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Gopher Tortoise (*Gopherus polyphemus*) Vertebrate Burrow Commensals within a Private, Working Forest Landscape

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The Gopher Tortoise (*Gopherus polyphemus*) is a keystone species endemic to the Coastal Plain ecoregion of the southeastern United States. Gopher Tortoises excavate extensive burrows that are used by over 60 vertebrate and 300 invertebrate species. Our understanding of burrow commensals has generally been limited to Longleaf Pine (*Pinus palustris*) savanna and xeric uplands and shrublands, excluding private, working pine (*Pinus* spp.) forests that are known to harbor tortoise populations. Therefore, we used passive infrared wildlife cameras to document vertebrate burrow commensals and evaluate differences in composition across burrow classifications (i.e., abandoned, active, and inactive) within a private, working Loblolly Pine (*Pinus taeda*) forest located in the Upper Coastal Plain ecoregion of Georgia, USA. Our study showed that the composition of vertebrate commensals did not differ across abandoned, active, or inactive tortoise burrows, indicating that burrows, regardless of classification, may provide a similar suite of resources (e.g., refugia, forage) to vertebrate commensals. Also, we observed numerous species using burrows that typically occur in other landscapes with known tortoise populations (e.g., Longleaf Pine savannah). We encourage continued monitoring of tortoise burrows and other potential refugia within working forests to better understand how these structures contribute to species abundance and persistence within these forests.

THE Gopher Tortoise (*Gopherus polyphemus*; hereafter, tortoise) is an ecosystem engineer and considered a keystone species within the southeastern Coastal Plain ecoregion of the United States (e.g., Boglioli et al., 2000; Kinlaw and Grasmueck, 2012; Pike and Mitchell, 2013; Catano and Stout, 2015; Dziadzio and Smith, 2016; Johnson et al., 2017). Tortoises excavate extensive burrows whose construction and maintenance alter local abiotic and biotic characteristics (Kaczor and Hartnett, 1990; Kinlaw and Grasmueck, 2012; Dziadzio and Smith, 2016). Burrow construction disturbs local soil conditions, providing appropriate conditions for pioneer plant species (Kaczor and Hartnett, 1990; Boglioli et al., 2000). Tortoise burrows also provide resources, such as refugia, forage, and nesting sites, for more than 300 invertebrate and 60 vertebrate species (Young and Goff, 1939; Witz et al., 1991; Lips, 1991; Alexy et al., 2003; Catano and Stout, 2015; Dziadzio and Smith, 2016; White and Tuberville, 2017; Potash et al., 2020; Murphy et al., 2021). However, uncertainty exists regarding the effects declining tortoise populations will have on abiotic and biotic processes associated with burrow construction and species that use tortoise burrows in some capacity (Hermann et al., 2002; McCoy et al., 2006; Berish and Leone, 2014; Catano and Stout, 2015).

Use of tortoise burrows by commensal vertebrate species has been described as obligate, facultative, frequent, or occasional, with burrow use varying in frequency based on the ecology of commensal species, vegetation composition and structure, season, and burrow density and classification (Jackson and Milstrey, 1989; Witz et al., 1991; Hyslop et al., 2009; Catano and Stout, 2015; Dziadzio and Smith, 2016; Potash et al., 2020). Of the documented vertebrate burrow commensals, only a few have received considerable attention with regard to why and when the burrow is used. These species include the Gopher Frog (*Lithobates capito*), Eastern Indigo Snake (*Drymarchon couperi*), and Florida Mouse (*Podomys floridanus*; Layne and Jackson, 1994; Kent et al., 1997; Alexy et al., 2003; Hyslop et al., 2009; Roznik and Johnson, 2009). Our understanding of the relationships and dynamics between tortoise burrows and many other vertebrate commensals is currently limited. We also have an incomplete understanding of the composition of vertebrate commensal communities across different forest types and land uses inhabited by tortoises (e.g., Longleaf Pine [*Pinus palustris*] savanna, xeric shrubland, private, working pine [*Pinus* spp.] forests), as burrow commensal studies have generally been restricted to a few study areas (Witz et al., 1991; Alexy et al., 2003; Catano and Stout, 2015; Dziadzio and Smith, 2016; Potash et al., 2020; Murphy et al., 2021).

Private lands have received considerable attention regarding their capacity to support tortoise populations and aid in conservation strategies (Hermann et al., 2002; Underwood et al., 2012). Currently, private lands encompass >80% of the species' range. However, private lands, especially private working lands, remain relatively understudied regarding tortoise ecology (Hermann et al., 2002; Underwood et al., 2012; Greene et al., 2020). Private working forests (hereafter working forest) are common within the range of the Gopher Tortoise, and tortoises are known to inhabit and persist within these landscapes (Jones and Dorr, 2004; Diemer Berish et al., 2012; Wigley et al., 2012; Duffie, 2020). Tortoises are generally distributed within and along permanently open areas, such as roadside verges or utility rights-of-way, or recently harvested forest stands exhibiting early successional vegetation conditions (e.g., sparse canopy cover, abundant herbaceous understory) within these forests (Jones and Dorr, 2004; Diemer Berish et al., 2012; Wigley et al., 2012; Duffie, 2020; Marshall et al., 2022). Although portions of working

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forests harbor tortoise populations, the composition of vertebrate burrow commensals is relatively unknown compared to other, more heavily studied landscapes, such as Longleaf Pine savannas and military installations.

Within working forests, stands are generally surveyed for tortoise burrows prior to forest management, with buffers established to reduce the risk of these activities disturbing burrows (Jones and Dorr, 2004; Wigley et al., 2012; Smith et al., 2015). It has been suggested that some surveys conducted within working forests focus solely on locating active burrows with the possible rationale being that active burrows are more likely to contain tortoises or are more easily detected than other classifications (Wigley et al., 2012). It is improbable that all working forests are surveyed exclusively for active burrows. However, those that heavily emphasize the detection of active burrows over other categories risk reduced mitigation rates (i.e., projects or programs that offset negative impacts to natural resources) and/or increased tortoise mortalities, as non-active burrows are known to contain tortoises (Witz et al., 1991; Tuberville and Dorcas, 2001; Smith et al., 2005; Marshall, 2021). Furthermore, an emphasis on detecting active burrows may also negatively affect vertebrate commensals, which have been documented using inactive and abandoned burrows in non-working forest landscapes (Witz et al., 1991; Dziadzio and Smith, 2016). It is likely that inactive and abandoned burrows are used by vertebrate commensals within working forests; however, to our knowledge, no published information exists regarding vertebrate use of tortoise burrows within these forests.

Our objectives were to identify vertebrate commensals using tortoise burrows and determine if vertebrate burrow commensal composition differed across active, inactive, and abandoned burrows in a working forest. We hypothesized that the composition of the vertebrate commensal community would differ across burrow classifications. We predicted that active burrows would support a distinct suite of vertebrate species compared to inactive and abandoned burrows, with this suite of species benefiting from recent tortoise activity (e.g., feces [coprophagous insects], burrow maintenance) within these burrows (Lips, 1991; Kent et al., 1997; Dziadzio and Smith, 2016). We predicted that vertebrate commensal composition of inactive and abandoned burrows would be similar with species using these burrow classifications being less reliant on recent tortoise activity to obtain resources from burrows than commensals associated with active burrows.

MATERIALS AND METHODS

Study area.—Our study was conducted in a working pine forest located in the Upper Coastal Plain ecoregion (Atlantic Southern Loam Plains subunit) of Toombs and Emanuel Counties in Georgia, USA. The site was 32.4 km^2 and consisted predominantly of managed Loblolly Pine (*Pinus taeda*) planted in even-aged stands (22.9 km^2). Adjacent pine stands differed in edaphic (e.g., elevation, soil characteristics) and vegetation conditions (e.g., understory composition and density, canopy cover) because of the timing of forest management (e.g., stand establishment, mid-rotational thinning, final harvest). Stand age classes within our study site ranged from 0–3 years, which includes recently harvested and planted stands, to ~30+ years. Chemical and mechanical site preparation were conducted prior to planting of pines to control woody plant species. Mechanical site preparation was excluded on soils conducive for tortoises. Banded weed control was applied over planted rows one year after stand establishment. This method was used to minimize chemical use and maintain a more diverse plant community. Pine stands were thinned between 12- and 15-years post-stand establishment, with stands thinned to a basal area of 16–17 m^2 (70–75 ft^2). Stands were assessed post-thin for mid-rotation release (i.e., herbicide application) to control woody plant species and identify fertilizer opportunities. Pine stands were generally harvested 25 years post-stand establishment. Managed pine stands were interspersed with streamside management zones and hardwood areas (5.49 km^2), roads (paved and unpaved; 0.78 km^2), non-forest areas (e.g., wildlife openings, food plots; 0.09 km^2), and utility rights-of-way (0.39 km^2). Lands surrounding our study area consisted of agricultural fields, Loblolly Pine stands managed primarily for timber production, suburban and rural development, and pine forests managed primarily for other objectives (e.g., hunting land). The climate was subtropical with a mean annual temperature of 18.5°C and mean annual precipitation of 130 cm (National Oceanic and Atmospheric Administration, 2021).

Field methods.—We used passive infrared wildlife cameras (Spartan SR1-BK, Duluth, GA, USA) to identify vertebrate commensals using tortoise burrows from June–August in 2018 and 2019. Burrows used in our study were derived from datasets of burrow detections from other studies conducted on the study site during 2018 and 2019 (Marshall, 2021; Marshall et al., 2022). Within these datasets, we classified burrows as active (half-moon shaped opening and entrance often having plastron skid marks or footprints), inactive (minimal sign of recent use), or abandoned (burrow opening collapsed or shape was altered; Auffenberg and Franz, 1982; Stober and Smith, 2010; Wigley et al., 2012). We only monitored adult Gopher Tortoise burrows (burrow width $\geq$ 23 cm; Alford, 1980; Doonan and Stout, 1994). We monitored all burrows for 14 days (a single set), with three sets occurring in 2018 and four sets in 2019. Within each set, we evenly split 18 cameras across a randomly selected set of abandoned, active, and inactive tortoise burrows (6 cameras per category). We set cameras with a trigger interval of five seconds and captured photos for 24 hours throughout each set. We set the photo resolution to five megapixels. We visually inspected all photos and identified detected vertebrates to species. We combined all detections of *Peromyscus* spp. into a single group due to difficulty in accurately identifying species. We recorded date, time, a unique burrow identifier, and burrow status (i.e., active, inactive, or abandoned) for each detected individual. We considered multiple detections of the same species within ten minutes of each other to be a single detection event to reduce the probability of counting the same individual multiple times. We conducted all research under the University of Georgia Institutional Animal Care and Use Committee (IACUC) protocol A2018 01-018-Y3-A0.

Statistical analyses.—We used rarefaction implemented in the vegan package in R to identify whether species richness differed across sampling years because of unequal sampling effort (Oksanen et al., 2020; R Core Team, 2020). We also

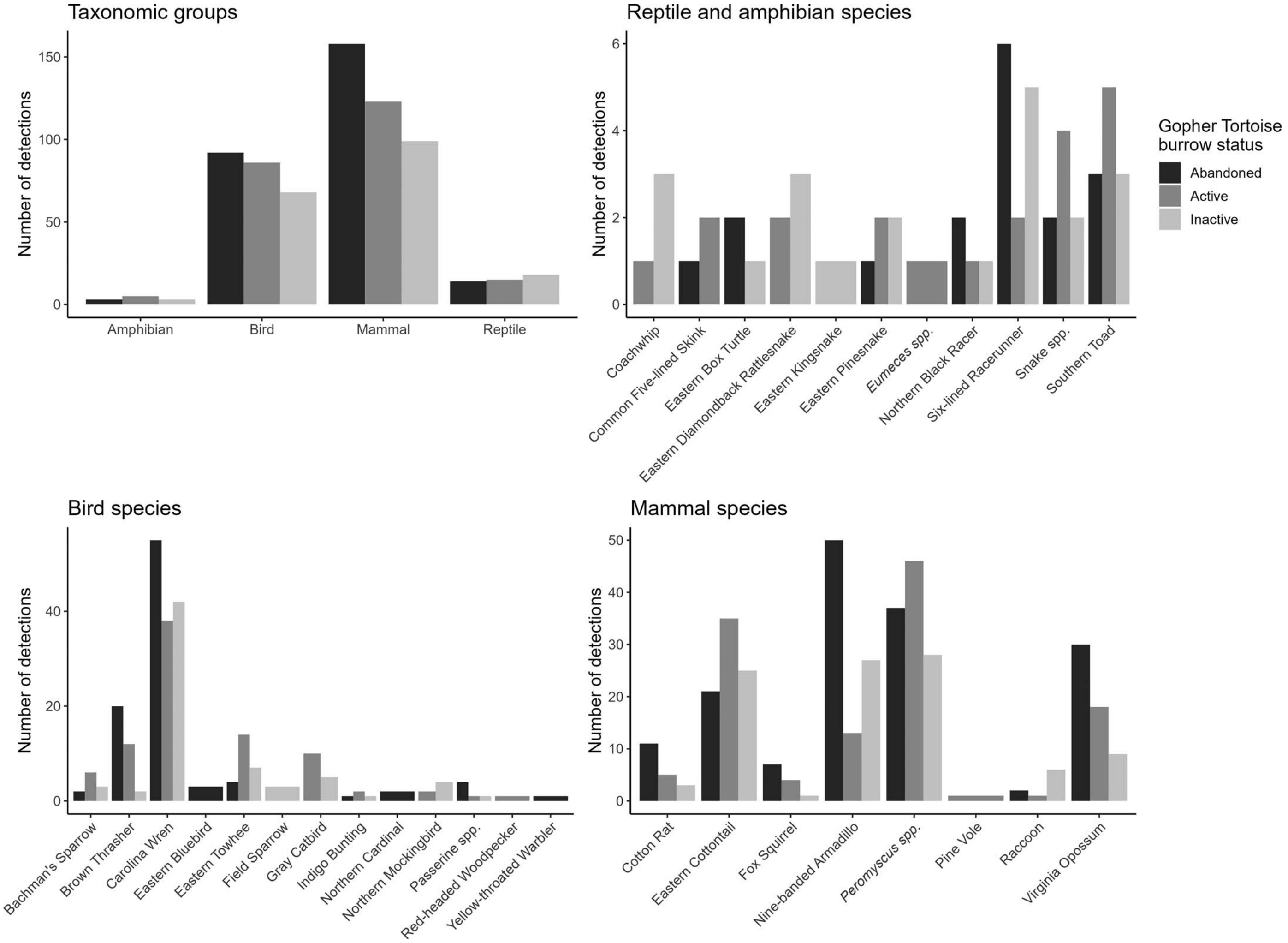

Fig. 1. Number of unique observations of vertebrate burrow commensals by taxonomic group (top left), reptile and amphibian species (top right), bird species (bottom left), and mammal species (bottom right). Vertebrate burrow commensal data were collected in a private, working forest landscape dominated by planted Loblolly Pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018–2019.

used linear regression to determine if unequal sampling across years resulted in differences in the number of observations. We used non-metric multidimensional scaling to investigate dissimilarity in vertebrate commensal community composition across burrow classifications. Non-metric multidimensional scaling was implemented using the vegan package in R (Oksanen et al., 2020). We used a Bray-Curtis distance measure, as this is a commonly used distance measure when conducting ordinations with ecological data. The Bray-Curtis distance measure is invariant to changes in units and has the capacity to deal with datasets containing multiple zeros (e.g., count data; Rees et al., 2004). We visually inspected Shepard plots and stress values (e.g., stress $\leq$ 0.05 provides an excellent representation of the data, stress $>$ 0.2 provides a poor representation of the underlying data) to determine if the data were being adequately represented within a certain number of dimensions (e.g., two or three dimensions; Clark, 1993). We then used the function "adonis" within the vegan package to test the significance of the environmental variables (i.e., burrow classification) using permutation tests (Oksanen et al., 2020). We considered all tests significant at $\alpha = 0.05$.

RESULTS

We had 698 detections encompassing 30 vertebrate species across 1,764 trap days and 125 tortoise burrows (Fig. 1). We removed one burrow from the dataset due to a malfunctioning camera. Sampling effort varied across years, with 756 sampling days in 2018 and 1,008 sampling days in 2019. We found no indication of differences in species richness or total observations ($z = -0.46$, $P = 0.63$) because of unequal sampling across survey years (Fig. 2). We detected 9 reptile (not including Gopher Tortoises), 1 amphibian, 12 bird, and 8 mammal species using tortoise burrows (Table 1). We were unable to determine the species of 8 snake and 6 bird observations. However, we identified the bird observations down to order Passeriformes. Non-metric multidimensional scaling attained a convergent three-dimensional solution with a stress value of 0.15. This stress value indicates that the underlying data were well represented in three dimensions. We could have continued to reduce the stress value by increasing the number of dimensions (e.g., 5-dimensional). However, increasing dimensionality beyond three would significantly reduce our ability to

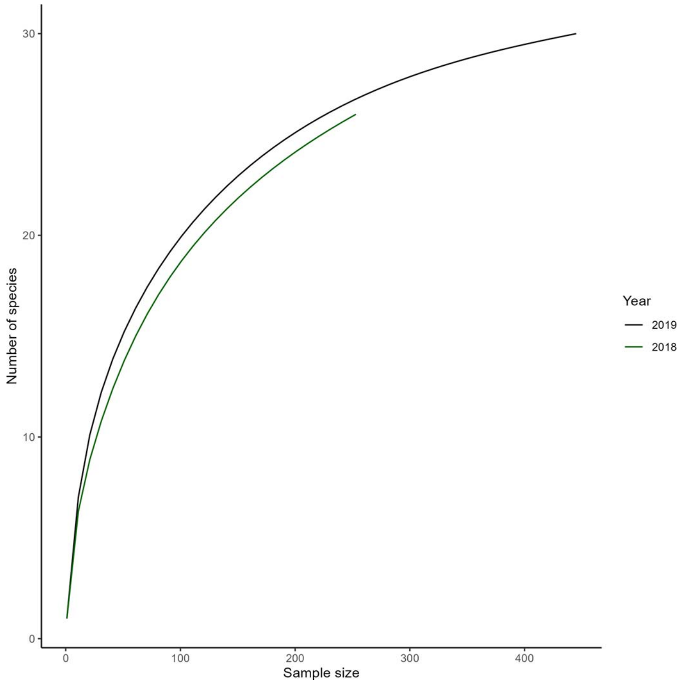

Fig. 2. Rarefaction curves of species richness during 2018 and 2019. Vertebrate burrow commensal data were collected in a private, working forest landscape dominated by planted Loblolly Pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018–2019.

Table 1. Number of unique observations of all commensal species detected using Gopher Tortoise (*Gopherus polyphemus*) burrows. Data were collected in a private, working forest landscape dominated by planted Loblolly Pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018–2019.

Birds	Detections
Carolina Wren (*Thryothorus ludovicianus*)	135
Brown Thrasher (*Toxostoma rufum*)	34
Eastern Towhee (*Pipilo erythrophthalmus*)	26
Gray Catbird (*Dumetella carolinensis*)	15
Bachman's Sparrow (*Peucaea aestivalis*)	11
Northern Mockingbird (*Mimus polyglottos*)	6
Passerine spp.	6
Indigo Bunting (*Passerina cyanea*)	4
Eastern Bluebird (*Sialia sialis*)	3
Field Sparrow (*Spizella pusilla*)	3
Northern Cardinal (*Cardinalis cardinalis*)	2
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	1
Yellow-throated Warbler (*Setophaga dominica*)	1
Mammals	Detections
Peromyscus spp.	112
Nine-banded Armadillo (*Dasypus novemcinctus*)	100
Eastern Cottontail (*Sylvilagus floridanus*)	83
Virginia Opossum (*Didelphis virginiana*)	57
Cotton Rat (*Sigmodon hispidus*)	19
Fox Squirrel (*Sciurus niger*)	12
Raccoon (*Procyon lotor*)	9
Pine Vole (*Microtus pinetorum*)	1
Reptiles	Detections
Snake spp.	8
Eastern Diamondback Rattlesnake (*Crotalus adamanteus*)	5
Eastern Pinesnake (*Pituophis melanoleucus*)	5
Northern Black Racer (*Coluber constrictor*)	4
Coachwhip (*Masticophis flagellum*)	4
Eastern Kingsnake (*Lampropeltis getula*)	1
Six-lined Racerunner (*Cnemidophorus sexlineatus*)	13
Common Five-lined Skink (*Eumeces fasciatus*)	3
Eumeces spp.	1
Eastern Box Turtle (*Terrapene carolina*)	3
Amphibians	Detections
Southern Toad (*Anaxyrus terrestris*)	11

interpret model results. Composition of the vertebrate burrow commensal community did not differ across abandoned, active, or inactive burrows ($r^2 = 0.1$, $P = 0.48$; Fig. 3). We conducted a *post hoc* ordination to determine if mammal species composition differed across burrow classifications. Visual inspection of the raw data revealed a greater number of mammal commensals using abandoned and inactive burrows compared to active burrows (Fig. 1). We found no difference in mammal species composition across abandoned, active, and inactive burrows ($r^2 = 0.14$, $P = 0.16$).

DISCUSSION

Contrary to our prediction, we documented a similar suite of vertebrate commensals using abandoned, active, and inactive tortoise burrows within our study site. Our results suggest that tortoise burrows, regardless of classification, may provide a similar suite of resources (e.g., forage, refugia) to vertebrate commensals inhabiting our study site. Previous studies documented differences in the frequency of burrow use by taxa (e.g., mammal, reptile) and species (e.g., Gopher Frog) among burrow classifications (Lips, 1991; Witz et al., 1991; Kent et al., 1997; Dziadzio and Smith, 2016). It has been suggested that differences in commensal burrow use arises from active burrows providing additional resources to commensal species, such as recently deposited tortoise feces, compared to abandoned and inactive burrows (Lips, 1991; Dziadzio and Smith, 2016). Documented differences in commensal composition may relate more to the spatial distribution of surveyed tortoise burrows than classification (Kent et al., 1997). In other words, surveyed active burrows may have been clumped within areas exhibiting specific vegetation characteristics (e.g., early successional pine community) or adjacent to important landscape features (e.g., ephemeral wetlands) that are well suited or required for specific taxa or species (Witz et al., 1991).

Commensal species observed in our study overlapped with those previously recorded at sites not classified as working forests (e.g., Longleaf Pine savanna, xeric uplands; e.g., Lips, 1991; Kent et al., 1997; Alexy et al., 2003; Pike and Grosse, 2006; Catano and Stout, 2015; Dziadzio and Smith, 2016; White and Tuberville, 2017; Murphy et al., 2021). This suggests that working forests, and tortoise burrows contained within, have the capacity to support some of the same vertebrate commensal species recorded at other sites (e.g., Longleaf Pine savannah, xeric uplands) inhabited by tortoises. Vegetation structure and composition within

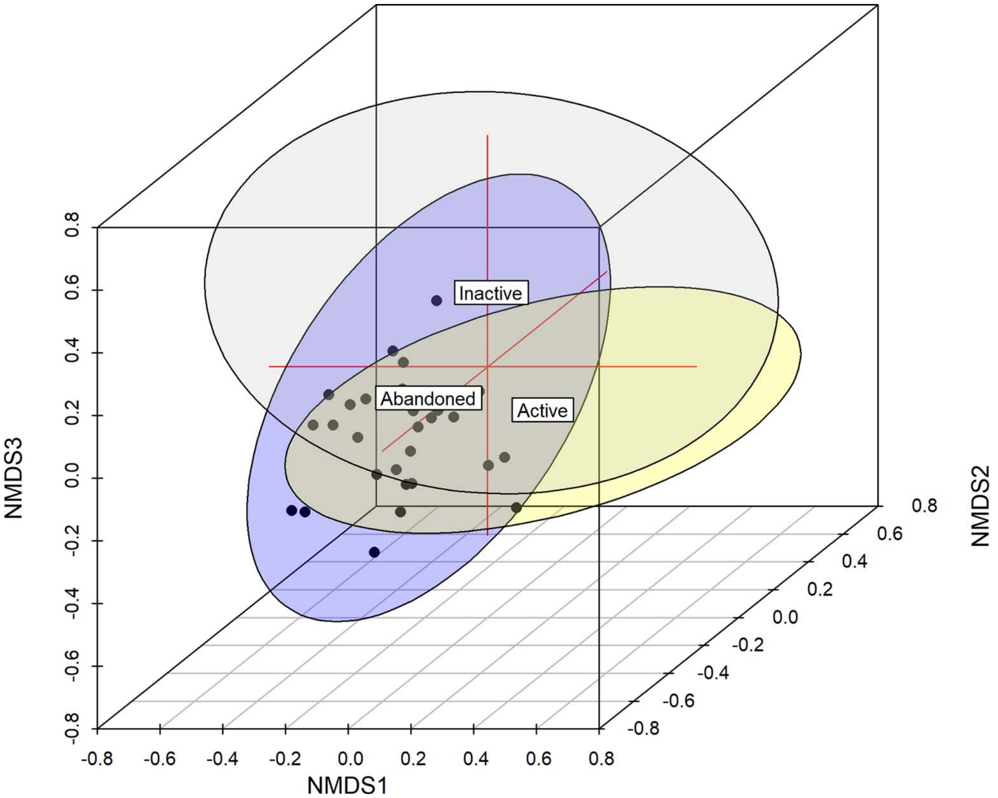

Fig. 3. Three axes of non-metric multidimensional scaling of the vertebrate commensal community across abandoned (blue), active (yellow), and inactive (gray) Gopher Tortoise (*Gopherus polyphemus*) burrows. Species detected are represented by the black points. Vertebrate burrow commensal data were collected in a private, working forest landscape dominated by planted Loblolly Pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018–2019.

forest stands, coupled with the presence of tortoise burrows, may provide a similar suite of resources (e.g., forage, refugia, nest sites) required by species observed at other sites. Some species, such as the Eastern Hog-nosed Snake (*Heterodon platyrhynos*), Northern Bobwhite (*Colinus virginianus*), and Striped Skunk (*Mephitis mephitis*), have been recorded using burrows at other sites (e.g., Lips, 1991; Kent et al., 1997; Dziadzio and Smith, 2016; White and Tuberville, 2017). These species were not observed using burrows during our study; however, these species were observed incidentally on site. This suggests that these species may be present within working forests and that chance most likely resulted in these species not being observed using burrows during our surveys.

A lack of observations of other vertebrate commensal species within our study site may be a result of a lack of available habitat (e.g., breeding wetlands, nest sites), seasonality, or the survey method employed (e.g., camera trapping). Habitat may have been absent within or proximate to our study site, resulting in known burrow commensals, such as Gopher Frogs, being absent from our records. Certain commensal species are known to increase the use of tortoise burrows during different seasons, such as Eastern Indigo Snakes increasing use during the winter (Lips, 1991; Hyslop et al., 2009). Sampling across multiple seasons within our study site may increase the number of commensal species observed and provide insight into how commensal use of tortoise burrows shifts in response to season (Lips, 1991). Using passive infrared cameras may have biased our observations towards larger species, as movements of smaller vertebrates may not have reliably triggered the cameras (Amber et al., 2021). Ectotherms and small mammals, such as shrews, voles, and mice, can have surface temperatures that are similar to background surfaces (e.g., plants, bare ground), resulting in the infrared sensor not detecting an individual (Glen et al., 2013; Amber et al., 2021). Coupling the timelapse setting, which takes a photo or photos at a constant time interval, with the standard motion trigger setting could also aid in detecting smaller vertebrate species that may not have triggered the motion sensor.

We observed two previously undocumented bird species, the Red-headed Woodpecker (*Melanerpes erythrocephalus*) and Yellow-throated Warbler (*Setophaga dominica*), using tortoise burrows. Based on the foraging habits (e.g., occasional ground forager) of the Red-headed Woodpecker, it is possible that the detected individual was foraging for invertebrates associated with burrows (Williams, 1975; White and Tuberville, 2017). To our knowledge, foraging at a burrow has yet to be documented in a woodpecker species. However, the behavior has been observed across multiple species (e.g., Carolina Wren [*Thryothorus ludovicianus*], Eastern Bluebird [*Sialia sialis*], and Northern Mockingbird [*Mimus polyglottos*]) with a relatively high frequency compared to other behaviors (e.g., dust bathing; Dziadzio and Smith, 2016; White and Tuberville, 2017). It is plausible that the observed Yellow-throated Warbler was using the burrow for reasons other than foraging (e.g., dust bathing, displaying), as the species is a foliage and bark gleaner of the upper forest canopy (Morse, 1974; Gabbe et al., 2002). Although not as common as foraging, other bird behaviors, such as dust bathing and displaying, have been observed at tortoise burrows (Dziadzio and Smith, 2016; White and Tuberville, 2017). However, we only had a single observation of each species, with these observations providing no indication of behavior, making it difficult to conclude how these species use tortoise burrows. It is also plausible that observations of these species were coincidental and not related to their use of tortoise burrows.

Our study demonstrates that abandoned, active, and inactive burrows support a similar suite of commensal species associated with working forests. We recommend that forest managers be conscientious of the presence of inactive and abandoned burrows and mitigate the effects of forest management activities on these burrows similar to active burrows. Mitigating across all burrow classifications may positively affect commensal species associated with working forests, including species of conservation concern (e.g., Florida Pine Snake [*Pituophis melanoleucus mugitus*]). Tortoise burrows may be an important form of refugia within working forests, as other forms of refugia may not exist or may be too ephemeral on the landscape to be used consistently by commensal species (Murphy et al., 2021). We encourage continued monitoring of tortoise burrows and commensals to better understand how burrows contribute to species abundance and persistence within working forest landscapes. We recommend using video recordings to monitor vertebrate commensals over photos when possible (Dziadzio and Smith, 2016; White and Tuberville, 2017). Video recordings would enable researchers to observe commensal behaviors and determine how and why commensal species may use burrows.

Our study also highlights the ability of working forests to support and, potentially, aid in the conservation efforts of vertebrate commensal species. With more than 80 percent of tortoise habitat being on privately owned lands, managing these lands in a manner that supports tortoise and commensal populations and continued production of merchantable products is imperative. Numerous conservation initiatives have been developed, such as the Natural Resources Conservation Service's Working Lands for Wildlife and Florida's Gopher Tortoise Payment for Ecosystem Services program, which provides a framework for private landowners to support tortoise and, therefore, commensal populations (see Underwood et al., 2012; Florida Fish and Wildlife Conservation Commission, 2022; Natural Resources Conservation Service, 2022). These programs provide technical and/or financial assistance to landowners interested in supporting tortoise populations while also being able to continue to work the land (e.g., timber production, grazing). Continuing to encourage and support private landowners to take part in these programs will be critical to supporting tortoise and, therefore, commensal populations throughout the species' range.

DATA ACCESSIBILITY

ACKNOWLEDGMENTS

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