bird species, most omnivore observations were of mammal species, and the total count of commensal visitation events was heavily influenced by mammal visitation.

Measures of burrow visitation were used as response variables in generalized linear models (GLMs) and linear models (LMs) with predictor variables set as microhabitat and burrow characteristics. Three sets of regressions were performed at the three levels of response; 1) full measures of commensal visitation: vertebrate species richness, Shannon-Wiener diversity index, and total number of observations of associate species, 2) total frequency of observations of each vertebrate class, and 3) total frequency of observations of each vertebrate guild. All models that used counts as a response variable included log trap nights of camera trap stations as an offset term to account for variation in sampling effort.

After forward and backward model selection via ‘stepAIC’, 3 out 13 predictors were found to have statistically significant effects on vertebrate species richness: easting ($\beta = 0.025$, SE = 0.0073, $P = 0.003$), burrow type (tortoise; $\beta = 4.22$, SE = 1.33, $P = 0.006$), and activity status (possibly occupied; $\beta = 2.74$, SE = 1.23, $P = 0.04$) (Table 6). A standard linear model detected five predictors that had a significant effect on Shannon-Wiener diversity: burrow type ($\beta = 0.19$, SE = 0.082, $P = 0.03$), northing ($\beta = -1.44\text{x}10^{-3}$, SE = $4.52\text{x}10^{-4}$, $P = 0.008$), burrowing intensity ($\beta = 0.056$, SE = 0.015, $P = 0.003$), light intensity ($\beta = 6.38\text{x}10^{-4}$, SE = $2.69\text{x}10^{-4}$, $P = 0.03$), and visibility of burrow entrance at five meters ($\beta = -1.01$, SE = 0.35, $P = 0.01$) (Table 6). Four burrow and microhabitat variables had statistically significant effects on total commensal visitation. Activity status (possibly occupied; $\beta = 106.6$, SE = 41.51, $P = 0.03$), northing ($\beta = 0.97$, SE = 0.38, $P = 0.03$), burrow type (tortoise; $\beta = 202.9$, SE = 36.49, $P = 0.004$), and tree species richness ($\beta = 266.8$, SE = 95.27, $P = 0.02$) had positive effects on total commensal visitation (Table 6).

For class level GLMs, burrow visitation frequency by mammals, birds, and herpetofauna were used as response variables. Of the 13 predictor variables, burrow type (tortoise; $\beta = 179.8$, SE = 28.88, $P < 0.001$), activity status (possibly occupied; $\beta = 122.8$, SE = 27.96, $P = 0.003$), and northing ($\beta = 0.69$, SE = 0.27, $P = 0.03$) had statistically significant positive effects on mammal visitation frequency (Table 7). For visitation by birds, tree species richness ($\beta = 68.29$, SE = 25.85, $P = 0.02$) had statistically significant positive effects while statistically significant negative effects were detected for canopy cover ($\beta = -1.15$, SE = 0.39, $P = 0.01$) and proportion of hardwood trees ($\beta = -260.2$, SE = 108.8, $P = 0.04$) (Table 7). For herpetofauna visitation, tree species richness ($\beta = 34.28$, SE = 10.22, $P = 0.007$) and distance from the nearest habitat edge ($\beta =0.31$, SE = 0.12, $P = 0.02$) had statistically significant positive effects, while activity status (possibly occupied; $\beta = -10.26$, SE = 4.43, $P = 0.04$), canopy cover ($\beta = -42.9$, SE = 17.22, $P = 0.03$), northing ($\beta = -0.15$, SE = 0.039, $P = 0.003$), and proportion of hardwood trees ($\beta = -64.11$, SE = 27.88, $P = 0.04$) had statistically significant negative effects (Table 7).

Guild level GLMs were performed using commensal visitation frequencies of carnivores, granivores, herbivores, insectivores, and omnivores as response variables (Table 8). No predictor variable had a statistically significant effect on visitation by carnivores, but near significant effects were detected for burrow type (tortoise; $\beta = 2.99$, SE = 1.46, $P = 0.06$), relative abundance of excavator species ($\beta = -0.014$, SE = 0.012, $P = 0.06$), and visibility of burrow entrance at five meters ($\beta = -8.57$, SE = 4.12, P = 0.06) (Table 8). For visitation by granivores, activity status (possibly occupied; $\beta = 2.61$, SE = 0.93, $P = 0.02$) and easting ($\beta = 0.026$, SE = 0.0093, $P = 0.02$) had statistically significant positive effects and distance from the nearest edge ($\beta = -0.11$, SE = 0.028, $P = 0.006$) and proportion of hardwood trees ($\beta = -0.28$, SE = 6.76, $P = 0.004$) showed statistically significant negative effects (Table 8). Statistically significant positive effects on visitation by herbivores were detected for burrow type (tortoise; $\beta = 4.39$, SE = 1.46, $P = 0.01$) and easting ($\beta = 0.025$, SE = 0.0085, $P = 0.01$) while a negative effect was observed for distance from the nearest habitat edge ($\beta = -0.081$, SE = 0.027, $P = 0.01$) (Table 8). For visitation by insectivores, statistically significant positive effects were found for northing ($\beta = 0.31$, SE = 0.11, $P = 0.02$) and tree species richness ($\beta = 96.03$, SE = 29.33, $P = 0.01$) while statistically significant negative effects were observed for canopy cover ($\beta = -1.48$, SE = 0.47, $P = 0.01$), vegetative density ($\beta = -509.3$, SE = 202.8, $P = 0.03$), and proportion of hardwood trees ($\beta = -334.7$, SE = 120.8, $P = 0.02$) (Table 8). Statistically significant positive effects on omnivore visitation were detected for burrow type (tortoise; $\beta = 169$, SE = 28.32, $P < 0.001$), initial activity status (possibly occupied; $\beta = 112.6$, SE = 27.42, $P = 0.004$), and northing ($\beta = 0.65$, SE = 0.26, $P = 0.04$) (Table 8).

G. Meta-Community Nestedness

Nested patterns were expected to be found across burrow locations with increasing distance from habitat edges and with decreasing burrowing intensity values as a measure of isolation due to these variables being applicable for nested patterns in island biogeography. Other variables selected as indices of habitat quality that were tested for influencing nested patterns were vegetative density and proportion of hardwood trees due to their negative influence on burrow visitation frequency in GLMs. When species RAI data were tested with data frame rows arranged by increasing distance from the habitat edges (Fig. 16A), the NODF value was 55.18 (*P* = 0.7), showing that nestedness across burrow associated communities based on increasing distance from habitat edges was not statistically significant when compared to the null hypothesis of a random pattern. Arranging data frame rows by decreasing co-intensity of burrowing produced an NODF value of 55.74 (*P* = 0.7) showing that a nested pattern in species data compared to a random pattern was not statistically significant based on an increasing degree of burrow isolation (Fig. 16B). Data arranged by increasing vegetative density (Fig. 16C) yielded an NODF value of 55.31 (*P* = 0.6) and arranging data by increasing proportion of hardwood trees (Fig. 16D) resulted in an NODF value of 53.85 (*P* = 0.7), neither of which were statistically significant in comparison to simulated random communities.

Discussion

This study is the first to compare vertebrate visitation between gopher tortoise and armadillo burrows in a syntopic population and the first to incorporate this type of analytical framework in assessments of commensal utilization for either burrow type. In the southeastern United States, the armadillo has been largely regarded as a nuisance species (Armstrong 1991; Bruggers et al. 2002; Mengak 2003) and listed as an invasive species in Georgia and Florida (FFWCC 2011;

GISTF 2011). Invasive species are considered a significant threat to imperiled species and biodiversity in general (Wilcove et al. 1998). However, my study, along with others (Taber 1945; Clark 1951; Platt et al. 2004) favors the concept that armadillos augment local biodiversity in a similar manner as the gopher tortoise (Butler 2020).

In my study, proportions of taxonomic classes of burrow associates differed from observations from a recent camera trapping study of tortoise burrow associates showing birds then mammals making up the majority of species richness and herpetofauna being less numerous (Dziadzio and Smith 2016). And these results differed from a similar study from the same region where herpetofauna then birds comprised the majority of the species richness of tortoise burrows and mammal species were less numerous (Murphy et al. 2021). For camera trapping studies of armadillo burrow associates, less research has been conducted. However, taxonomic proportions of burrow associate species in my study also differed from a recent camera trapping study on armadillo burrows which found that birds contributed the most to species richness with mammals and herpetofauna exhibiting less richness (Butler 2020).

While species composition overlapped between burrow types, tortoise burrows were visited more frequenty (in terms of total observations of associate fauna). Tortoise burrows were also visited more frequently by all classes and guilds. In addition, of the 40 vertebrate taxa observed interacting with burrows in this study, 15 were observed with greater-than-expected frequency at tortoise burrows (as compared to a proportional null model), suggesting these animals may have a stronger association with tortoise burrows. Then again, 11 species were observed at frequencies that were not significantly different between burrow types, suggesting that they may benefit from the presence of either burrow type. Several species of concern were observed visiting burrows in this study, namely the eastern box turtle which is both vulnerable and in decline and the northern bobwhite which is near threatened and a commercially important game species (Dozier and Bramwel 2010; BirdLife International 2016). No obligate tortoise burrow commensals [i.e., eastern indigo snake (*Drymarchon couperi*), gopher frog (*Lithobates capito*), and Florida mouse (*Podomys floridanus*)], as identified by Jackson and Milstery (1989), were observed during this study.

Median species richness, mean biodiversity and the PERMANOVA test for community dissimilarity were not statistically different between burrow types. However, the test result for dissimilarity was near significant and both median species richness and mean Shannon-Weiner diversity were greater at tortiose burrows. Additionally, greater species richness and biodiversity for tortoise burrows was further supported by the GLM and LM (Table 6). This suggests that armadillo burrows potentially support similar communities of associate vertebrates as tortoise burrows but may not be perfect syrogates in open canopy pine-forest ecosystems. That said, associate vertebrates may have more opportunities to benefit from armadillo burrows because the majority of burrows in our study were armadillo. Thus, within the study site armadillo burrows likely provided the greatest overall support for many taxa.

Burrow visitation was affected by several microhabitat and burrow characteristics. In general, possibly occupied tortoise burrows in areas with high tree species richness were associated with increased commensal visitation. This result may be due to habitat heterogeneity in these areas as biodiversity is expected to be greater near the ecotonal habitats of the pine stand (Harris 1988; Lidicker 1999) where increased resource availability from diverse tree communities likely increases species richness.

Microhabitat variables influenced the composition of assemblages visiting burrows as certain taxa’s burrow visitation frequency was affected differently by certain habitat characteristics. Althought statistically higher than expected at tortoise burrows, visitation by birds was not strongly associated with burrow type, but was positively affected by increased tree species richness which could be due to increased resource availability in these areas (May-Uc et al. 2020). However, increased canopy cover and proportion of hardwood trees negatively affected bird visitation of burrows. This may be due to these variables obscuring aerial visability of burrows for birds which rely heavily on vision for foraging (Fernandez-Juricic et al. 2004). Additionally, many frenquently observed birds in this study (10/14) were insectivores or omnivores which may use burrows as a food resource, relying on burrows with high arthropod abundance facilitated by tortoise excrement within heavily used tortoise burrows (Young and Goff 1939; Lips 1991; Dziadzio and Smith 2016; White and Tuberville 2017). However, this hypothesis may require further research in the context of burrow commensalism by way of measuring intra-burrow arthropod abundance and testing for associations with bird visititation.

Mammalian visitation was also higher than expected at tortoise burrows and positively associated with possibly occupied burrows. This suggests mammals observed in our study show interest in well-maintained tortoise burrows. Potentially, burrows that were identified as possibly occupied are higher quality sources of refugia for mammals or may be a viable food resource.

Herpetofauna visitation was higher than expected at tortoise burrows, although the deviation from expected visitation frequency by herpetofauna was much lower when compared to birds and mammals. Additionally herpetofauna visitation of burrows was not strongly associated with burrow type, but was associated with abandoned burrows and areas of low canopy cover with a low proportion of hardwood trees. As expected, low canopy cover and low hardwood proportion increased herptile visitation of burrows likely due to increased thermal stress in less shaded areas. Herpetofauna may also display an aversion for occupied burrows whereas abandoned burrows in areas with open canopy may be important sources of thermal refugia (Taylor et al. 2020). Higher visitation at abandoned burrows may be due to negative interactions between herptiles and burrow engineers or may indicate that these species are less reliant on possibly occupied burrows as a food resource.

Microhabitat variables also affected visitation by different feeding guilds observed in this study. Granivore visitation was associated with possibly occupied burrows near habitat edges in areas with low proportion of hardwood trees. However, granivore visitation counts were heavily influenced by observations of northern cardinal (*Cardinalis* cardinalis) whose presence is associated with habitat edges (Woodward et al. 2001), and all granivores observed in this study were birds which were also negatively associated with increased canopy cover and proportion of hardwoods. Burrow visitation by herbivores was also associated with burrows near habitat edges, specifically tortoise burrows, but was not associated with a particular activity status. This result may be due to the increased diversity of plant species associated with the ecotonal edges of the pine stand, and the lack of association with a burrow activity status suggests herbivores are not reliant on burrows for a food resource. Insectivore visitation of burrows was positively associated with increased tree species richness. However, burrows in areas with a higher proportion of hardwood trees, increased vegetative density, and increased canopy cover were visited less by insectivores. Insectivore GLM results were similar to the GLM results for bird visitation, with the exception of a significant effect from vegetative density, due to the majority of insectivore observations being from bird species despite the fact that less than half (4/11) of insectivores were birds. Visitation by omnivores was positively associated with tortoise burrows, particularly those that were possibly occupied, which is consistent with the concept of burrows serving as a food resource facilitated by cascading effects of tortoise dung. Additionally, omnivore observations were heavily influenced by mouse spp. which were the most frequently observed taxa for both burrow types. No burrow characteristics or microhabiat variables had a statistically significant effect on carnivore visitation, despite carnivore visitation being higher than expected at tortoise burrows.

Although not consistent for all GLM responses, burrow variables that repeatedly showed positive effects on visitation by associate species were tortoise burrows and possibly occupied burrows. Most likely, these results reflect the necessity of high quality refugia in this environment as tortoise burrows have greater overall volume than armadillo burrows allowing occupancy by more individuals, and possibly occupied burrows are well maintained and potentially more easily accessible to associate species. Furthermore, microhabitat variables showing repeated significant effects across responses also reiterate the importance of burrows as sources of refugia as canopy cover, vegetative density, and proportion of hardwood trees were negatively associated with burrow visitation by several categories of vertebrates. These results imply that resources provided by burrows (i.e., thermal refugia and food resources) may be less important for associate species in areas with abundant canopy cover, high proportions of hardwoods, and dense vegetation.

One limitation of this study was small sample size which was constrained by the number of available cameras and so, we were not able to survey more than 20 burrows at a time. This prevented us from using generalized linear mixed models (GLMMs) which would have accounted for random effects and provided more clairity to the effects of microhabitat characteristics on commensal burrow visitation. Neverthless, the addition of UTM coordinates as a covariate may have accounted for effects of variation in burrow location. In future studies, adding burrow dimension as an explanatory variable to a study using this framework could uncover associations between commensal use and burrow volume. Lastly, future studies should include monitoring of random sites which may be needed to assess the degree of burrow use by associate fauna compared to randomly selected locations serving as a control group.

There was not strong evidence of meta-community nestedness (Ulrich et al. 2009) associated with any examined variable. At the spatial scale of the study area, the dispersal potential of most vertebrate associates was presumably high relative to the average nearest-neighbor distance between burrows, so it is not necessarily suprising that we did not observe nested subsets of species with increasing distance from the stand edge (Wright et al. 1998). On the other hand, it would not be suprising to find subsets of commensal species in some isolated burrows, compared to areas where both species burrow intensively as the degree of isolation may play a part in limiting the number and types of species capable of using burrows that were not excavated near others. However, the degree of habitat heterogeneity and small area of the study site may have produced confounding effects (Clark 2010), and this hypothesis will require futher investigation, ideally at a larger spatial scale and in a study site with less habitat heterogeneity, to obtain a more clear result on the effects burrow isolation may have on associate community nestedness.

Biodiversity has long been associated with ecosystem function and efficiency (Naeem et al. 1994). It is clear that both armadillo and tortoise burrows provide important habitat features that support local biodiversity and these features may facilitate increased biodiversity and ecosystem processes (Hacker and Gaines 1997; Hooper et al. 2005). It is reasonable to suspect that burrow associate species would be adversly affected in areas where tortoise populations have been eliminated (Jackson and Milstery 1989; Read et al. 2008; Kinlaw and Grasmueck 2012; Hofstede and Dziminski 2017), and in turn the health of the ecosystem would decline as well. This presents a clear benefit to the increasing presence of armadillos in the United States, as many tortoise burrow associate species in our study were observed visiting armadillo burrows. It has recently been demonstrated that armadillos in insular systems within their introduced range support local biodiversity where gopher tortoises have never occurred (Butler 2020). However, commensal use of armadillo burrows remains an understudied aspect of armadillo ecology and future research should focus on mainland regions where this species has expanded its range to areas where gopher tortoises and other medium-sized burrowers are not present.

One factor that could be playing a part in the range expansion of armadillos is climate change (Wilson et al. 2005). Warming temperatures may allow dispersal of this species into higher latitudes (Taulman and Robbins 2014), and this could prove beneficial to native vertebrates in these areas as increased thermal stress could be mitigated by the availability of medium-sized burrows (Pike and Mitchell 2013). Additionally, shifts in vegetative communities associated with climate change (Kullman 2001; Kimball et al. 2010), which could potentially result in succesional, heterogeneous habitats that either increase in aridity and/or predation risk, could result in armadillo burrows being essential habitat features for maintaining biodiversity in these high stress environments.

Tortoises and armadillos are both medium-sized vertebrate excavators that can cohabitate the same environment, which could result in competitive interactions between the two species (Case and Gilpin 1974; Alley 1982). Although negative interactions between armadillos and tortoises occur (Degroote et al. 2013; Smith et al. 2012), the two excavators differ in food habits, temporal activity patterns, and microhabitat preferences (Kronfeld-Schor and Dayan 1999; Houadria et al. 2015; Bhandari 2019). A concerning result from this study is that armadillos were observed visiting tortoise burrows more frequently than their own. This may be problematic as armadillos are a known nest predator of the gopher tortoise (Smith et al. 2012). It has been demonstrated recently that armadillos do not exhibit preference or attraction toward tortoise eggs (Degroote et al. 2013) and that a long implicated negative interaction between armadillos and sea turtles has been largly overstated (Butler et al. 2020). But considering the armadillo’s foraging style and the fact that tortoises mostly nest on their burrow apron (Lamb et al. 2013), armadillos may be more likely to discover tortoise nests in areas where these species co-occur. The range of the gopher tortoise has become reduced with the reduction of longleaf pine forests of the Coastal Plain (Hermann et al. 2002), and with the expansion of the armadillo (Taulman and Robbins 2014), the gopher tortoise is now fully sympatric with the armadillo. This may have severe direct negative consequences for tortoise recruitment as well as indirect consequences for several obligate tortoise commensals with restricted ranges whose populations may suffer further declines in the absence of tortoise colonies (Diemer and Speake 1983; Eisenberg 1983; Layne and Jackson 1994; Roznik and Johnson 2009; Kinlaw and Grasmueck 2012). More research should be conducted on interactions between armadillos and gopher tortoises, obligate commensals of gopher tortoise burrows, and all species of conservation concern that occur within the introduced range of the armadillo before prioritizing armadillo control efforts.

This thesis should provide novel insight for land managers who are looking to make informed decisions as to whether or not armadillos should be controlled in certain areas based on their management goals. The results of this study will also inform conservationists attempting to re-establish or optimize the ecological functions of degraded longleaf pine ecosystems and identify habitats for gopher tortoise relocation projects where their keystone function will be most advantageous. Furthermore, this study provides a framework for investigating the community level effects of introduced ecosystem engineers that will increase our knowledge of interactions between medium-sized burrowers in novel ecosystem networks and the effects of syntopic populations of burrowing species on local biodiversity.

Conclusion

Armadillo burrows were utilized by dozens of species in this study, many of which are considered associates of gopher tortoises and had not been considered associates of armadillos. I did not observe any noteworthy instances of a species consistently visiting only one burrow type, and many species that were observed at armadillo burrows had not been previously documented in the literature.

The remaining gaps in research regarding armadillo burrow commensalism, the diversity of vertebrate utilization of armadillo burrows reported by Butler (2020), and the similarity in richness, diversity, and community composition between armadillo and tortoise burrows observed in this study highlights the need for range-wide monitoring of armadillo burrows. Future research should also include comparisons between sites that include armadillos and those that exclude them as well as between sites with and without tortoises to better clarify the effects that these excavators have on local biodiversity.

My study may support the notion of armadillos being important ecosystem engineers in xeric, open-canopy environments with increased thermal stress. However, burrows may be less important for local biodiversity in areas where other sources of refugia are abundant. Furthermore, differences in tortoise and armadillo burrow site selection (Bhandari 2019) could mean that armadillo burrows, by default, will be utilized less by associate vertebrates since they are typically excavated in shadier areas with greater vegetative density. Thus, the gopher tortoise should retain its status as the more important burrowing species for local biodiversity.

Keystone function of gopher tortoises may be optimized by habitat management to include prescribed fire and removal of excessive hardwood encroachment, to prevent the development of a closed canopy, while retaining some richness of tree species. Lastly, the removal of armadillos from areas containing gopher tortoise populations may be advised as armadillos were observed visiting tortoise burrows more frequently than their own which may have implications of negative effects on tortoise demographics but will require further investigation.

Literature Cited

Akaike H (1974) A New Look at the Statistical Model Identification. *IEEE Transactions on Automatic Control* 19: 716-723

Alexy JK, Brunjes KJ, Gassett JW, and Miller KV (2003) Continuous Remote Monitoring of Gopher Tortoise Burrow Use. *Wildlife Society Bulletin* 31: 1240–1243

Alford RA (1980) Population Structure of *Gopherus polyphemus* in Northern Florida. *Journal of Herpetology* 14: 177-182

Alley TR (1982) Competition Theory, Evolution, and Concept of an Ecological Niche. *Acta Biotheoretica* 31: 165-179

Almeida-Neto M, Guimaraes P, Guimaraes PR, Loyola RD, and Ulrich W (2008) A Consistent Metric for Nestedness Analysis in Ecological Systems: Reconciling Concept and Measurement. *Oikos* 117: 1227-1239

Anker A, Murina GV, Lira C, Vera Caripe JA, Palmer AR, and Jeng MS (2005) Macrofauna Associated with Echiuran Burrows: A Review with New Observations of the Innkeeper Worm, *Ochetostoma erythrogrammon* (Leuckart and Rüppel), in Venezuela. *Zoological Studies* 44: 157-190

Armstrong JB (1991) Extension Wildlife Damage Management in Alabama. *Proceedings of the Eastern Wildlife Damage Control Conference* 5: 148–150

Atmar W and Patterson BD (1993) The Measure of Order and Disorder in the Distribution of Species in Fragmented Habitat. *Oecologia* 96: 373-382

Audubon JJ and Bachman J (1854) The Quadrupeds of North America. Audubon JJ, New York

Auffenberg W and Franz R (1982) The Status and Distribution of the Gopher Tortoise (*Gopherus polyphemus*). In Bury RB (ed) North American Tortoises: Conservation and Ecology. U.S. Fish and Wildlife Service, Wildlife Research Report No.12: 95–126

Aya-Cuero C, Rodriquez-Bolanos A, and Superina M (2017) Population Density, Activity Patterns, and Ecological Importance of Giant Armadillos (*Priodontes maximus*) in Colombia. *Journal of Mammalogy* 98: 770-778

Baddeley A, Rubak E, and Turner R (2015) Spatial Point Patterns: Methodology and Applications with R. London: Chapman and Hall/CRC Press. https://www.routledge.com/Spatial-Point-Patterns-Methodology-and-Applications-with-R/Baddeley-Rubak-Turner/9781482210200/

Bailey HH (1924) The Armadillo in Florida and how it Reached There. *Journal of Mammalogy* 5: 264-265

Bhandari N (2019) Impact of Microhabitat Selection on Burrow Distribution of Nine-Banded Armadillos and Gopher Tortoises in a Pine Plantation (Master's thesis). Valdosta State University

BirdLife International. 2016. *Colinus virginianus*. The IUCN Red List of Threatened Species 2016. https://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22728956A95000808.en.

Bivand R, Keitt T, and Rowlingson B (2021) rgdal: Bindings for the 'Geospatial' Data Abstraction Library. R package version 1.5-23. https://CRAN.R-project.org/package=rgdal

Bray JR and Curtis JT (1957) An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs* 27: 325-349

Bruggers RL, Owens R, and Hoffman T (2002) Wildlife Damage Management Research Needs: Perceptions of Scientists, Wildlife Managers, and Stakeholders of the USDA/Wildlife Services Program. *International Biodeterioration and Biodegradation* 4: 213-223

Bruno JF, Stachowicz JJ, and Bertness MD (2003) Inclusion of Facilitation into Ecological Theory. *Trends in Ecology and Evolution* 18: 119-125

Butler ZP (2020) Assessing the Ecological Roles of Nine-banded Armadillos (*Dasypus novemcinctus*) on Georgia's Barrier Islands (Master's thesis). University of Georgia

Butler ZP, Wenger SJ, Pfaller JB, Dodd MG, Ondich BL, Coleman S, Gaskin JL, Hickey N, Kitchens-Hayes K, Vance RK, and Williams KL (2020) Predation of Loggerhead Sea Turtle Eggs Across Georgia's Barrier Islands. *Global Ecology and Conservation* 23: e01139

Caravaggi A, Banks PB, Burton AC, Finlay CMV, Haswell PM, Hayward MW, Rowcliffe MJ, and Wood MD (2017) A Review of Camera Trapping for Conservation Behaviour Research. *Remote Sensing in Ecology and Conservation* 3: 109-122

Case TJ and Gilpin ME (1974) Interference Competition and Niche Theory. *Proceedings of the National Academy of Sciences of the United States of America* 71: 3073-3077

Catano CP and Stout IJ (2015) Functional Relationships Reveal Keystone Effects of the Gopher Tortoise on Vertebrate Diversity in a Longleaf Pine Savanna. *Biodiversity and Conservation* 24: 1957-1974

Chamberlain PA (1980) Armadillos: Problems and Control. *Proceedings of the 9th Vertebrate Pest Conference* 164-169

Clark WK (1951) Ecological Life History of the Armadillo in the Edwards Plateau Region. *American Midland Naturalist* 46: 337-358

Clark WR (2010) Principles of Landscape Ecology. *Nature Education Knowledge* 3: 34

Cox J, Inkley D, and Kautz R (1987) Ecology and Habitat Protection Needs of Gopher Tortoise (*Gopherus polyphemus*) Populations Found on Lands Slated for Large-scale Development in Florida. Florida Game and Fresh Water Fish Commission Nongame Wildlife Program Technical Report No. 4. Tallahassee, Florida

Degroote LW, Ober HK, McDonough CM, and Mizell RF (2013) An Evaluation of the Nine-banded Armadillo as Predators of Gopher Tortoise and Northern Bobwhite Quail Nests in Florida. *The American Midland Naturalist* 169: 74-85

Di Blanco YE, Desbiez ALJ, di Francescantonio D, and Di Bitetti MS (2020) Excavations of Giant Armadillos Alter Environmental Conditions and Provide New Resources for a Range of Animals. *Journal of Zoology* 311: 227-238

Diemer JE (1986). The Ecology and Management of the Gopher Tortoise in the Southeastern United States. *Herpetologica* 42: 125-133

Diemer JE and Speake DW (1983) The Distribution of the Eastern Indigo Snake, *Drymarchon corais couperi*, in Georgia. *Journal of Herpetology* 17: 256-264

Doonan TJ and Stout IJ (1994) Effects of Gopher Tortoise (*Gopherus polyphemus*) Body Size on Burrow Structure. *The American Midland Naturalist* 131: 273-280

Dozier WA and Bramwell K (2010) Bobwhite Quail Production and Management Guide. University of Georgia Cooperative Extension Bulletin 1215. University of Georgia

Dziadzio MC, Smith LL, Chandler RB, and Castleberry SB (2016) Effect of Nest Location on Gopher Tortoise Nest Survival. *The Journal of Wildlife Management* 80: 1314-1322

Dziadzio MC and Smith LL (2016) Vertebrate Use of Gopher Tortoise Burrows and Aprons. *Southeastern Naturalist* 15: 586-594

Eisenberg JF (1983) The Gopher Tortoise as a Keystone Species. In Bryant RJ and Franz R (Eds). The Gopher Tortoise: A Keystone Species. Proceedings of the 4th Annual Meeting of the Gopher Tortoise Council: 1-4. Florida State Museum, Gainesville

Ernst CH, Barbour RW, and Lovich JE (1994) Turtles of the United States and Canada. Smithsonian Institute Press, Washington D.C.

Fernandez-Juricic E, Erichsen JT, and Kacelnik A (2004) Visual Perception and Social Foraging in Birds. *Trends in Ecology and Evolution* 19: 25-31

FFWCC. 2011. Nonnative Mammals. Available online at http://myfwc.coni/wildlifehabitats/nonnatives/mammals/

Friend GR (1993) Impact of Fire on Small Vertebrates in Mallee Woodlands and Heathlands of Temperate Australia: A Review. *Biological Conservation* 65: 99–114

GISTF. 2011. Invasive mammals of concern in Georgia. Available online at http://www.gainvasives.org/mammals.html

Hacker SD and Gaines SD (1997) Some Implications of Direct Positive Interactions for Community Species Diversity. *Ecology* 78: 1990-2003

Hansen KL (1963) The Burrow of the Gopher Tortoise. *Quarterly Journal of the Florida Academy of Sciences* 26: 353-360

Harris LD (1988) Edge Effects and Conservation of Biotic Diversity. *Conservation Biology* 2: 330-332

Hermann SM, Guyer C, Waddle JH, and Nelms MG (2002) Sampling on Private Property to Evaluate Population Status and Effects of Land Use Practices on the Gopher Tortoise, *Gopherus polyphemus*. *Biological Conservation* 108: 289-298

Hijmans RJ (2020) raster: Geographic Data Analysis and Modeling. R Package Version 3.4-10. https://CRAN.R-project.org/package=raster

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vila M, Zamora R, and Zobel M (2006) Novel Ecosystems: Theoretical and Management Aspects of the New Ecological World Order. *Global Ecology and Biogeography* 15: 1-7

Hofstede L and Dziminski MA (2017) Greater Bilby Burrows: Important Structures for a Range of Species in an Arid Environment. *Australian Mammalogy* 39: 227-237

Holcomb SR and Carr JL (2013) Mammalian Depredation of Artificial Alligator Snapping Turtle (*Macrochelys temminckii*) Nests in North Louisiana. *Southeastern Naturalist* 12: 478-491

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, and Wardle DA (2005) Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecological Monographs* 75: 3-35

Houadria M, Salas-Lopez A, Orivel J, Bluthgen N, and Menzel F (2015) Dietary and Temporal Niche Differentiation in Tropical Ants – Can They Explain Local Ant Coexistence? *Biotropica* 47: 208-217

Humphrey SR (1974) Zoogeography of the Nine-Banded Armadillo (*Dasypus novemcinctus*) in the United States. *BioScience* 24: 457-462

Hunt TP (1959) Breeding Habits of the Swamp Rabbit with Notes on its Life History. *Journal of Mammalogy* 40: 82-91

Jackson DR and Milstrey EG (1989) The Fauna of Gopher Tortoise Burrows. In: Diemer J, Jackson, DR, Landers JL, Layne JN, Wood DA (Eds). *Gopher Tortoise Relocation Symposium Proceedings*. Florida Game and Freshwater Fish Commission, Nongame Wildlife Program Technical Report 5: 86–98

Jones CG, Lawton JH, and Shachak M (1994) Organisms as Ecosystem Engineers. *Oikos* 69: 373-386

Jones CG, Lawton JH, and Shachak M (1997) Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology* 78: 1946-1957

Kent DM and Snell E (1994) Vertebrates Associated with Gopher Tortoise Burrows in Orange County, Florida. *Florida Field Naturalist* 22: 8-10

Kimball S, Angert AL, Huxman TE, and Venable L (2010) Contemporary Climate Change in the Sonoran Desert Favors Cold-adapted Species. *Global Change Biology* 16: 1555-1565

Kinlaw AE (1999) A Review of Burrowing by Semi-fossorial Vertebrates in Arid Environments. *Journal of Arid Environments*. 41: 127-145

Kinlaw AE (2006) Burrow Dispersion of Central Florida Armadillos. *Southeastern Naturalist* 5: 523-534

Kinlaw AE and Grasmueck M (2012) Evidence for and Geomorphologic Consequences of a Reptilian Ecosystem Engineer: The Burrowing Cascade Initiated by the Gopher Tortoise. *Geomorphology* 157-158: 108-121

Knapp DD, Howze JM, Murphy CM, Dziadzio MC, and Smith LL (2018) Prescribed Fire Affects Diurnal Vertebrate Use of Gopher Tortoise (*Gopherus polyphemus*) Burrows in a Longleaf Pine (*Pinus palustrus*) Forest. *Herpetological Conservation and Biology* 13: 551-557

Kolowski JM and Forrester TD (2017) Camera Trap Placement and the Potential for Bias Due to Trails and Other Features. *PLOS ONE* 12: e0186679

Kronfeld-Schor N and Dayan T (1999) The Dietary Basis for Temporal Partitioning: Food Habits of Coexisting *Acomys* Species. *Oecologia* 121: 123-128

Kullman L (2001) 20th Century Climate Warming and Tree-limit Rise in the Southern Scales of Sweden. *AMBIO: A Journal of the Human Environment* 30: 72-80

Kush JS (2016) The Longleaf Pines are Few and Far Between. *Ecological Restoration* 34: 15-16

Laidre ME (2018) Evolutionary Ecology of Burrow Construction and Social Life. Chapter 11. In Wellborn GA and Thiel M (Eds.) Life Histories 279– 301. Oxford University Press. New York, New York

Lamb JY, Ennen JR, and Qualls CP (2013) Environmental Characteristics of Nest Sites Selected by Gopher Tortoises (*Gopherus polyphemus*) in Southern Mississippi. *Chelonian Conservation and Biology* 12: 227-234

Layne JN (1997) *Nonindigenous Mammals. Strangers in paradise: Impact and Management of Nonindigenous Species in Florida* (D. Simberloff, D. C. Schmitz, and T. C. Brown, Eds.). Island Press, Washington, D.C.

Layne JN and Jackson RJ (1994) Burrow Use by the Florida Mouse (*Podomys floridanus*) in South-central Florida. *American Midland Naturalist* 131: 17-23

Lidicker WZ (1999) Responses of Mammals to Habitat Edges: An Overview. *Landscape Ecology* 14: 333-343

Lips KR (1991) Vertebrates Associated with Tortoise (*Gopherus polyphemus*) Burrows in 4 Habitats in South-Central Florida. *Journal of Herpetology* 25: 477–481

Loughry WJ and McDonough CM (2013) *The Nine-Banded Armadillo: A Natural History*. University of Oklahoma Press, Norman

Loughry J, McDonough C, and Abba AM (2014) *Dasypus novemcinctus*. The IUCN Red List of Threatened Species: e.T6290A47440785. https://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T6290A47440785.en

Loughry WJ, Superina M, McDonough CM, and Abba AM (2015) Research on Armadillos: A Review and Prospectus. *Journal of Mammalogy* 96: 635-644

MacArthur RH and Wilson EO (1963) An Equilibrium Theory of Insular Zoogeoraphy. *Evolution* 17: 373-387

Machicote M, Branch LC, and Villarreal D (2004) Burrowing Owls and Burrowing Mammals: Are Ecosystem Engineers Interchangeable as Facilitators? *Oikos* 106: 527-535

May-Uc Y, Nell CS, Parra-Tabla V, Navarro J, and Abdala-Roberts L (2020) Tree Diversity Effects Through a Temporal Lens: Implications for the Abundance, Diversity and Stability of Foraging Birds. *Journal of Animal Ecology* 89: 1775-1787

McCoy ED, Mushinsky HR, and Lindzey J (2006) Declines of the Gopher Tortoise on Protected Lands. *Biological Conservation* 128: 120-127

McDonough CM, DeLaney MA, Le PQ, Blackmore MS, and Loughry WJ (2000) Burrow Characteristics and Habitat Associations of Armadillos in Brazil and the United States of America. *Revista de Biologia Tropical* 48: 109-120

Mengak MT (2003) Wildlife Damage Management Education Needs: Survey of Georgia County FASAT Agents. *Proceedings of the Wildlife Damage Management Conference* 10: 7-15

Mukherjee A, Pilakandy R, Kumara HN, Manchi SS, and Bhupathy S (2017) Burrow Characteristics and its Importance in Occupancy of Burrow Dwelling Vertebrates in Semiarid Area of Keoladeo National Park, Rajasthan, India. *Journal of Arid Environments* 141: 7-15

Murphy CM, Smith LL, O'Brien JJ, and Castleberry SB (2021) A Comparison of Vertebrate Assemblages at Gopher Tortoise Burrows and Stump Holes in the Longleaf Pine Ecosystem. *Forest Ecology and Management* 482: 118809

Naeem S, Thompson LJ, Lawler SP, Lawton JH, and Woodfin RM (1994) Declining Biodiversity can Alter the Performance of Ecosystems. *Nature* 368: 734- 737

Niedballa J, Sollmann R, Courtiol A, and Wilting A (2016) camtrapR: An R Package for Efficient Camera Trap Data Management. *Methods in Ecology and Evolution* 7: 1457-1462

Noss RF (1989) Longleaf Pine and Wiregrass: Keystone Components of an Endangered Ecosystem. *Natural Areas Journal* 9: 211-213

Noss RF, LaRoe ET, and Scott JM (1995) Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. USDI National Biological Service, Biological Report No. 28

Ober H, DeGroote LW, McDonough CM, Mizell RF, and Mankin RW (2011) Identification of an Attractant for the Nine-Banded Armadillo, *Dasypus novemcinctus*. *Wildlife Society Bulletin* 35: 421-429

O’Brien TG, Kinnaird MF, and Wibisono HT (2003) Crouching Tigers, Hidden Prey: Sumatran Tiger and Prey Populations in a Tropical Forest Landscape. *Animal Conservation* 6: 131-139

O’Connell AF, Nichols JD, and Karanth KU (2011) *Camera Traps in Animal Ecology: Methods and Analyses*. Springer Publishing Company. New York City, New York

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, and Wagner H (2020) vegan: Community Ecology Package. R Package Version 2.5-7. https://CRAN.R-project.org/package=vegan

Oliver MA and Webster R (1990) Kriging: A Method of Interpolation for Geographical Information Systems. *International Journal of Geographical Information Systems* 4: 313-332

Paine RT (1966) Food Web Complexity and Species Diversity. *American Naturalist* 100: 65-75

Pebesma EJ (2004) Multivariable Geostatistics in S: the gstat Package. *Computers and Geosciences* 30: 683-691

Pike DA and Mitchell JC (2013) Burrow-dwelling Ecosystem Engineers Provide Thermal Refugia Throughout the Landscape. *Animal Conservation* 16: 694-703

Platt SG, Rainwater TR, and Brewer SW (2004) Aspects of the Burrowing Ecology of Nine-Banded Armadillos in Northern Belize. *Mammalian Biology* 69: 217-224

Pristo de Medeiros Oliveira IV, Deps P, and Azevedo de Paula Antunes JM (2019) Armadillos and Leprosy: From Infection to Biological Model. *Revista do Instituto de Medicina Tropical de São Paulo* 61: e44

R Core Team (2021). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Read JL, Carter J, Moseby KM, and Greenville A (2008) Ecological Roles of Rabbit, Bettong, and Bilby Warrens in Arid Australia. *Journal of Arid Ecology* 72: 2124-2130

Reid FA (2006) A Field Guide to Mammals of North America, North of Mexico. Houghton Mifflin, New York

Riggs TR, Pascarella JB, and Bechler DL (2010) The Ethno- and Research History of the Lake Louise Field Station, Valdosta State University, Valdosta, GA. *Georgia Journal of Science* 68: 149-165

Rodriquez TF, Mantellatto AMB, Superina M, and Chiarello AG (2019) Ecosystem Services Provided by Armadillos. *Biological Reviews* 95: 1-21

Rolshausen G, Hallman U, Dal Grande F, Otte J, Knudsen K, and Schmitt I (2020) Expanding the Mutualistic Niche: Parallel Symbiont Turnover Along Climactic Gradients. *Proceedings of the Royal Society B* 287: 20192311

Roznik EA and Johnson SA (2009) Burrow Use and Survival of Newly Metamorphosed Gopher Frogs (*Rana capito*). *Journal of Herpetology* 43: 431-437

Sawyer CF, Brinkman DC, Walker VD, Covington TD, and Stienstraw EA (2012) The Zoogeomorphic Characteristics of Burrows and Burrowing by Nine-Banded Armadillos (*Dasypus novemcinctus*). *Geomorphology* 157: 122-130

Smith LL, Tuberville TD, and Seigel RA (2006) Workshop on the Ecology, Status, and Management of the Gopher Tortoise (*Gopherus polyphemus*), Joseph W. Jones

Ecological Research Center, 16-17 January 2003: Final Results and Recommendations. *Chelonian Conservation and Biology* 5: 326-330

Smith LL, Steen DA, Conner LM, and Rutledge JC (2012) Effects of Predator Exclusion on Nest and Hatchling Survival in the Gopher Tortoise. *The Journal of Wildlife Management* 77: 352-358

Smith RB, Tuberville TD, Chambers AL, Herpich KM, and Berish JE (2005) Gopher Tortoise Burrow Surveys: External Characteristics, Burrow Cameras, and Truth. *Applied Herpetology* 2: 161-170

Staller EL, Palmer WE, Carroll JP, Thornton RP, and Sisson DC (2005) Identifying Predators at Northern Bobwhite Nests. *Journal of Wildlife Management* 69: 124-132

Taber FW (1945) Contribution on the Life History and Ecology of the Nine-Banded Armadillo. *Journal of Mammalogy* 26: 211-226

Tamaki A, Kagesawa T, Takeuchi S, Ohashi H, Yang S, and Sassa S (2018) Facultative Commensalism of a Free-burrowing Urothoid Amphipod with a Deep Burrow-Dwelling Callianassid Shrimp in Intertidal Sand. *Marine Biology* 165

Taulman JF and Robbins LW (2014) Range Expansion and Distributional Limits of the Nine-Banded Armadillo in the United States: An Update to Taulman & Robbins (1996). *Journal of Biogeography* 41: 1626-1630

Taylor EN, Diele-Viegas LM, Gangloff EJ, Hall JM, Halpern B, Massey MD, Rodder D, Rollinson N, Spears S, Sun BJ, and Telemeco RS (2020) The Thermal Ecology and

Physiology of Reptiles and Amphibians: A User's Guide. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 335: 13-44

Ter Braak CJF (1986) Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. *Ecology* 67: 1167-1179

Thomas KR (1974) Burrow Systems of the Eastern Chipmunk (*Tamias striatus pipilans* Lowery) in Louisiana. *Journal of Mammalogy* 55: 454-459

Tortoise & Freshwater Turtle Specialist Group (1996) *Gopherus polyphemus*. The IUCN Red List of Threatened Species. https://dx.doi.org/10.2305/IUCN.UK.1996.RLTS.T9403A12983629.en

Ulrich W, Almeida-Neto M, and Gotelli NJ (2009) A Consumer's Guide to Nestedness Analysis. *Oikos* 118: 3-17

University of Georgia (2021) Lizards of South Carolina and Georgia. University of Georgia Savannah River Ecology Laboratory. http://srelherp.uga.edu/lizards/index.htm

University of Michigan (2020) Animal Diversity Web. University of Michigan Museum of Zoology. https://animaldiversity.org/

Van Beneden PJ (1887) Animal Parasites and Messmates. Appleton, New York

Venables WN and Ripley BD (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York

Villete P, Krebs CJ, and Jung TS (2017) Evaluating Camera Traps as an Alternative to Live Trapping to Estimate the Density of Snowshoe Hares (*Lepus americanus*) and Red Squirrels (*Tamiasciurus hudsonicus*). *European Journal of Wildlife Research* 63

White KN and Tuberville TD (2017) Birds and Burrows: Avifauna Use and Visitation of Burrows of Gopher Tortoise at Two Military Sites in the Florida Panhandle. *The Wilson Journal of Ornithology* 129: 792-803

Wilcove DS, Rothstein D, Dubow J, Phillips A, and Losos E (1998) Quantifying Threats to Imperiled Species in the United States. *BioScience* 48: 607-615

Wilson RJ, Gutierrez D, Gutierrez J, Martinez D, Agudo R, Monserrat VJ (2005) Changes to the Elevational Limits and Extent of Species Ranges Associated with Climate Change. *Ecology Letters* 8: 1138-1146

Witz BW, Wilson DS, and Palmer MD (1991) Distribution of *Gopherus polyphemus* and its Vertebrate Symbionts in 3 Burrow Categories. *American Midland Naturalist* 126: 152-158

Woodward AA, Fink AD, and Thompson FR (2001) Edge Effects and Ecological Traps: Effects on Shrubland Birds in Missouri. *Journal of Wildlife Management* 65: 668-675

Wright DH, Patterson BD, Mikkelson GM, Cutler A, and Atmar W (1998) A Comparative Analysis of Nested Subset Patterns of Species Composition. *Oecologia* 113: 1-20

Young FN and Goff CC (1939) An Annotated List of Arthropods Found in the Burrows of the Florida Gopher Tortoise, *Gopherus polyphemus* (Daudin). *Florida Entomologist* 22: 53-62

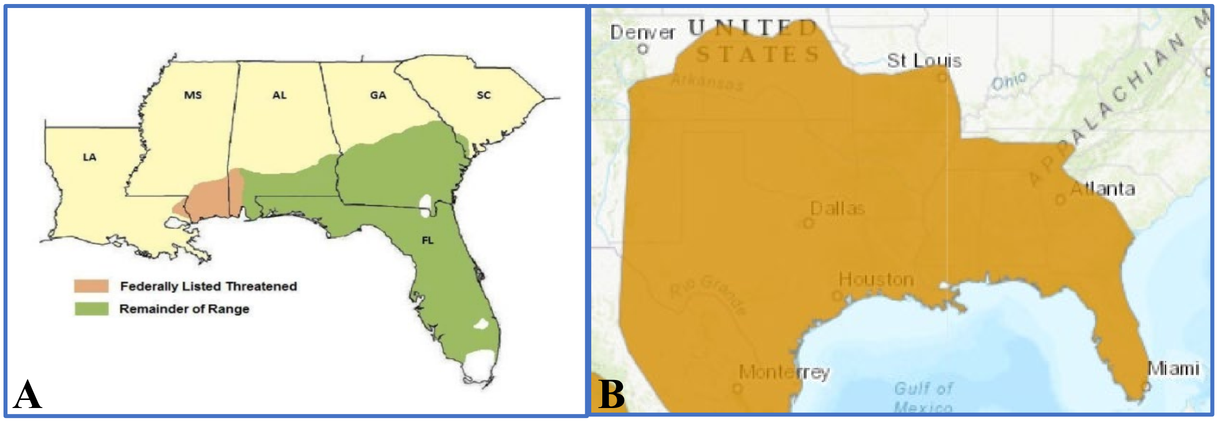

Figure 1. (A) Current geographic range of the gopher tortoise (https://gophertortoisecouncil.org/gopher-tortoise). Red portions of the range map indicate areas where the gopher tortoise is federally listed as threatened and green portions indicate areas where it is not listed as a threatened species. (B) Current geographic range of the nine-banded armadillo within the United States (Loughry et al. 2014).

Figure 2. Satellite view of Lake Louise Field Station (LLFS) in Lowndes County, GA, USA. The light blue line represents the dirt road edge that is the boundary of the 10.4-hectare pine stand. The highway to the west of the pine stand is Interstate 75 and the body of water directly south of the pine stand is Lake Louise.

Figure 3. A typical armadillo burrow (A) and a typical gopher tortoise burrow (B). Note the difference in shape between the two burrow entrances: the armadillo burrow is more circular/ovular while the tortoise burrow displays a characteristic half-moon shape. Another important difference to note between burrow types is the burrow apron. The tortoise burrow apron is notably larger and apron soil coloration is in stark contrast with the surrounding ground.

Figure 4. Example of camera trap setup at a gopher tortoise burrow. Camera mount legs are staked into the ground on either side of the burrow mouth as to minimize interference with burrow use by vertebrates. The camera lens is positioned to include the full burrow opening and only a small portion of surrounding ground on all sides of the burrow mouth in its field of view.

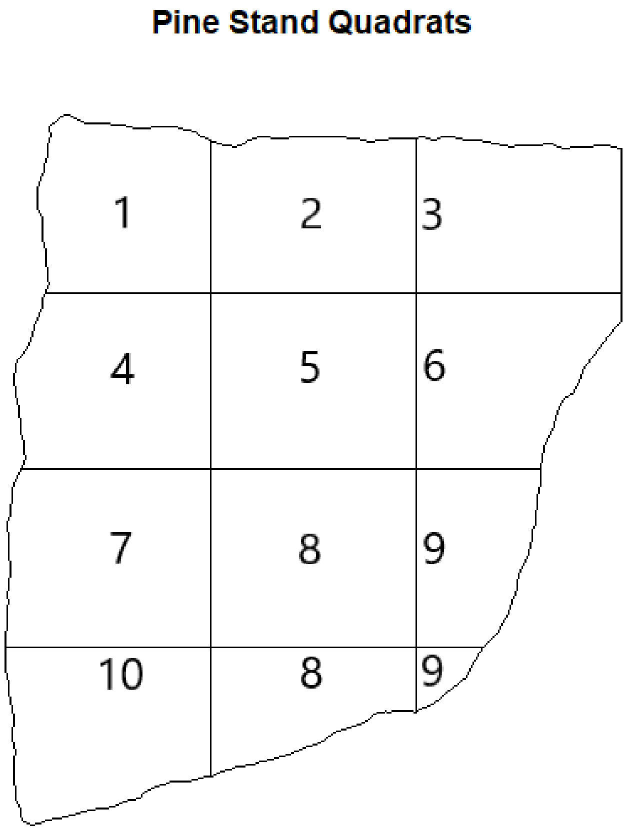

Figure 5. Shapefile of the Lake Louise pine stand separated into quadrats. This quadrat system was used to space camera traps sufficiently throughout the study area. Two camera traps were deployed, after random selection of one armadillo burrow and one tortoise burrow for monitoring, within each quadrat. Each quadrat is labeled with its respective identification number. In our analyses, quadrats 11 and 12 (labeled 8 and 9 on the bottom row) in the southeastern portion of the stand were combined with the quadrats on their northern border due to their small area.

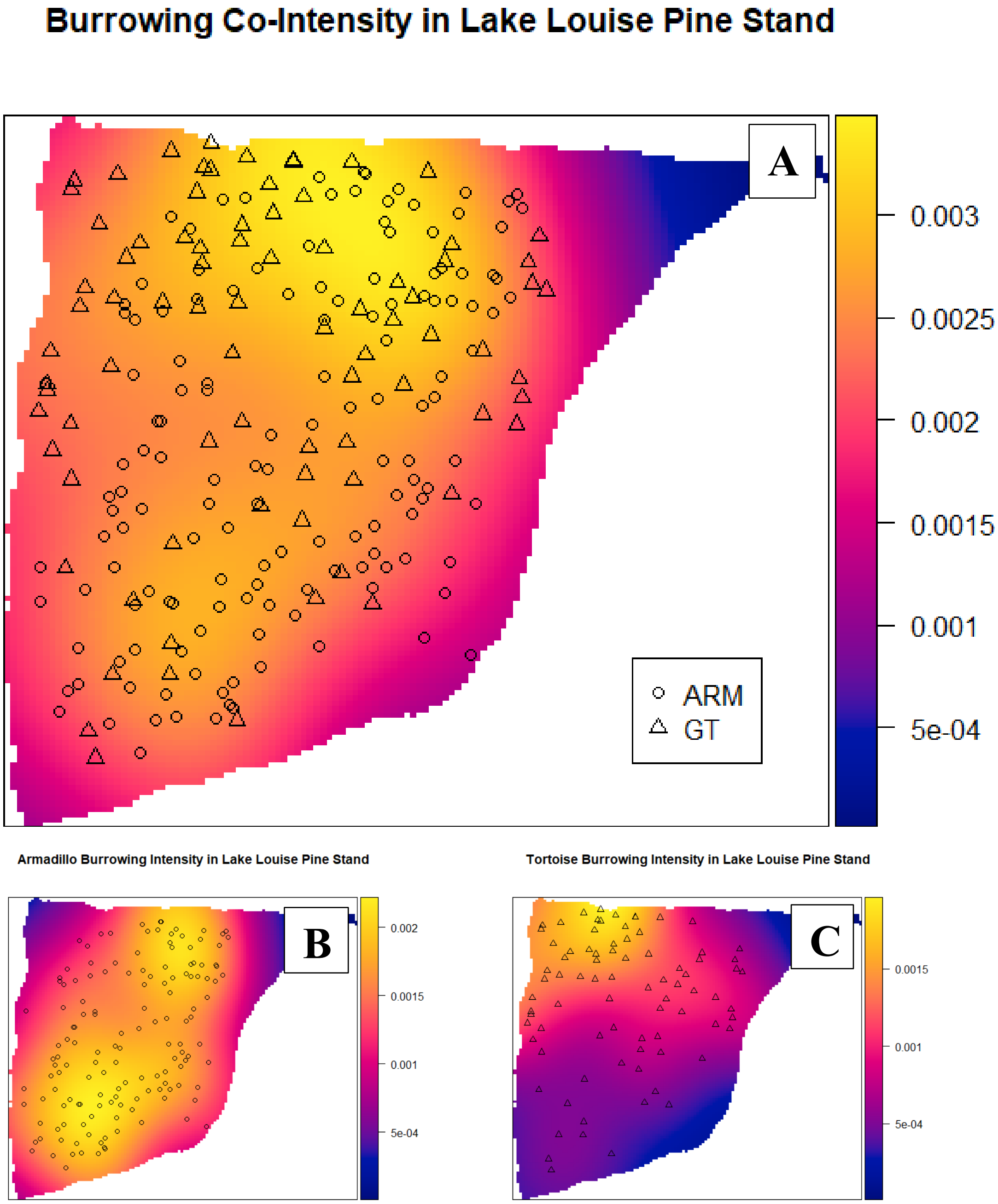

Figure 6. Plots showing kernel-smoothed burrowing co-intensity (A), armadillo burrowing intensity (B), and tortoise burrowing intensity (C) within the Lake Louise pine stand. Lighter colors represent areas of high burrowing intensity. Open circles indicate armadillo burrow locations and open triangles represent tortoise burrow locations. Legend labels indicate density values as the number of burrows per meter.

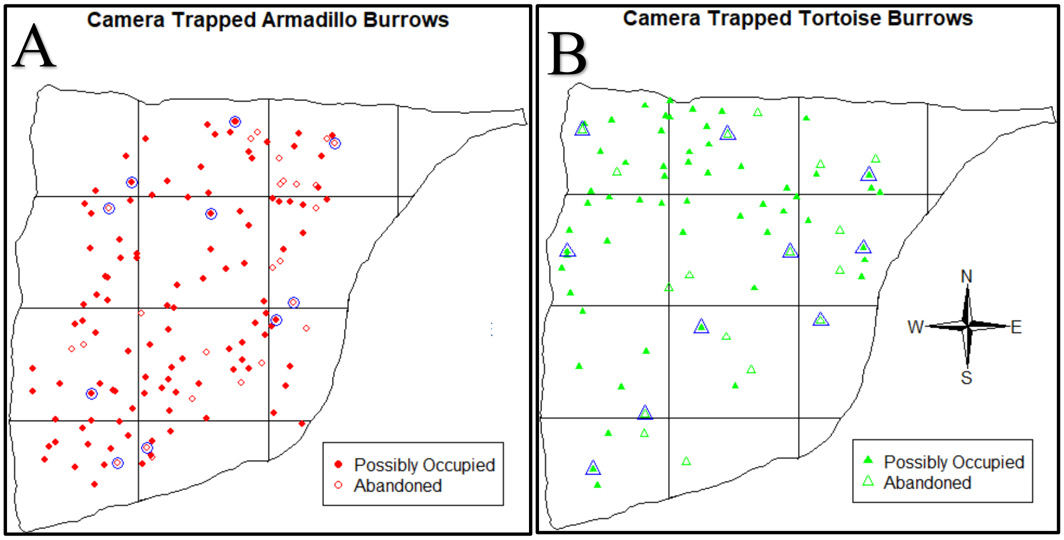

Figure 7. Armadillo burrow locations (A) and tortoise burrow locations (B) within the pine stand. Filled symbols represent possibly occupied burrows while open symbols represent abandoned burrows. Camera trapped burrows are outlined in blue.

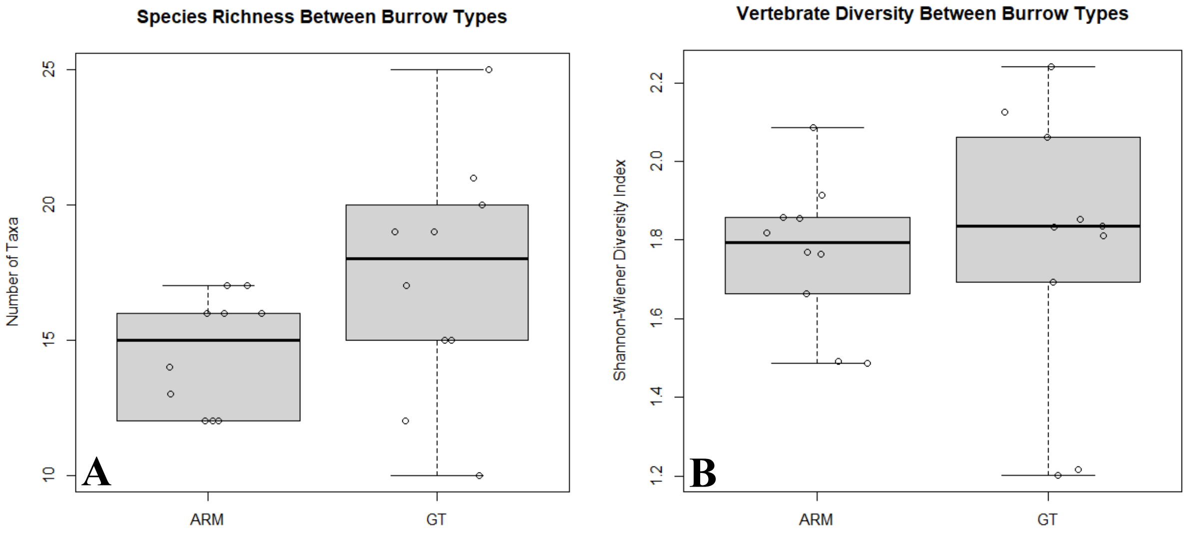

Figure 8. Boxplots with stripcharts overlayed displaying ranges of species richness (A) and Shannon-Wiener diversity indices (B) between armadillo and tortoise burrows. Data points in the stripchart have been randomly jittered for maximum visibility.

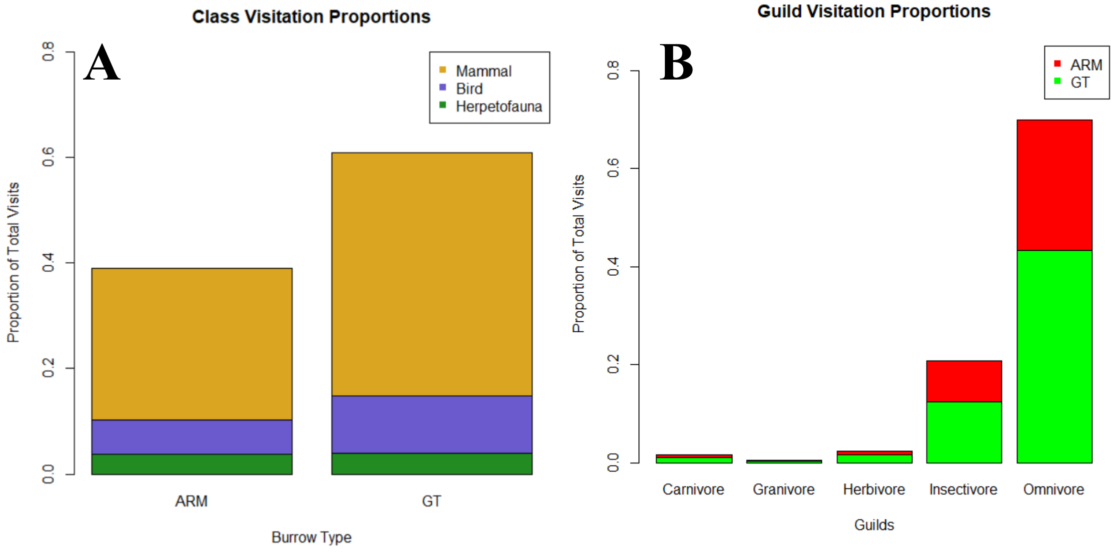

Figure 9. Proportions of class level commensal burrow visitation frequency separated by burrow type (A): The bar labeled "ARM" represents armadillo burrows and the bar labeled "GT" represents tortoise burrows. Classes of associate species are colored coded (yellow = mammals, blue = birds, and green = herpetofauna). Proportions of total commensal visitation frequency separated by associate species guilds (B): Guild bars are color coded by burrow type with red portions representing armadillo burrows and green portions representing tortoise burrows. Proportions of total visitation for all classes and guilds were higher for tortoise burrows, but relative proportions of each category were consistent for burrow type-specific visitation totals.

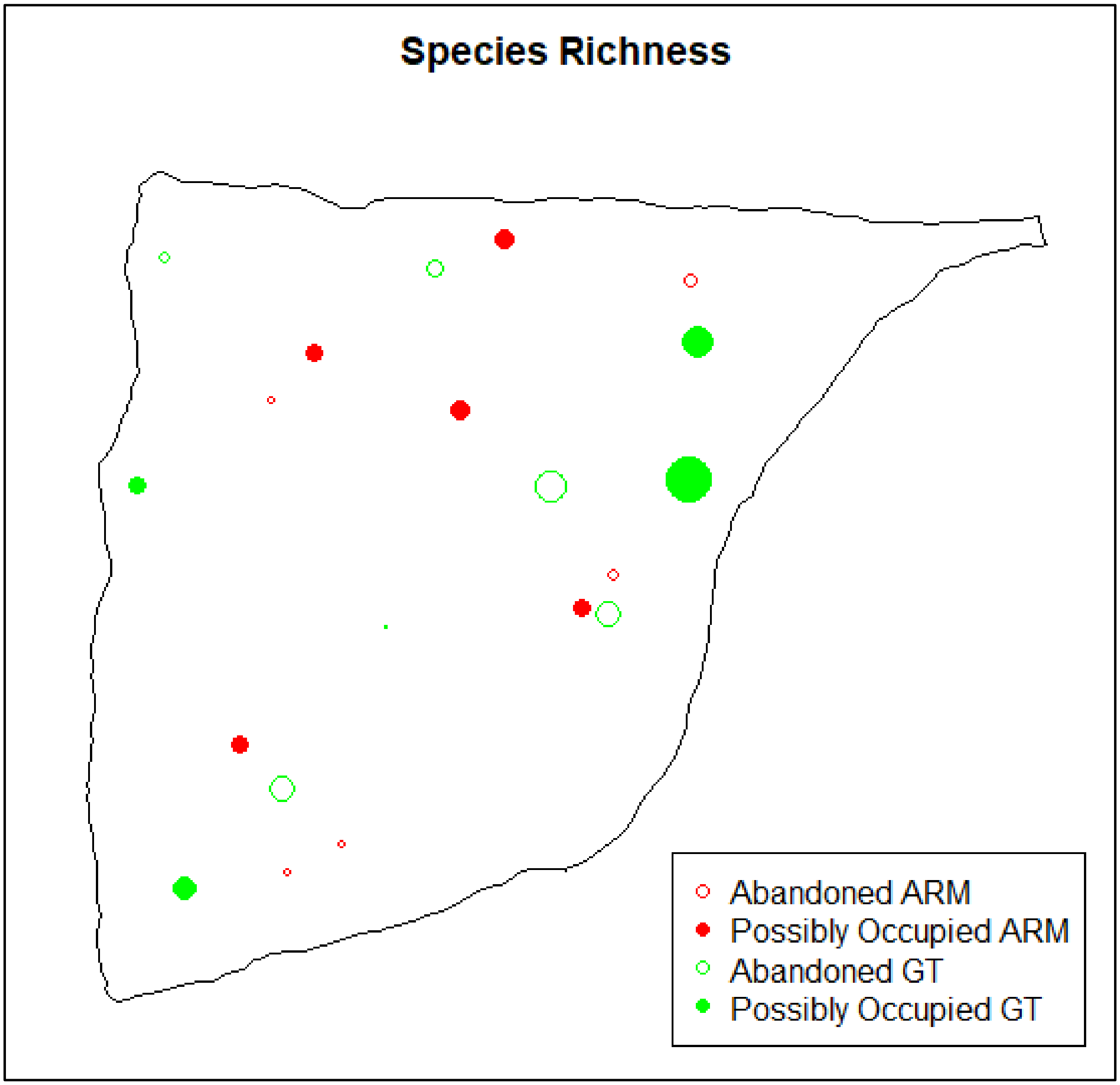

Figure 10. Map of species richness across sampled burrows in the study area. Red points represent armadillo burrows while green points represent tortoise burrows. Abandoned burrows are plotted as open circles and possibly occupied burrows are displayed as filled circles. Species richness values ranged from 10 to 25 taxa and are indicated by point size with larger points representing burrows with higher species richness.

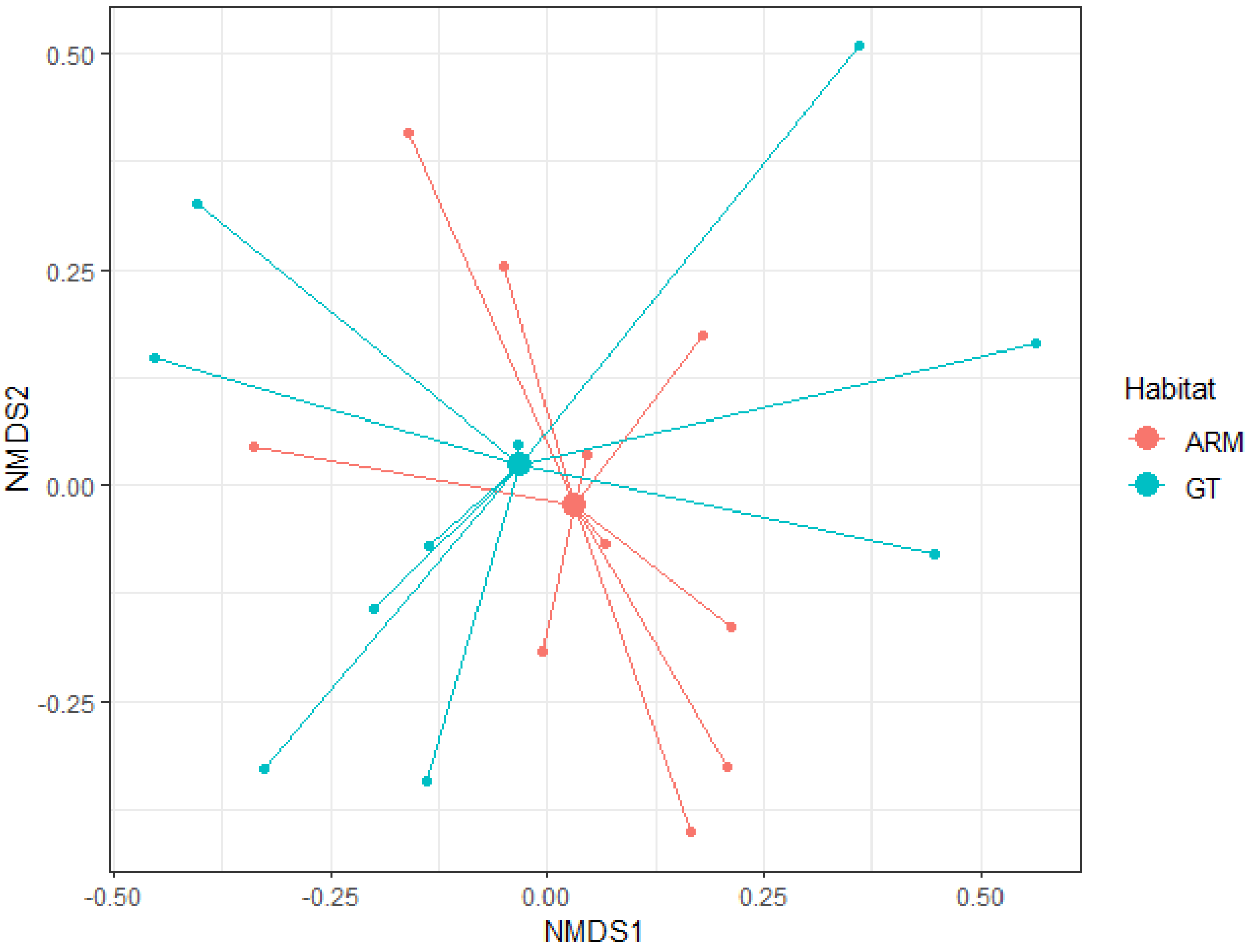

Figure 11. Spider plot showing community dissimilarity distances between monitored burrows. Plot centroids represent mean dissimilarity scores for armadillo and tortoise burrows. Orange points represent armadillo burrows and blue points represent tortoise burrows. The overlapping point clouds indicates minimal separation between communities visiting either burrow type, showing that there is little dissimilarity between species composition at armadillo and tortoise burrows. Additionally, there is a greater degree of spread for tortoise burrow dissimilarity scores than for armadillo burrows, indicating higher variance in community composition for tortoise burrows.

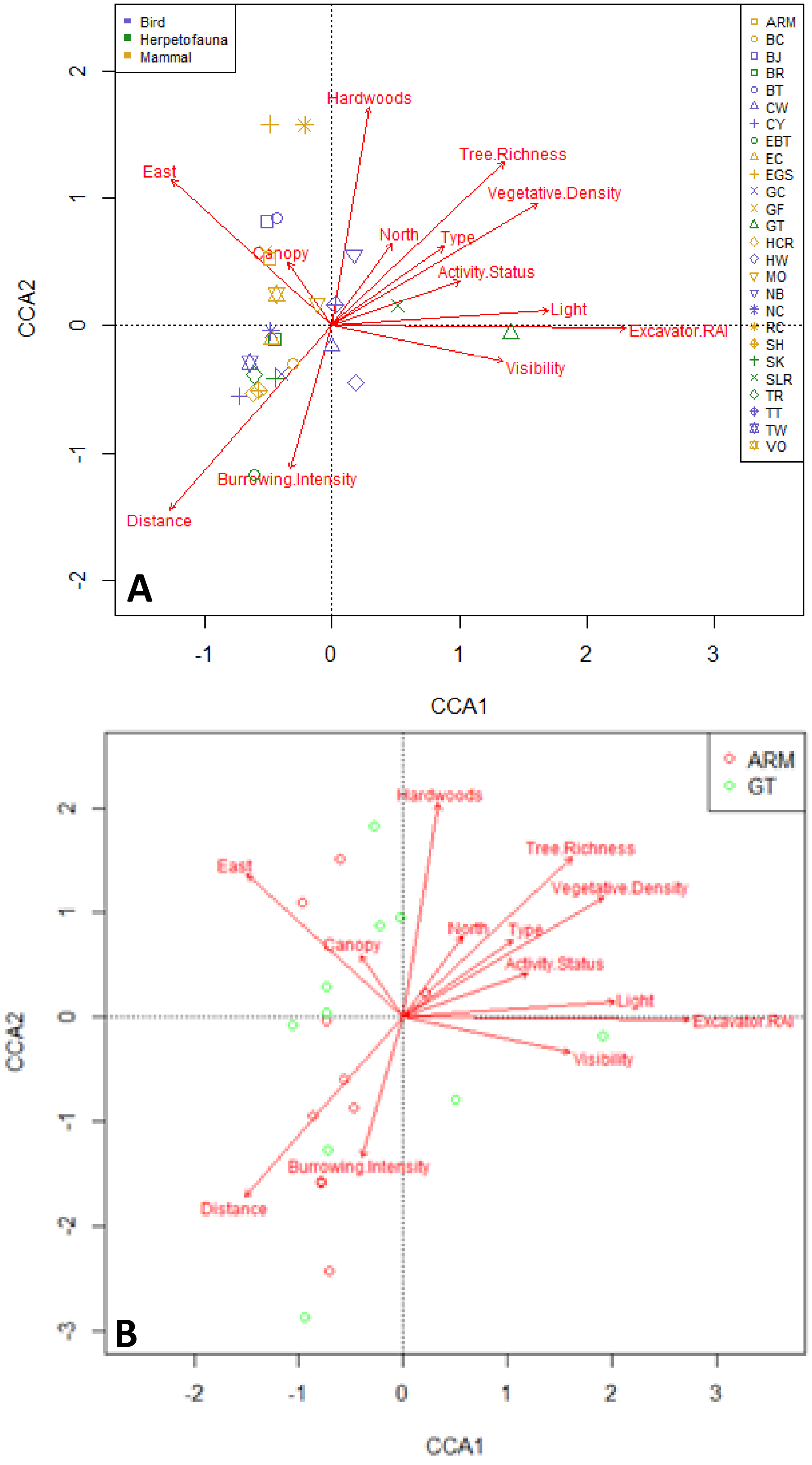
Bird
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Figure 12. Canonical correspondence analysis biplots showing each environmental variable's influence on burrow visitation by individual species (A) and similarity in species composition among monitored burrows (B). Symbols are color coded by class (blue = bird, green = herpetofauna, and yellow = mammal). Legend abbreviations are alphabetized and listed as follows: armadillo (ARM), bobcat (BC), blue jay (BJ), black racer (BR), brown thrasher (BT), Carolina wren (CW), common yellowthroat (CY), eastern box turtle (EBT), eastern cottontail (EC), eastern gray squirrel (EGS), gray fox (GF), gopher tortoise (GT), hispid cotton rat (HCR), house wren (HW), mouse spp. (MO), northern bobwhite (NB), northern cardinal (NC), raccoon (RC), shrew spp. (SH), skink spp. (SK), six lined racerunner (SLR), timber rattlesnake (TR), tufted titmouse (TT), towhee (TW), and Virginia opossum (VO). Green circles represent monitored tortoise burrows and red circles represent monitored armadillo burrows.

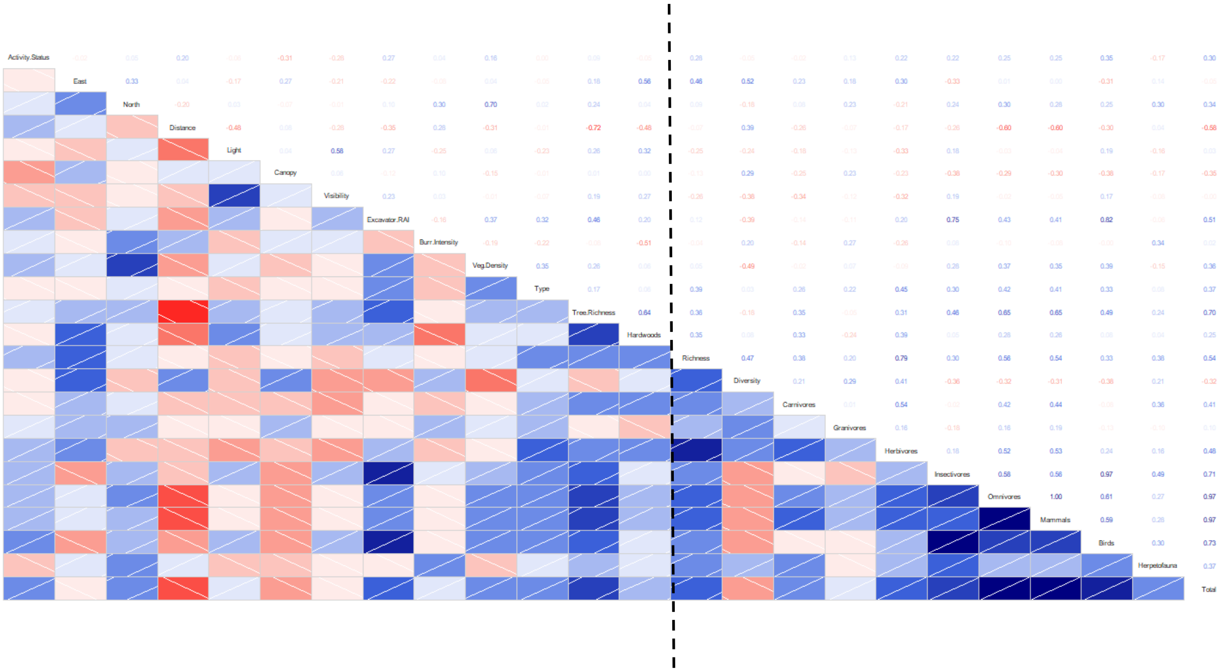
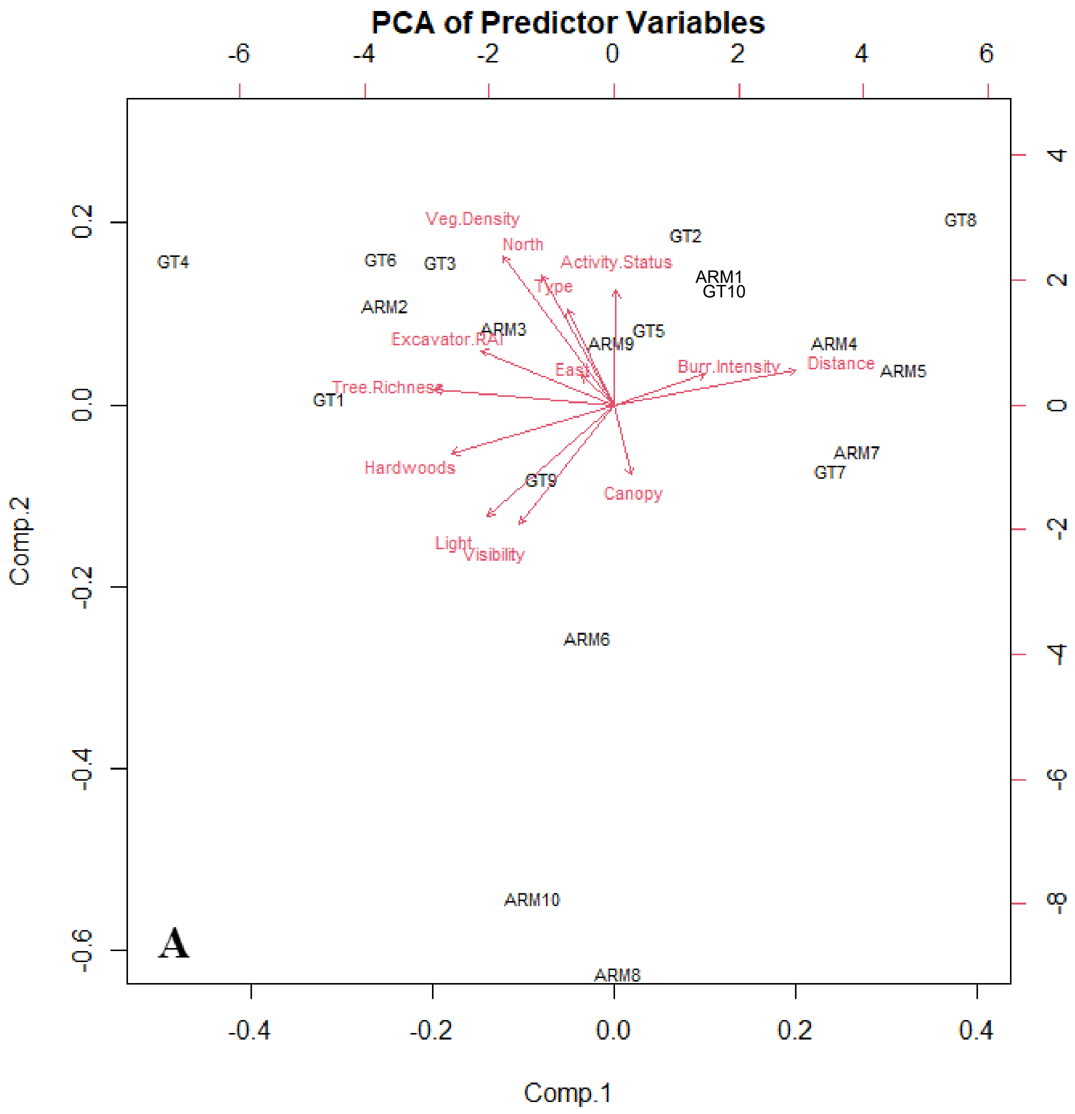


Figure 13. Correlogram showing all pairwise Pearson product moment correlations between predictor and response variables. The upper panel displays correlation coefficients and lower panel boxes indicate the direction of the correlation. Both panels are color coded with blue boxes and text representing positive correlations and red boxes and text representing negative correlations. Variable labels are displayed on the diagonal. The dashed line separates predictor variables (left) from response variable (right). The variable labeled “Status” is coded in binary with 0 indicating abandoned burrows and 1 indicating possibly occupied burrows. The variable “Type” is also coded in binary with 0 for armadillo burrows and 1 for tortoise burrows.


PCA of Predictor Variables
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Comp.2
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Comp.1
GT4
GT6
GT3
GT2
GT8
ARM1
GT10
ARM2
ARM3
GT5
ARM9
ARM4
ARM5
GT1
ARM7
GT7
GT9
ARM6
ARM10
ARM8
Veg.Density
North
Activity.Status
Type
Excavator.RAI
East
Burr.Intensity
Distance
Tree.Richness
Hardwoods
Canopy
Light
Visibility
A

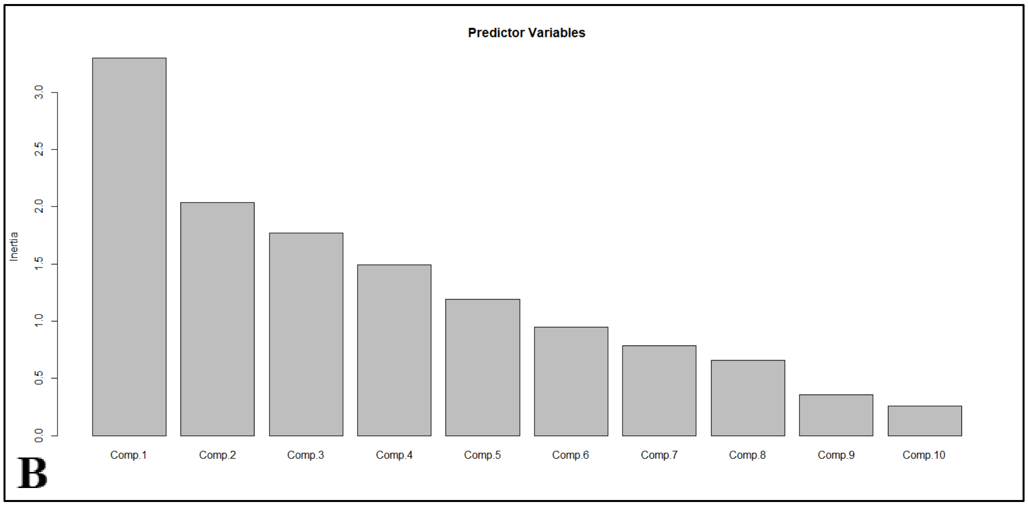

Predictor Variables
Inertia
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Comp.1
Comp.2
Comp.3
Comp.4
Comp.5
Comp.6
Comp.7
Comp.8
Comp.9
Comp.10
B

Figure 14. (A) Correlational principal components analysis biplot showing associations between predictor variables and (B) associated scree plot. The biplot shows where each burrow falls within the two-dimensional space of environmental variables, with sampling locations plotted as abbreviations, “ARM” for armadillo burrows and “GT” for tortoise burrows, followed by the quadrat number where the burrow was located.

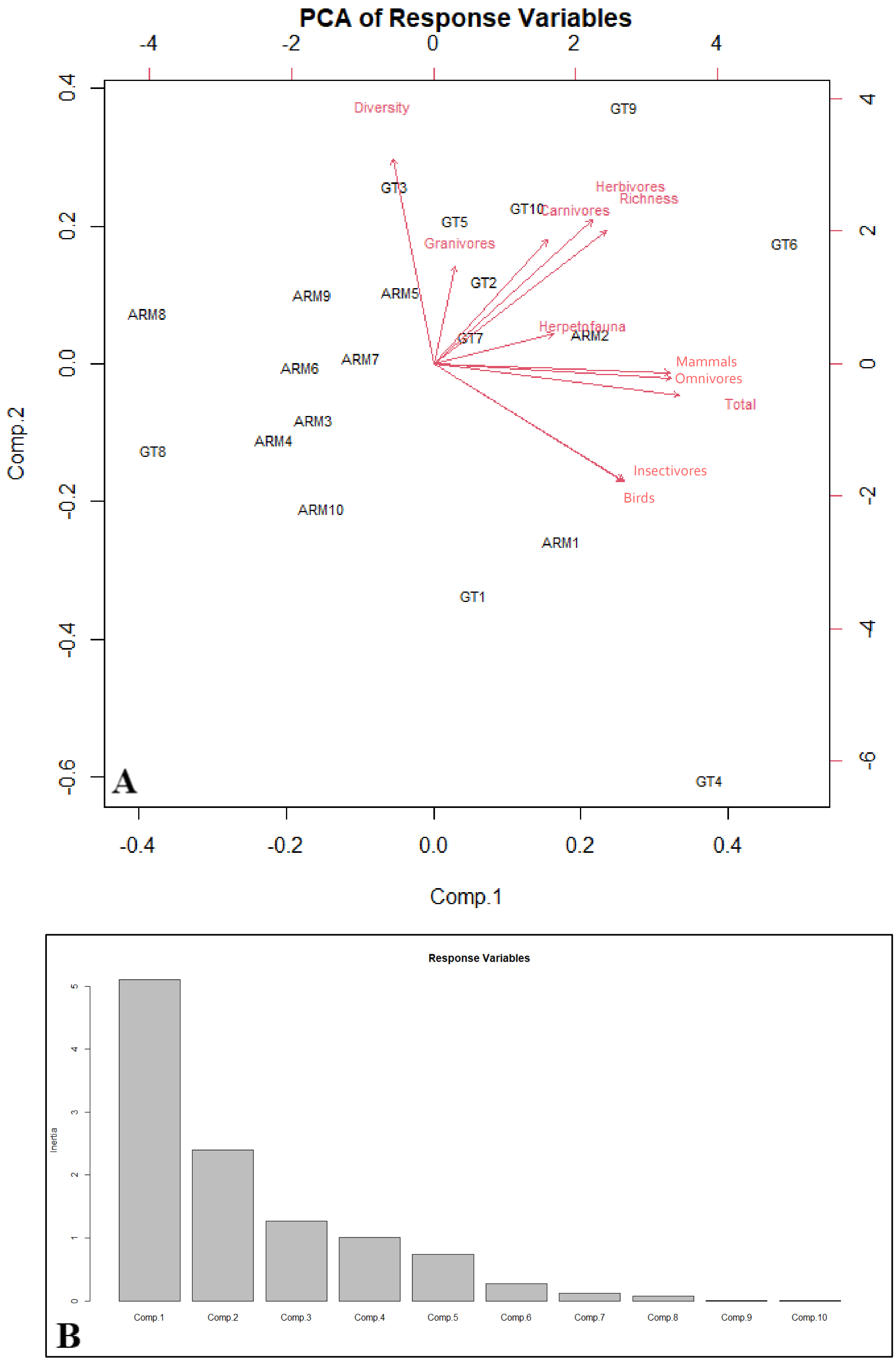
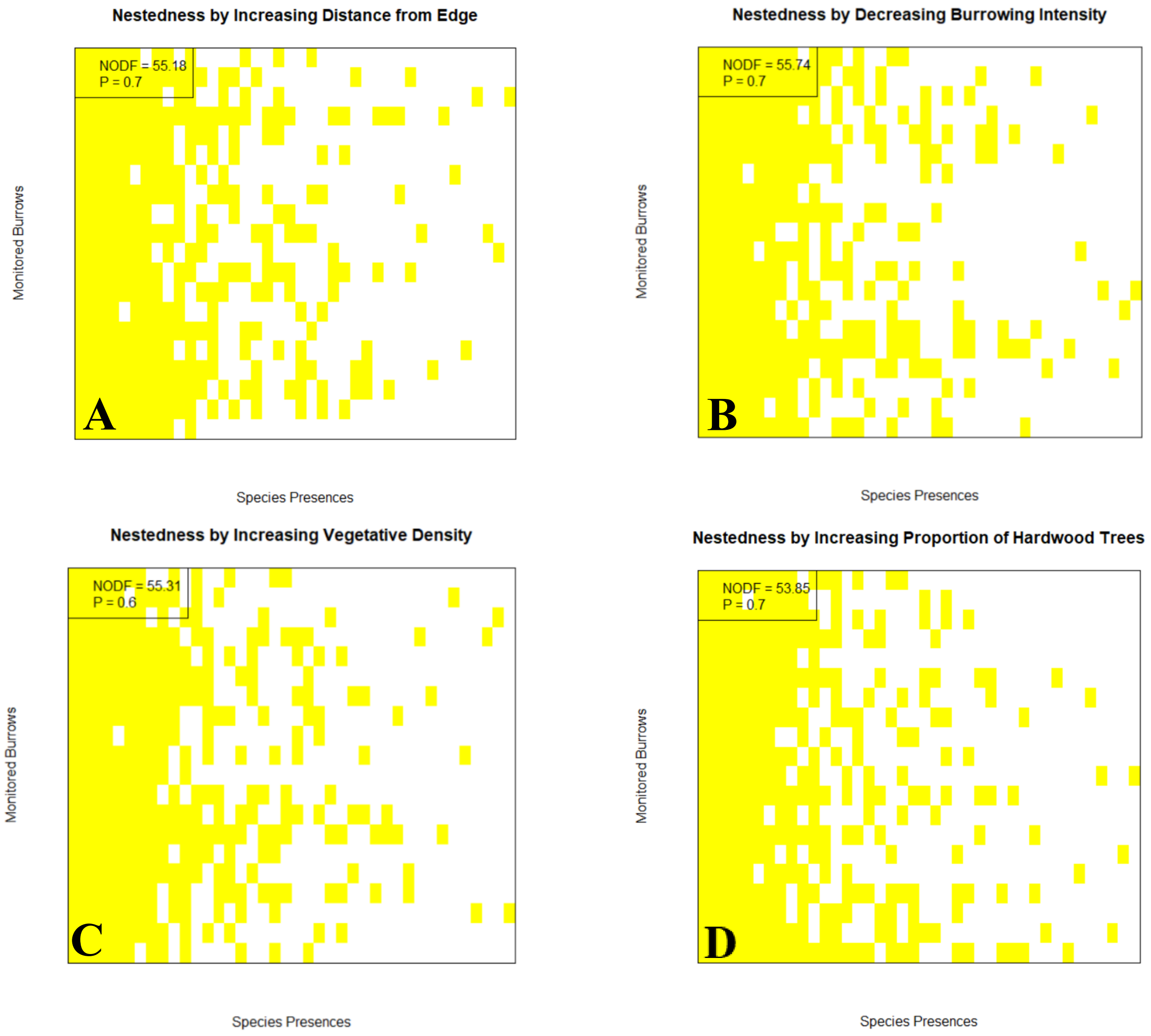

PCA of Response Variables
Comp.1
Comp.2
-0.4
-0.2
0.0
0.2
0.4
0.4
0.2
0.0
-0.2
-0.4
-0.6
-4
-2
0
2
4
4
2
0
-2
-4
-6
Diversity
GT9
GT3
Herbivores
Richness
GT10
Carnivores
GT5
Granivores
GT6
GT2
ARM9
ARM5
ARM8
Herpetofauna
GT7
ARM2
ARM7
ARM6
Mammals
Omnivores
Total
ARM3
ARM4
GT8
Insectivores
Birds
ARM10
ARM1
GT1
GT4
A
Response Variables
Inertia
0
1
2
3
4
5
Comp.1
Comp.2
Comp.3
Comp.4
Comp.5
Comp.6
Comp.7
Comp.8
Comp.9
Comp.10
B

Figure 15. (A) Correlational principal components analysis biplot showing associations between response variables and (B) associated scree plot. The biplot shows where each burrow falls within the two-dimensional space of environmental variables, with sampling locations plotted as abbreviations, “ARM” for armadillo burrows and “GT” for tortoise burrows, followed by the quadrat number where the burrow was located.


Nestedness by Increasing Distance from Edge

Nestedness by Decreasing Burrowing Intensity

Nestedness by Increasing Vegetative Density

Nestedness by Increasing Proportion of Hardwood Trees

Figure 16. Nestedness matrix plots with monitored burrows arranged by (A) increasing distance from habitat edges, (B) decreasing burrowing intensity values, (C) increasing vegetative density, and (D) increasing proportion of hardwood trees. X-axes represent species presences and Y-axes represent monitored burrows. A typical nested pattern would display an ordered decrease in species richness across sites that corresponds with a predictor variable with few to no gaps between species presences within each site row. These results show that dispersal to, and utilization of distant and isolated burrows, and burrows located in low quality habitat, may not have limiting effects on many species observed in this study.

Table 1. Game camera parameters, parameter selection, and selection description/rational for all camera traps deployed in the study area.

Parameter	Selection	Description
Mode	Hybrid	Each trigger produces images and a video
Image Size	8m pixel	Produced high quality images without depleting SD card storage
Video Size	1920x1080m pixels per frame	Highest video quality for accurate species identification
Image Format	Full screen	Widest field of view for improved image review
Image Number	2	Each trigger produced two consecutive still images
Video Length	10 seconds	Each trigger produced a 10 second video following the two images
Interval	2 seconds	Two second lag time between consecutive triggers
LED Control	Low	Lowest LED setting; prevented overexposure of light from reflective soil
Senor Level	Low	Lowest camera sensitivity setting; prevented excess accumulations of false triggers
NV Shutter	High	Highest night vision shutter setting; prevented blurring of night vision images

Table 2. List of observed species with total number of observations (*n.* obs.), relative abundance at armadillo burrows (RAI ARM), and relative abundance at tortoise burrows (RAI GT).

Class	Common Name	Latin Name	Guild	Conservation Status	*n* obs.	RAI ARM	RAI GT
Amphibia	Eastern narrowmouth toad[a]	*Gastrophryne carolinensis*	Insectivore	LC	1	0.03	0
	Southern toad	*Anaxyrus terrestris*	Insectivore	LC	1	0	0.03
	Frog[a]	*Anura*	Insectivore	N/A	2	0.03	0.03
Aves	Barred owl[a]	*Strix varia*	Carnivore	LC	1	0.03	0
	Blue jay[a]	*Cyanocitta cristata*	Omnivore	LC	5	0.08	0.06
	Brown thrasher	*Toxostoma rufum*	Omnivore	LC	18	0.13	0.39
	Carolina wren	*Thryothorus ludovicianus*	Insectivore	LC	624	5.91	12.58
	Common yellowthroat[g]	*Geothlypis trichas*	Insectivore	LC	7	0.03	0.18
	Eastern phoebe	*Sayornis phoebe*	Insectivore	LC	1	0	0.03
	Gray catbird	*Dumetella carolinensis*	Omnivore	LC	31	0.37	0.52
	Hermit thrush[g]	*Catharus guttatus*	Omnivore	LC	2	0	0.06
	House wren	*Troglodytes aedon*	Insectivore	LC	208	0.24	0.55
	Mourning dove	*Zenaida macroura*	Granivore	LC	1	0	0.03
	Northern bobwhite	*Colinus virginianus*	Herbivore	NT	12	0.08	0.61
	Northern cardinal	*Cardinalis cardinalis*	Granivore	LC	27	0.24	0.55
	Towhee	*Pipilo erythrophthalmus*	Omnivore	LC	25	0.34	0.37
	Tufted titmouse[a]	*Baeolophus bicolor*	Omnivore	LC	14	0.08	0.34
Mammalia	Armadillo	*Dasypus novemcinctus*	Omnivore	LC	594	4.8	12.73
	Bobcat[a]	*Lynx rufus*	Carnivore	LC	14	0.24	0.21
	Eastern cottontail	*Sylvilagus floridanus*	Herbivore	LC	115	1.19	2.14
	Eastern gray squirrel	*Sciurus carolinensis*	Omnivore	LC	31	0.29	0.61
	Eastern woodrat	*Neotoma floridana*	Herbivore	LC	2	0	0.06
	Gray fox[a]	*Urocyon cinereoargenteus*	Carnivore	LC	15	0.11	0.34
	Hispid cotton rat	*Sigmodon hispidus*	Omnivore	LC	838	11.43	12.61
	House cat[g]	*Felis catus*	Carnivore	LC	4	0	0.12
	Marsh rice rat[g]	*Oryzomys palustris*	Omnivore	LC	1	0	0.03
	Mouse	*Muroidea*	Omnivore	N/A	2574	27.06	47.74
	Norway rat	*Rattus norvegicus*	Omnivore	LC	1	0.03	0
	Virginia opossum	*Didelphis virginiana*	Omnivore	LC	219	2.19	4.15
	Raccoon	*Procyon lotor*	Omnivore	LC	3	0	0.15
	Shrew	*Soricidae*	Insectivore	N/A	20	0.26	0.31
Reptilia	Black racer	*Coluber constrictor*	Carnivore	LC	55	0.63	0.95
	Common garter	*Thamnophis sirtalis*	Carnivore	LC	1	0	0.03
	Eastern box turtle[a]	*Terrapene carolina*	Omnivore	VU	8	0.13	0.09
	Gopher tortoise[a]	*Gopherus polyphemus*	Herbivore	VU	1045	2.98	29.21
	Gray ratsnake[a]	*Pantherophis spiloides*	Carnivore	LC	3	0.03	0.06
	Green anole	*Anolis carolinensis*	Insectivore	LC	3	0.03	0.06
	Six-line racerunner	*Aspidoscelis sexlineatus*	Insectivore	LC	27	0.08	0.73
	Skink	*Plestiodon*	Insectivore	LC	349	4.69	5.31

	Timber rattlesnake[a]	*Crotalus horridus*	Carnivore	LC	6	0.08	0.09

[a] Species that have not been previously documented utilizing armadillo burrows.

[g] Species that have not been previously documented utilizing gopher tortoise burrows.

Table 3. Monitored burrow types, activity statuses (**PO** for possibly occupied and **Ab** for abandoned), identification number, and quadrats where each was located in the pine stand at the Lake Louise Field Station. "Associate Visits" describes the count of visitation events from vertebrates other than the respective excavator species while "Engineer Visits" are visitation events from the burrow specific excavator.

Type	Status	ID#	Quadrat#	Associate Visits	Engineer Visits	Total Visits
Armadillo	PO	2189	1	434	4	438
Armadillo	PO	2382	2	554	31	585
Armadillo	Ab	87	3	223	24	247
Armadillo	Ab	2107	4	149	0	149
Armadillo	PO	2389	5	256	5	261
Armadillo	Ab	494	6	183	17	200
Armadillo	PO	2154	7	227	5	232
Armadillo	Ab	2169	8	46	2	48
Armadillo	PO	62	9	174	90	264
Armadillo	Ab	2176	10	213	4	217
Tortoise	Ab	2111	1	397	8	405
Tortoise	Ab	2302	2	405	3	408
Tortoise	PO	90	3	220	30	250
Tortoise	PO	2119	4	596	776	1372
Tortoise	Ab	2319	5	228	84	312
Tortoise	PO	89	6	655	50	705
Tortoise	Ab	2351	7	317	4	321
Tortoise	PO	485	8	57	2	59
Tortoise	Ab	64	9	413	0	413
Tortoise	PO	2162	10	390	0	390

Table 4. Chi-square Goodness of Fit test (to a proportional model) table listing expected vs. observed visitation frequency, Pearson standardized residuals, X^2 statistics, and *P*-values for associate species classes and guilds at each burrow type.

Associate Species Category	**Observed ARM**	**Observed GT**	**Expected ARM**	**Expected GT**	**ARM r_p**	**GT r_p**	***X2***	***P***
Class								
Bird	397	652	562.52	486.48	-6.98	7.5	105.01	< 0.001*
Herpetofauna	225	243	250.96	217.039	-1.64	1.76	5.79	0.01*
Mammal	1729	2783	2419.51	2092.49	-14.04	15.09	424.94	< 0.001*
Guild								
Carnivore	42	59	54.16	46.84	-1.65	1.78	5.89	0.01*
Granivore	9	19	15.01	12.99	-1.55	1.67	5.19	0.02*
Herbivore	53	92	77.75	67.25	-2.81	3.02	16.99	< 0.001*
Insectivore	508	750	674.59	583.41	-6.41	6.89	88.71	< 0.001*
Omnivore	1596	2616	2258.64	1953.36	-13.94	14.99	419.2	< 0.001*
Total	2459	3678	3290.91	2846.09	-14.50	15.59	453.46	< 0.001*

* Indicates statistical significance at 0.05 significance level.

Table 5. Binomial and Chi-square Goodness of Fit test (to a proportional model) table listing expected vs. observed visitation frequency, Pearson standardized residuals, X^2 statistics, and *P*-values for common associate species at each burrow type. Binomial tests were used for species with less than five observations at one or both burrow types.

Common Name	Captures ARM	Captures GT	Expected ARM	Expected GT	Arm r_p	GT r_p	X^2	*P*
Bird								
Blue jay^b	3	2	2.68	2.32	-	-	-	1
Brown thrasher^c	5	13	9.65	8.35	-1.50	1.61	4.84	0.03*
Carolina wren^c	224	412	341.05	294.95	-6.34	6.82	86.62	0.001*
Common yellowthroat^b	1	6	3.75	3.25	-	-	-	0.054
Gray catbird^c	14	17	16.62	14.38	-0.64	0.69	0.89	0.3
House wren^c	89	119	111.54	96.46	-2.13	2.29	9.82	0.005*
Northern bobwhite^b	3	20	12.33	10.67	-	-	-	$< 0.001^*$
Northern cardinal^c	9	18	14.48	12.52	-1.44	1.55	4.47	0.04*
Towhee^c	13	12	13.41	11.59	-0.11	0.12	0.027	1
Tufted titmouse^b	3	11	7.51	6.49	-	-	-	0.02*
Herpetofauna								
Black racer^c	24	31	29.49	25.51	-1.01	1.09	2.21	0.1
Eastern box turtle^b	5	3	4.29	3.71	0.34	-0.37	-	0.7
Gopher tortoise^c	113	957	573.78	496.22	-19.24	20.68	797.89	0.001*
Six-line racerunner^b	3	24	14.48	12.52	-	-	-	$< 0.001^*$
Skink spp. ^{c}	178	174	188.76	163.24	-0.78	0.84	1.32	0.2
Timber rattlesnake^b	3	3	3.22	2.78	-	-	-	1
Mammal								
Armadillo^c	182	417	321.21	277.79	-7.77	8.35	130.09	0.001*
Bobcat^c	9	7	8.58	7.42	0.14	-0.15	0.044	1
Eastern cottontail^c	45	70	61.67	53.33	-2.12	2.28	9.71	0.001*
Eastern gray squirrel^c	11	20	16.62	14.38	-1.38	1.48	4.1	0.053
Gray fox^b	4	11	8.04	6.96	-	-	-	0.04*
Hispid cotton rat^c	433	413	453.66	392.34	-0.97	1.04	2.03	0.1
Mouse spp. ^{c}	1025	1564	1388.33	1200.67	-9.75	10.49	205.03	0.001*
Opossum^c	83	136	117.44	101.56	-3.18	3.42	21.77	0.001*
Raccoon^b	0	5	2.68	2.32	-	-	-	0.02*
Shrew spp. ^{c}	10	10	10.72	9.28	-0.22	0.24	0.11	0.8

b Indicates implementation of binomial test.

c Indicates implementation of Chi-square Goodness of Fit test.

* Indicates statistical significance at 0.05 significance level.

Table 6. Regression tables for generalized linear models with response variables: richness, diversity, and total commensal visitation of burrows. Variables listed in the “Model Variable” column are those retained from the full model after model selection via ‘stepAIC’. ΔAIC values describe the magnitude of information contributed to the model by each variable. The *t*-scores were determined using Wald tests (*β*/SE) and represent the direction of the effect of each variable’s deviation from zero (no effect of predictor variable). P-values show the probability of obtaining a result less than or equal to the *t*-score.

Response	**Model Variables**	**Δ AIC**	***β***	**SE**	***t*-value**	***P*-value**
Species Richness	Intercept	-	-7.15x10^{3}	2.09x10^{3}	-3.43	0.003*
	Offset	3.2	6.89	3.26	2.11	0.051
	Activity Status	3.69	2.74	1.23	2.22	0.04*
	Type	8.25	4.22	1.33	3.17	0.006*
	Easting	11.12	0.025	0.0073	3.42	0.003*
Shannon-Weiner Diversity	Intercept	-	4.44x10^{3}	1.43x10^{3}	3.09	0.01*
	Hardwood Proportion	1.11	1.16	0.85	1.36	0.2
	Easting	3.1	0.0016	8.69x10^{-4}	1.79	0.1
	Tree Richness	4.06	-3.18	0.16	-1.97	0.07
	Type	6.27	0.19	0.082	2.37	0.03*
	Light Intensity	6.28	6.38x10^{-4}	2.69x10^{-4}	2.38	0.03*
	Visibility	9.44	-1.01	0.35	-2.91	0.01*
	Northing	11.03	-1.44x10^{-3}	4.52x10^{-4}	-3.18	0.008*
	Burrowing Intensity	13.81	0.056	0.015	3.64	0.003*
Total Commensal Visitation	Intercept	-	-3.43x10^{6}	1.26x106	-2.72	0.02*
	Easting	0.93	0.49	0.47	1.05	0.3
	Visibility	2.05	200.6	160	1.25	0.2
	Canopy Cover	2.15	-257.7	202.8	-1.27	0.2

	Hardwood Proportion	3.94	-737.9	474.2	-1.56	0.1
	Burrowing Intensity	4.83	-15.49	9.18	-1.69	0.1
	Excavator RAI	5.81	0.66	0.36	1.83	0.1
	Vegetative Density	8.09	-1.37x10^{3}	640.1	-2.14	0.06
	Northing	11.07	0.97	0.38	2.54	0.03*
	Activity Status	11.28	106.6	41.51	2.57	0.03*
	Tree Richness	13.03	266.8	95.27	2.8	0.02*
	Offset	18.05	381.7	41.29	3.48	0.01*
	Type	22.99	202.9	36.49	5.56	0.004*

* Indicates statistical significance at 0.05 significance level.

Table 7. Regression table for generalized linear models for class level visitation. Variables listed in the “Model Variable” column are those retained from the full model after model selection via ‘stepAIC’. ΔAIC values describe the magnitude of information contributed to the model by each variable. The *t*-scores were determined using Wald tests (*β*/SE) and represent the direction of the effect of each variable’s deviation from zero (no effect of predictor variable). P-values show the probability of obtaining a result less than or equal to the *t*-score.

Response	**Model Variable**	**Δ AIC**	***β***	**SE**	***t*-value**	***P*-value**
Bird Visitation	Intercept	-	$-6.96x10^{5}$	$3.55x10^{5}$	-1.96	0.08
	Excavator RAI	2.27	1.11	$7.39x10^{-1}$	1.51	0.1
	Visibility	2.81	0.745	0.46	1.61	0.1
	Vegetative Density	3.04	-300.2	181.5	-1.65	0.1
	Distance	3.31	$4.55x10^{-1}$	$2.67x10^{-1}$	1.7	0.1
	Burrowing Intensity	4.32	-5.49	2.91	-1.88	0.09
	Northing	4.76	2.05	$1.04x10^{-1}$	1.96	0.08
	Hardwood Proportion	7.34	-260.2	108.8	-2.39	0.04*
	Tree Richness	8.9	68.29	25.85	2.64	0.02*
	Canopy	10.86	-1.15	0.39	-2.95	0.01*
Herpetofauna Visitation	Intercept	-	$-4.95x10^{5}$	$1.33x10^{5}$	-3.74	0.003*
	Type	0.06	4.49	4.31	1.04	0.3
	Burrowing Intensity	4.54	-1.8	0.92	-1.97	0.07
	Hardwood Proportion	6.49	-64.11	27.88	-2.29	0.04*
	Activity Status	6.6	-10.26	4.43	-2.32	0.04*
	Canopy	7.65	-42.9	17.22	-2.49	0.03*
	Distance	7.99	0.31	0.12	2.55	0.02*
	Tree Richness	13.08	34.28	10.22	3.36	0.007*
	Northing	15.46	-0.15	0.039	3.74	0.003*
Mammal	Intercept	-	$-2.48x10^{6}$	$9.03x10^{5}$	-2.74	0.02*

Visitation						
	Excavator RAI	1.89	0.32	0.26	1.23	0.2
	Visibility	2.42	145.8	110.8	1.32	0.2
	Tree Richness	2.84	98.24	70.97	1.38	0.2
	Distance	4.03	-1.33	0.85	-1.57	0.1
	Hardwood Proportion	4.33	-473.4	293.2	-1.62	0.1
	Easting	4.71	0.47	0.28	1.67	0.1
	Burrowing Intensity	4.96	-11.85	6.94	-1.71	0.1
	Vegetative Density	8.85	-102.1	455	-2.25	0.059
	Northing	11.21	0.69	0.27	2.56	0.03*
	Activity Status	24.47	122.8	27.96	4.39	0.003*
	Offset	27.99	380.7	77.14	4.94	0.001*
	Type	35.56	179.8	28.88	6.23	< 0.001*

* Indicates statistical significance at 0.05 significance level.

Table 8. Regression table for generalized linear models for guild level visitation. Variables listed in the "Model Variable" column are those retained from the full model after model selection via 'stepAIC'. ΔAIC values describe the magnitude of information contributed to the model by each variable. The *t*-scores were determined using Wald tests (*β*/SE) and represent the direction of the effect of each variable's deviation from zero (no effect of predictor variable). P-values show the probability of obtaining a result less than or equal to the *t*-score.

Response	Model Variable	AIC	*β*	SE	*t*-value	*P*-value
Carnivore Visitation	Intercept	-	-3.71×10^{4}	3.24×10^{4}	-1.15	0.2
	Northing	0.27	0.011	0.0095	1.15	0.2
	Excavator RAI	0.33	-0.014	0.012	-1.17	0.2
	Hardwood Proportion	1.05	7.31	5.43	1.35	0.2
	Canopy	1.3	-7.98	5.69	-1.4	0.1
	Vegetative Density	1.79	-27.33	18.05	-1.51	0.1
	Distance	2.34	-0.045	0.027	-1.63	0.1
	Type	4.49	2.99	1.46	2.05	0.06
	Visibility	4.63	-8.57	4.12	-2.08	0.06
Granivore Visitation	Intercept	-	-3.49×10^{4}	3.05×10^{4}	-1.15	0.2
	Northing	0.13	0.0082	0.0092	0.89	0.4
	Burrowing Intensity	1.25	-0.19	0.18	-1.11	0.3
	Light Intensity	1.28	-0.0042	0.0038	-1.12	0.3
	Excavator RAI	2.48	-0.011	0.0085	-1.33	0.2
	Offset	4.3	-5.25	3.26	-1.61	0.1
	Type	5.34	1.87	1.06	1.76	0.1
	Vegetative Density	7.33	-31.96	15.67	-2.04	0.08
	Visibility	8.71	8.33	3.74	2.23	0.06
	Easting	12.75	0.026	0.0093	2.76	0.02^{*}
	Activity Status	13.02	2.61	0.93	2.79	0.02^{*}

	Distance	20.93	-0.11	0.028	-3.88	0.006*
	Hardwood Proportion	22.58	-27.79	6.76	-4.11	0.004*
Herbivore Visitation	Intercept	-	2.64x10^{4}	3.42x10^{4}	1.07	0.3
	Northing	0.6	-0.013	0.01	-1.24	0.2
	Vegetative Density	0.78	-23.26	18.17	-1.28	0.2
	Canopy	2.94	-11.01	6.27	-1.76	0.1
	Activity Status	3.29	2.51	1.38	1.83	0.09
	Light Intensity	3.87	-0.0075	0.0039	-1.94	0.07
	Easting	9.43	0.025	0.0085	2.91	0.01*
	Distance	9.99	-0.081	0.027	-3.01	0.01*
	Type	10.01	4.39	1.46	3.01	0.01*
Insectivore Visitation	Intercept	-	-1.06x10^{6}	3.96x10^{5}	-2.68	0.02*
	Activity Status	0.73	-13.39	12.06	-1.11	0.2
	Excavator RAI	2	1.12	0.82	1.37	0.2
	Visibility	3.86	0.89	0.53	1.7	0.1
	Burrowing Intensity	7.51	-7.38	3.24	-2.28	0.052
	Distance	7.57	0.73	0.32	2.29	0.051
	Vegetative Density	9.05	-509.3	202.8	-2.51	0.03*
	Northing	10.18	0.31	0.11	2.68	0.02*
	Hardwood Proportion	10.78	-334.7	120.8	-2.77	0.02*
	Canopy	13.49	-1.48	0.47	-3.18	0.01*
	Tree Richness	14.16	96.03	29.33	3.27	0.01*
Omnivore Visitation	Intercept	-	-2.32x10^{6}	8.86x10^{5}	-2.62	0.03*
	Distance	1.34	-0.93	0.83	-1.13	0.2
	Excavator RAI	2.3	0.33	0.26	1.29	0.2
	Tree Richness	2.56	93.21	69.6	1.34	0.2
	Hardwood Proportion	2.8	-396.2	287.5	-1.38	0.2

	Visibility	3.38	159.7	108.6	1.47	0.1
	Easting	3.73	0.42	0.28	1.52	0.1
	Burrowing Intensity	4.46	-11.13	6.91	-1.63	0.1
	Vegetative Density	6.54	-861.7	446.2	-19	0.09
	Northing	10.39	0.65	0.26	2.45	0.04*
	Activity Status	22.52	112.6	27.42	4.11	0.004*
	Offset	28.01	373.5	75.65	4.94	0.001*
	Type	34.13	169	28.32	5.97	< 0.001*

* Indicates statistical significance at 0.05 significance level.