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THESIS APPROVAL

Candidate:

Kennedy Norris

Major:

Biology

Thesis Title:

Distribution of carrion-associated beetles and their phoretic mites along an urban rural gradient in northeast Alabama

Approval:

422Q

Dr. Lori Tolley-Jordan Associate Professor of Biology

Major Professor

Dr. Mark Sciuchetti

Assistant Professor of Geography

Dr. Grover Brown

Assistant Professor of Ecology

Channing R. Ford

Dr. Channing R. Ford Dean, Graduate Studies

15 pl <u>2022</u> Date

Date

7/15/22

Date

July 27, 2022

Date

JACKSONVILLE STATE UNIVERSITY

COLLEGE OF SCIENCE AND MATHEMATICS

DISTRIBUTION OF CARRION-ASSOCIATED BEETLES AND THEIR PHORETIC MITES ALONG AN URBAN-RURAL GRADIENT IN NORTHEAST ALABAMA

By

Kennedy Norris

A Thesis Submitted to the Graduate Faculty of Jacksonville State University in Partial Fulfillment of the Requirements for the Degree of Master of Science with a Major in Biology

2022

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Kennedy Norris

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Kennedy Norris

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ABSTRACT

Global insect decline has been linked to urbanization, most notably by habitat fragmentation. These insects perform important ecological functions such as pollination, managing pests, and decomposing carrion to recycle nutrients back into the environment. Despite the importance of nutrient recycling behavior displayed by carrion-associated beetles, little research has been done on them in the southeastern US. Previous studies have found a relationship between urbanization, less favorable environmental conditions, carrion availability, and decreased insect diversity. However, no studies have been conducted in the southeastern United States on the relationship of these beetles to their environment despite having the highest rates of urbanization. The purpose of my research was to investigate the landscape variables and habitat variables that influence the carrion-associated beetle assemblages and their obligate phoretic mites found on those beetles in the southeastern US. Results from the landscape variable analyses showed considerable range in percent urban cover, patch size, and habitat heterogeneity across the 11 sites. Microhabitat variables were similar across all sites. Results of beetle and mite collections yielded a total of 263 beetles in 20 species and 40 mites of one species with similar evenness values across all sites. PCA and multiple regression analysis did not show significant relationships to environmental conditions. While these findings suggest that carrion associated ground beetles and their mites are not affected by fragmented habitats, caveats to this study include a limited number of sites, low beetle detection, and low intensity of developed landscape as in a major metropolitan area.

Keywords: land use, habitat fragmentation, biodiversity, Silphidae, Parasitidae

CHAPTER ONE

INTRODUCTION

One of the most important processes on the planet is decomposition of organic matter. Carrion decomposition generally refers to the breakdown of vertebrate carcasses. This usually occurs in four stages of decay including: initial, bloat, putrefaction, and dry decay. All stages are associated with a unique assemblage of bacteria, fungi, and carrion feeding animals. Multiple taxa of beetles are important in these stages of decomposition, albeit the roles of each group vary such that adults of some taxa feed on the beetles while larvae of other taxa are ones responsible for carrion consumption. These beetles are divided into three functional roles: necrophilous, necrophagous, and omnivorous (Zanetti et al, 2015). Necrophilous species predate on other arthropods found on the carcass. Necrophagous species use the carcass as their primary food source. Finally, omnivorous species are those that feed on the carcass while also predating on the other arthropods.

Beetle families associated with carrion decomposition are outlined below. In the family Trogidae, species are necrophagous directly feeding on the carcass (Battán and Linhares, 2011). These beetles are commonly called "hide beetles". Scarabaeidae, most notably species in the genera *Onthophagus, Canthon*, and *Copris* are necrophagous beetles with adults feed directly on the carcasses (Larsen et al, 2006; Stone and Jameson, 2021). Silphidae are considered omnivorous with the larvae and adults feeding on the carcass, but the adults also feed on larvae of other insects, most notably fly larvae (Ratcliffe, 1980). Carabidae are considered necrophilous as adults only come to feed on other insects found on the carcass (Lovei and Sunderland, 1996). Histeridae are also considered necrophilous feeding on fly larvae and other Histeridae species (Geden et al, 1987; Kaufman et al, 2000). Staphylinidae are considered highly necrophilous

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feeding on eggs, larvae, and adults of various species of insects found on carrion, as well as the phoretic mites found on carrion (Frank et al, 1992; Balog et al, 2010).

A focal group of this study are called carrion beetles (Silphidae) as they are the only group responsible for carrion decay based on larval consumption and are considered obligate carrion specialists (Scott, 1998). These beetles are distinguished by their shortened elytra; clubbed antenna; and flat, black bodies with yellow, orange, or red markings. They are important for nutrient recycling by burying carrion for food and for nurseries in their habitats which affect soil quality by altering soil nutrients, soil pH, and microbes found in the soil (Barton et al, 2013). The approximate 200 species of silphids are divided into two subfamilies: Silphinae and Nicrophorinae. Within Silphinae, there are 113 species in 14 genera that appear in late successional stages of decomposition of larger vertebrate carcasses. These beetles do not participate in bi-parental care or use carcasses as part of their reproduction, instead laying their eggs in the soil near large carcasses (Anderson, 1982a). There are 65 species of Silphids in three genera Eonecrophorus, Nicrophorus, Ptomascopus of which 60 of these are in Nicrophorus - the only genus that occurs in the US. Nicrophorus spp. exhibit complex behaviors such as carcass burying, which is less common in other Nicrophorinae species (Burke, 2019). All Nicrophorus *spp.* target small carrion early in successional stages of carrion decomposition and bury carrion. They preserve the carrion with anal secretions and then lay their eggs on the carrion. After oviposition, the species provide biparental care on the carcass (Hoback et al, 2004). North American species show a strong preference for small rodent and bird carcasses (Coyle and Larsen, 1998).

Carrion beetles are found in temperate regions, primarily in Europe and Asia, and are absent in more extreme climates such as those found in Antarctica, sub-Saharan Africa, and Australia (Sikes and Venables, 2013). In fact, the few species found in the tropics but are limited to higher elevations and cooler temperatures (Sikes and Venables, 2013). Carrion beetles are less successful in the tropics since they are often outcompeted by competitors such as flies and ants and is a noted problem in other studies (Trumbo, 1990; Matuszewski and Madra-Bielewicz, 2021; Suzuki and Nagano, 2006; Scott et al, 1987). Forty-six species of silphids are in North America, and five are currently found in Alabama. The three species of Nicrophorinae are: Margined Burying Beetle (*Nicrophorus mariginatus*), Pustulated Carrion Beetle (*Nicrophorus pustulatus*), and Tormentose Burying Beetle (*Nicrophorus tomentosus*). The three species of Silphinae include the: Red-lined Carrion Beetle (*Necrodes surimanensis*), *Oiceoptoma inaequale*, and historically the American Carrion Beetle (*Necrophila americana*) which is now extirpated from the state.

In general, these beetles have limited dispersal capabilities (Ikeda et al, 2008) but can detect carrion several kilometers away (Kalinová et al, 2009). As mentioned, many species are habitat specialists that require specific soil types, temperatures, and vegetation cover (Willemssens 2015, Chemnitz et al. 2020). As such, multiple species of *Nicrophorus spp*. beetles in Europe are considered threatened or endangered (Anderson 1982b), while in the US the American Burying beetle (*N. americanus*) is federally listed as endangered. This listing is a result of the loss of individuals from approximately 90% of its historic range due primarily to habitat fragmentation and loss of preferred carrion, small birds and mammals (Kozol et al., 1988; Nichols et al. 2007, Creighton et al. 2009, Harris et al. 2019, Méndez-Rojas et al. 2021). Habitat fragmentation due to land conversion of natural habitats to intensive agriculture or urbanization is considered the primary driver for projections that 40% of the world's insect diversity will be lost over the next

several decades (Sánchez-Bayo and Wyckhuys, 2019), including beetle taxa that require specific substrates (e.g., carrion, wood, or dung) for rearing young.

Silphid species richness and abundance is significantly decreased in fragmented areas (Gibbs, 2001). However, some beetles can still thrive in fragmented habitats, but these are typically smaller generalists (Gibbs, 2001). Habitat fragmentation can negatively affect the of silphids (Gibbs, 2001). Soil quality is poorer in urban fragmented areas due to heavy metals in soils and rockier soil areas being left out of land development (Gibbs, 2001). An increase in vertebrate scavengers such as skunks, racoons, and rodents (subsidized predators) are seen in fragmented habitats, as well as an increase in insect competitors such as ants and flies (Trumbo, 2000; Gibbs, 2001). Fragmented habitat also has more unfavorable microclimates with drier and warmer conditions (Wilson et al, 2016).

The Southeastern US, particularly watersheds in Alabama and Tennessee, is considered a global hotspot of aquatic biodiversity (Elkins et al, 2019), including insects with obligate aquatic nymph or larval stages (Morse et al, 1997). Yet, far less is known about the biodiversity of terrestrial insects, which is most likely very high but underreported as recently shown in Georgia in which a survey for small, wood beetles (Monomitidae) increased reported diversity in the state from 0 to 9 species (Mcelrath and Mchugh 2018). As the landscape is rapidly changing due to increasing population sizes in urban centers and with urban sprawl (Milesi et al. 2003), this results in significant habitat fragmentation that may lead to declines or extirpation in insect taxa for which very little biology is known (Liu et al. 2016).

According to the International Union for Conservation of Nature (IUCN) and NatureServe, *N. mariginatus*, *N. pustulatus*, *N. tomentosus and Necrodes surimanensis* are burying beetles widespread in the eastern US (including Alabama) and are considered of no conservation concern (Stable G5 ranking, Natureserve.org). However, dispersion within the range is unknown and is most likely patchy (Trumbo & Bloch 2000). In addition to the underreported diversity of insects in the southeastern US, the relationships of the phoretic mites (Acari: Parasitidae) that are commonly associated with carrion beetles (Wilson 1983, Schwarz and Müller 1992) to changing land use is poorly understood; albeit limited evidence suggests that mite densities on carrion beetles also vary with urban cover and habitat fragmentation (Gibbs and Stanton 2001) Mites are a common phoront among burying beetles as they cannot sense and move to new carcasses, so they rely on carrion beetles to take them from carcass to carcass (Schwarz and Müller, 1992).

Some common families associated with burying beetles are Uropodidae, Anoetidae, Parasitidae, and Macrochelidae (Wilson, 1983). In the family Parasitidae, *Poecilochirus* species are found on all species of burying beetles (Schwarz and Müller, 1992). *Nicrophorus* also often sees more complex mite interactions with phoretic mites (Brown and Wilson, 1992). Interestingly, these mites are associated with other carrion associated beetles (Perotti et al, 2000; Nickel, 1969) although the complexities of these relationships are poorly understood.

Although previous studies in Europe (Esh and Oxbrough, 2021; Von Hoermann et al, 2018) and the Northern US (Sikes and Raithel, 2002; Gibbs, 2001; Trumbo, 2000) have shown that beetle taxa with limited dispersal capabilities (poor flyers) and habitat specialists (such as many silphid taxa for their carrion) are affected by differences in habitat and fragmentation due to land use change, this has not been shown for carrion associated beetles in the Southeastern US. The overall goal of this research is to test the prediction that the diversity (species richness and abundance) of carrion associated beetles and their phoretic mites will decline with increasing urban landcover.

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To evaluate this goal, I addressed the following questions: (1) Is there a relationship between percent urban land cover, carrion associated beetle diversity, and mite densities? (2) Is there a relationship between landscape fragmentation, carrion associated beetle diversity, and mite densities? (3) Is there a relationship between site specific habitat characteristics (soil temperature and soil composition), carrion associated beetle diversity, and mite densities?

CHAPTER TWO

METHODS

2.1 Study Sites

Although Calhoun County is predominantly rural, the 25 mile north-south corridor between Pleasant Valley and Oxford, AL (Figure 1 and Table 1) provides an urban-rural gradient ranging from primarily forest cover to high intensity urban cover. This corridor is ideal as it has a similar elevation (all sites are in a valley between two ridges), underlying geology (primarily cherty limestone), soil type (clay/loam), and vegetation (forest). As managed fields (dominated by grasses and intermittently mowed) are available across all land-use intensities, these habitats were selected for the 11 sites along the sampling corridor (Figure 2).

2.2 Landscape Variables

The National Land Cover Dataset (NLCD) from ArcGIS Online for May 19, 2021, was downloaded at a 30-meter resolution for the landcover data associated with this study. Once the raster data was downloaded from ArcGIS Online, it was converted from a raster image to a vector (polygon) so each pixel could be smoothed and joined to census blocks for site analysis. Using the raster to polygon conversion tool with the field of "Land Cover" chosen for the conversion to preserve the land cover types, the raster was converted, and the polygons were simplified. The land use data was joined to the block polygon data containing all variables and boundary information using a spatial join. The join was based on a one-to-one join where the land use polygons intersected the census block polygons.

Landcover land-use for the corridor between Pleasant Valley and Oxford was generated and used to select 11 sample sites along the forest, urban, and agricultural land cover was calculated ArcGIS Pro (Esri Inc., 2020). The Landsat Thematic Mapper-based land cover data from the National Landcover dataset for 2021 at 30-m resolution was used to describe the landcover along the corridor from Pleasant Valley to Oxford (Figure 3). The shades of red indicated the intensity of urban cover. Initially, 20 sites were selected to maximize patch sizes and percent urban cover differences, however only 11 sites were included in the study.

This study's habitat fragmentation is based on patch size and landscape heterogeneity due to urbanization. Patch size is defined by a census block (US Census Bureau, 2019) – a unit of area delineated by boundaries such as roads (urban) or streams (rural) and is independent of population density (Zhou and Troy, 2008). The scale of the block unit was chosen because it provides a method to adequately characterize the heterogeneity of land cover at each study site without issues with classification because of very high-resolution imagery in urban areas (Zhou and Troy, 2008). Percent urban cover and fragmentation (patch size) are correlated, small patches are usually more associated with a higher percent urban cover. The intensity of fragmentation at a site is variable as some urban sites have undeveloped, abandoned, or other urban habitats that are not impervious (Francis and Chadwick, 2012). Therefore, we included a measure of landscape heterogeneity in each patch. A heterogeneity index (HI) was calculated from a network analysis of the surrounding land use of patches adjacent to the study site patch. A count of all land use types in each patch was calculated and compared to the total area of the patch. The number of land use types across all patches and adjoining patches provided a total number of land use types in the entire study area to make comparisons of the study patches to the study area. A network analysis then compared each study site block to the neighboring site for differences in percent land use, providing an overall % heterogeneity of each site. Finally, the percentage of land use types in each patch compared to the number of land use types in the

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census blocks created the heterogeneity index (Gibbs and Stanton, 2001; DeMontis, et al., 2016). For the habitat heterogeneity index, the lower the value, the greater the landscape heterogeneity present at each patch. More homogeneous landscapes (higher HI) tend to occur in the most undeveloped areas, primarily forested in this study, and in the most densely developed residential centers that do not include open, undeveloped space (Figure 4). All analyses were conducted in ArcGIS Pro (Esri Inc., 2020).

2.3 Habitat Variables

To measure soil composition at each site, 130 grams of soil were collected from underneath one of the traps for each site. Soil percentages (clay, silt, and sand) were measured using the soil test analysis method following Jeffers (2019) and entered in the Natural Resources Conservation Service (NRCS) soil calculator to determine soil type (NRCS Web Soil Survey). Soil types are based on USDA soil composition grouping values (Ditzler et al., 2017). Vegetation composition was measured using a 50-meter transect method to attain the relative proportion of forbs to grasses for each site. The transect was placed for each site down the center of the field, ensuring the traps were found along the transect. Measurements were taken every 1 meter along the 50-meter transect for each side to get a total of 50 measurements of grass to forb presence for each field. In addition, the number of ants found was calculated based on the percentage of traps swarmed with ants each week as ants prevent carrion-associated beetles (Scott et al., 1987). Mean temperatures were collected using HOBO temperature logger (Onset Data Corporation) and iButton temperature loggers (Embedded Data Systems). Loggers were secured under the rain cover for only one trap per site. Readings were taken every 12 hours each day for the study duration.

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2.4 Beetle and Mite Collections

To collect the beetles and their phoretic mites, baited pitfall traps made from four 540 ml plastic containers were used. Approximately 40 grams of raw chicken wrapped in panty hose (to exclude ants) was placed in each container. All containers were then covered with 35x30 cm piece of chicken wire to exclude large scavengers (e.g., raccoons). Finally, the traps were covered in a rain cover made from a 30 x 25cm piece of corrugated plastic with two 15cm 5x5cm pieces of wood stapled underneath the plastic for lift (Figure 5). Five traps were set at each collection site within the middle of the field with at least 5 meters between each trap. Depending on species, the activity period ranges from early summer to late fall (Scott, 1998; Lingafelter, 1995) which resulted in the sampling period of May 06th 2022 through June 10th, 2022, for this study. Live specimens were collected from each trap. Specimens were taken back to the lab and stored in the freezer for 24 hours in separate containers for each trap. Individuals were identified to species per Sikes and Peck (2000). Mites were also collected from each specimen, counted, and identified by morphotype, but no taxonomic identifications were completed. Beetles were dry mounted, and mites preserved in ethanol. All specimens were deposited in the university's collection.

2.5 Statistical Analyses

The Catch per Unit Effort was standardized by the number of cups, traps, bait size, and deployment period, so the sampling effort was equal across all sites. As the sampling design is based on the colonization of traps by beetles, total beetle abundance per site was determined by summing all beetles per species during the study. Beetle abundance per site is based on the total number collected during the length of the study. Diversity estimates included taxa richness (number of species per site) and diversity indices based on the Shannon-Wiener index $(H=\sum[(pi)*ln(pi)])$ where pi is the proportion of individuals of each species belonging to species I, and Simpson's index $(D = \sum[pi*(pi - 1) / (N*(N - 1)]))$. Mite densities for each site were based on the total number of mites collected per the number of beetles, species, and sites.

To determine the relationship between the habitat variables (soil composition, vegetation cover, soil temperature, and percent ants), landscape variables (% urban cover, patch size, and heterogeneity index), and the presence of beetle taxa; a principal components analysis was conducted. The principal component axes that captured at least 75% of the variation among the environmental variables were subsequently used in a multiple linear regression. This analysis determined if the relationships of the beetles to their environment based on landscape and habitat scale physical variables were statistically significant. All statistical analyses were conducted in PAST v 4.0.

CHAPTER THREE

RESULTS

3.1 Habitat, Patch size, Urban Cover and Habitat Heterogeneity

Based on the soil composition analysis results using the particle separation system, soils across all sites were either loam or sandy loam with particle sizes dominated by sand and silt with low percentages of clay (Table 2 and Figure 6). As sites were standardized based on low-managed fields, vegetation composition did not vary significantly in the grass to forb ratio (Table 2). Soil temperature also did not vary significantly based on site (Figure 7). Percent land use across the sites ranged from 4.51% to 95.64%, patch size ranged from 27.30 hectares to 400.74 hectares, and habitat heterogeneity ranged from 8.6 to 80 across the 11 sites (Figure 3, Figure 4, and Table 3).

3.2 Carrion-associated beetle and mite distributions

In total, 20 species of carrion-associated beetles from six families were collected from 8 of the 11 sites where traps were placed. Taxa abundance ranged from three individuals (Site 8) to 66 individuals (Site 6), richness ranged from one to 12 at sites 3 and 6, respectively (Table 4). *Onthophagus hecate* was most collected (n=81) followed by two species of Silphidae: *Necrophila americana* (n=39), and *Oiceoptoma inaequale* (n=20). Most species were collected at only one or two sites and differences among taxa collected are reflected in Shannon (H) and Simpsons diversity (D) that were highest at site 6 (JV3) and lowest at 9 (AN2) (Shannon's and Simpson's, respectively).

Other carrion associated beetles were captured during this study but at much lower numbers. These included Staphylinidae (n=17), Histeridae (n=16), and Trogidae (n=2). One

individual of Elateridae and two of Chrysomelidae were collected from site 7 (AN1). However, these beetles are not carrion-associated and were incidental captures not included in further analyses.

Forty-four individuals of a single morphotype of mite (Acari: Parasitidae) were found on *Onthophagus hecate*, *Necrophila americana*, and *Oiceoptoma inaequale* across all sites (Table 5) and ranged in densities between one mite per beetle individual to six mites per individual beetle. Most mites were found on *Necrophila americana*, and generally were observed on the pronotum, elytra, and ventral side.

3.3 Relationships between habitat, landscape, and beetle diversity

Principal component analysis results showed that PC axis one (PC1) explained 57 percent variation and PC axis 2 (PC2) explained 21 percent of variation of the distribution of all carrion-associated beetles based on the habitats and land use conditions where they were found (Table 6 and Figure 8). The most positively loading variable for PC1 was heterogeneity index and percent urban, and the most negatively loading variable was patch size and vegetation while for PC2 the most positively loading variable was percent urban and percent ants, and the most negatively loading variable beetle collected, *Onthophagus hecate*, was widely distributed across habitats as shown by its distribution throughout the PC space. Despite only a few individuals that were collected for *Canthon probus*, *Galerita bicolor*, and Trogidae sp. these were also widely distributed across the PC space while taxa such as Staphylinidae sp. A, Staphylinidae sp. C, Histeridae sp. A, Histeridae sp. B, Carabidae sp. were found only in specific habitats (Figure 8) as they were restricted to specific regions of the PC space. As carrion associated beetles have distinct functional roles in the decomposition process, the distribution of these groups based on habitat associations showed that necrophilous beetle taxa and phoretic

mites were positively influenced by patch size, ant exposure, and percent grass. Necrophagous and omnivorous species were most positively associated with habitats dominated by vegetation of mixed grass and forbs (Figure 9 and Table 6).

Although some taxa appeared to group based on specific landscape and habitat conditions, these relationships were not significant as the PC scores did not significantly explain the relationship of the abundance of each beetle species to environmental conditions found in the principal components analyses (Table 7).

CHAPTER 4

DISCUSSION

Habitats across the 11 sites were similar with respect to soil temperature and soil composition, which is most likely because similar fields were targeted for this study. A detailed community study of vegetation composition was not conducted in this study as most research suggests that vegetation type is not informative in describing carrion beetle distributions (Lee et al, 2012). However, a cursory description of grasses to forbs was conducted to describe, to a degree, the types of vegetation found in managed fields along an urban-rural gradient.

Despite the low degree of variability in the habitat conditions among sites, a wide range of urban cover, patch size, and heterogeneity were found among these nine sites. It is a novel use of including block analyses, a method usually reserved for census data, but we found it to be a good estimator of mixed land use at a fine scale. This was reflected in that small patches could still include a diverse setting of landscapes.

Originally, 11 sites were to be included in this study, but three sites (OX1-3) failed to collect any beetles. For other sites, 11 taxa were single occurrences, and most taxa had few individuals, except for *Onthophagus hecate* (Appendix A). In general, the lack of beetles was associated with the fact that these are managed fields that were intermittently mowed. In some sites, traps would be destroyed from mowing despite the traps being clearly marked. Ants were also a major problem (Appendix B) and would swarm traps despite baits being secured in pantyhose to keep ants out, and this is documented in multiple studies looking at ground beetles or carrion-associated beetles (Trumbo, 1990; Marschalek and Deutschmanm 2022). All sites had

considerable fly activity which has been linked to carrion beetles being outcompeted due to their eggs being consumed by the fly larvae (Gibbs and Stanton, 2001; Scott, 1998).

At least five species of silphids are known from this region of silphids, however, only two species, Necrophila americana (Silphinae) and Oiceoptoma inaequale (Silphinae), were recovered. It is unclear if other taxa regularly occur in this area because no systematic surveys of the region have been conducted. Therefore, the distribution and abundance are unknown, and we cannot draw conclusions that the absence of taxa in the area is due to land use practices found here. Also, some beetle taxa may be more associated with wooded environments than fields (Lingafelter, 1995; Bishop et al, 2002; Arellano et al, 2008; Vernes et al, 2005; Daria et al, 2011) which were not used in this study as urban environments often do not have woods associated with them and only brown fields or other open habitats. As such, this study selected for beetles associated with carrion found in fields which excludes woodland specialists. Further, I elected to control for carrion size to attract beetles in Nicrophorinae that tend to occur in early successional stages and are attracted to small carrion which are easier to work with in collections. Chicken has been documented as a successful bait in a variety of studies (Coyle and Larsen, 1998), and beetles were attracted here, but other baits that are not as prone to ant swarming would be a good alternative. Other baits used in studies included artificial chemical attractants, fish, beef liver, piglet, and rodents (Coyle and Larsen, 1998; Podskalská et al, 2009; Kalinová et al, 2009). Determining which baits best deter ants is necessary before continuing surveys in the region.

When evaluating relationships of beetle distributions to habitat and landscape variables, most taxa were found in all habitat conditions regardless of urban cover, habitat heterogeneity, patch size or habitat variables. This suggests that all these beetles are generalists. However, the fact that beetles that were strongly associated with carrion grouped separately from weak

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associated beetles suggests that some trends in habitat or landscape variables could be present but a broader sampling array across more habitats is required.

My study highlights the difficulties of documenting carrion-associated beetle diversity which are a common phenomenon. Even though efforts such as this are difficult, long-term datasets with repeated surveys during the active time periods of beetles could allow a better pattern of beetle distributions and their relationships to urban environments to occur. It is also possible that Calhoun County simply does not possess the range of landscape and habitat conditions necessary to meet the ecological threshold to find any relationships among these beetles and their environment. Despite these difficulties and the inconclusive results, carrionassociated beetles are a poorly studied group, especially in the southeastern United States, and this study lays a foundation for approaches to evaluate landscape variables, considerations for altering site-specific conditions, and caveats to interpreting relationships of beetles and mites to environmental conditions along an urban-rural gradient.

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TABLES

Table 1. Site locations and descriptionsLatitude and longitude coordinates and descriptions of each site used in the beetle/mite survey. Site IDs correspond to region (PV is Pleasant Valley, JV is Jacksonville, AN is Anniston and OX is Oxford).

ID	Coordinates	Descriptions
PV1	33.834290, -85.793183	Large, open field dominated by grasses and forbs. Bordered by woods, roads, and residential.
PV2	33.831854, -85.794342	Large, open fields dominated by grasses. Bordered by woods on all sides.
PV3	33.88234, -85.74205	Small field nestled between a forked road. Dominated by grasses and forbs. Bordered by roads and a small stream.
JV1	33.812683, -85.764717	Small field dominated by grasses. Bordered by small stream, roads, woods, and residential.
JV2	33.805041, -85.760239	Large field dominated by grasses. Bordered by businesses, roads, and woods.
JV3	33.793237, -85.752693	Small field dominated by grasses and located in a floodplain. Bordered by woods, roads, and residential.

Table 1.	(Continued)
1 4010 11	(Commaca)

AN1	33.710922, -85.821314	Large, open field dominated by grasses. Bordered by woods and residential.
AN2	33.704252, -85.815690	Large, open field dominated by grasses. Bordered by highways and a stream.
OX1	33.609815, -85.824388	Small field dominated by grasses and forbs. Bordered by businesses, woods, and stream.
OX2	33.600385, -85.784981	Large, open field dominated by grasses. Bordered by roads, woods, and construction.
OX3	33.585805, -85.783800	Large field dominated by grasses and forbs. Bordered by woods, roads, and residential.

		Vegetation	Data	Soil Data							
Sites	% grass	% forb	% grass+forb	% sand	% silt	% clay	Soil type				
PV 1	52	10	38	44.44	44.44	11.11	loam				
PV 2	62	4	34	48.8	46.5	4.65	sandy loam				
PV 3	44	12	44	50	44	6	sandy loam				
JV 1	70	4	26	56.4	41.03	2.56	sandy loam				
JV 2	64	2	34	45	42.5	12.5	loam				
JV 3	82	0	18	45.45	45.45	9.1	loam				
AN 1	16	16	68	63	30	6.5	sandy loam				
AN 2	82	0	18	63.8	31.9	4.26	sandy loam				
OX 1	70	10	20	56.8	40.9	2.27	sandy loam				
OX 2	66	4	30	47.17	47.17	5.66	sandy loam				
OX 3	50	8	42	46	46	8	loam				

Table 2. Summary of habitat variables per site

			Heterogeneity
ID	% Urban	Area (ha)	Index
PV1	5.41	511.92	13.58
PV2	5.41	511.92	13.58
PV3	26.58	27.30	41.17
JV1	59.88	58.51	19.04
JV2	95.64	85.71	26.31
JV3	40.18	400.75	11.21
AN1	70.29	23.54	80
AN2	30.65	496.29	8.6
OX1	68.22	262.73	15.55
OX2	41.14	11.498	54.54
OX3	4.51	218.11	26.92

Table 3. Summary of land use variables per site

Table 4. Collections by site

Carrion-associated beetle species and mites collected for each site. No beetles were collected for sites 9-11.

Site	Species	Beetle Counts	Mite Counts
PV 1	Necrophila americana	7	6
	Onthophagus hecate	1	0
	Ground beetle spp.	1	0
	Ontholestes cingulatus	1	0
	Hister B sp.	4	5
PV 2	Necrophila americana	4	4
	Canthon probus	2	1
	Scarab A sp.	1	0
	Onthophagus hecate	1	0
	Ground beetle spp.	1	0
	Hister B sp.	1	0
PV 3	Necrophila americana	15	6
	Oiceoptoma inaequale	5	1
	Canthon probus	2	2
	Hister A sp.	2	0
	Trogidae sp.	1	0
JV 1	Necrophila americana	2	1
	Oiceoptoma inaequale	1	0
	Onthophagus hecate	18	0
	Rover A sp.	2	0
	Rove B sp.	1	0
	Rove C sp.	3	0
	Hister A sp.	1	0
JV 2	Onthophagus hecate	22	3
	Aphonus castaneous	1	0
	Rove C sp.	3	0
	Belonuchus rufipennis	1	0
	Hister A sp.	1	0
	Hister B sp.	1	0

Table 4. (Continued)

Site	Species	Beetle counts	Mite counts
JV 3	Onthophagus hecate	31	3
	Ground beetle spp.	1	0
	Necrophila americana	10	6
	Oiceoptoma inaequale	11	6
	Rove A sp.	2	0
	Rove C sp.	2	0
	Rove D sp.	1	0
	Hister A sp.	1	0
	Hister B sp.	3	0
	Saprinus pennsylvanicus	1	0
	Agonum extensicolle	1	0
	Galerita bicolor	2	0
AN 1	Hister B sp.	2	0
	Ground beetle spp.	8	0
	Galerita bicolor	1	0
	Oiceoptoma inaequale	3	0
	Onthophagus hecate	8	0
	Necrophila americana	1	0
	Canthon probus	1	0
	Phyllophaga sp.	1	0
	Maladera castanea	1	0
	Trogidae sp.	1	0
AN 2	Ground beetle spp.	3	0

Table 5. Summary of beetle diversity and abundance

Diversity of beetles as collected from 8 sites. Where number of individuals is the total count of beetles collected for each site, species richness is the number of different species caught per site, Shannon's diversity index, and Simpson diversity index. No data was collected for sites OX1 to OX3 and these sites are not included in the table.

Site	Number of individuals	Species richness	Shannon's Index (H')	Simpson's Index (1-D)
PV1	14	5	1.705	0.7763
PV2	10	6	1.922	0.8223
PV3	25	5	1.707	0.7713
JV1	28	7	1.673	0.7115
JV2	29	6	1.475	0.643
JV3	66	12	2.057	0.8214
AN1	27	10	2.046	0.83
AN2	3	1	0.5623	0.375

Table 6. PCA eigenvalues and varianceEigenvalues and percent variance of beetle and mite presence explained by habitat and landscape variables found at 8 sites where specimens were collected from 06 May 2022 to 10 June 2022.

PC	Eigenvalues	Percent variance
1	1971.96	57.164
2	728.174	21.109

Effect	Coefficient	Std. Error	Std. Coef	Tolerance	Т	P (2 tail)
Constant	24.842	5.842	0.000	-	4.252	0.003
PC1	- 0.745	0.334	- 0.710	0.587	- 2.227	0.057
PC2	- 0.448	0.433	- 0.314	0.647	- 1.035	0.331
PC3	- 1.365	0.553	- 0.692	0.761	- 2.470	0.039

Table 7. Results of linear regression analyses of beetle and mite abundance regressed against principal components 1, 2, and 3.

Adjusted squared multiple R: 0.343 and Standard error of estimate 19.299.

FIGURES

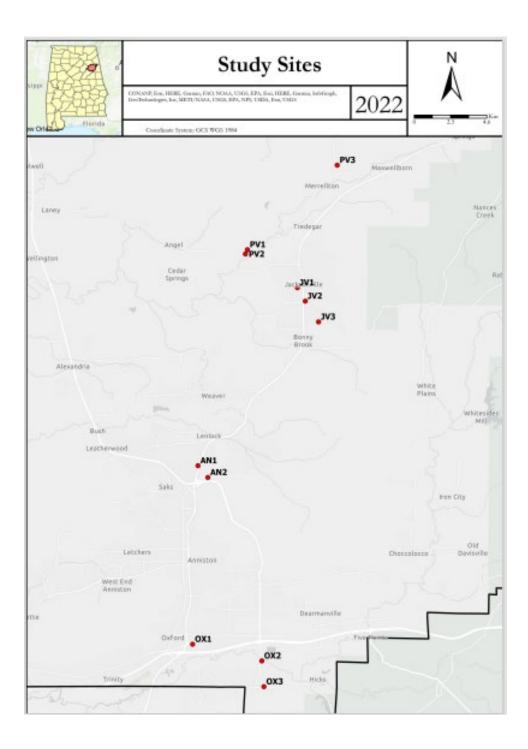


Figure 1. Map of collection sites

Distribution of beetle/mite collection sites along the north-south corridor of Calhoun County, AL. The northern most sites were in Pleasant Valley (PV), followed by Jacksonville (JV), Anniston (AN) and Oxford (OX).



PV1

PV2

PV3



JV1

JV2



AN1

AN2

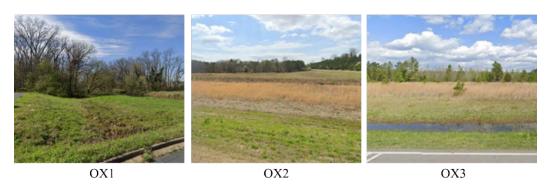


Figure 2. Site photos

Site photos of 11 sites used in survey from Pleasant Valley to Oxford, Calhoun County, AL. Sites were chosen following a standardized characteristic of grass dominant, intermittently mowed fields.

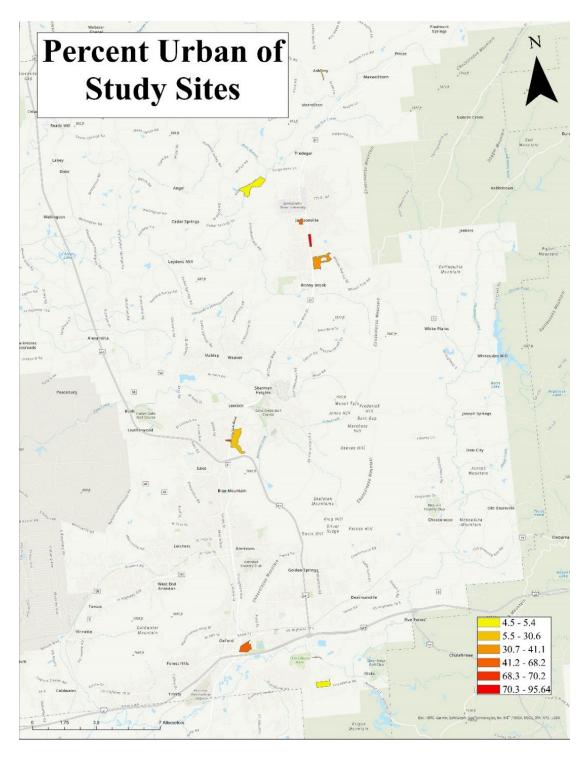


Figure 3. Percent land cover map

Percent land cover defined as urban in each of 11 sites in the north-south corridor of from Pleasant Valley to Oxford. Yellow indicates sites with lowest urban cover and red are sites with high % urban cover.

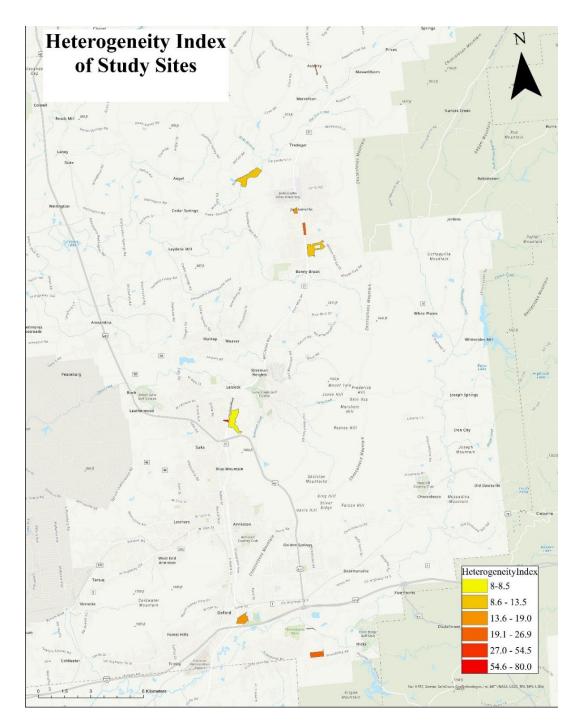


Figure 4. Heterogeneity index map

Heterogeneity index values of 11 sites in the north-south corridor of from Pleasant Valley to Oxford. A value of 100 corresponds to only one type of landcover type and a value of 0 corresponds to each parcel in the patch is a different landcover type.



Figure 5. Pitfall trap construction

The right panel shows 4 collection containers flush with hole in ground, top left panel shows chicken bait, and lower panel shows completed construction with rain barrier.

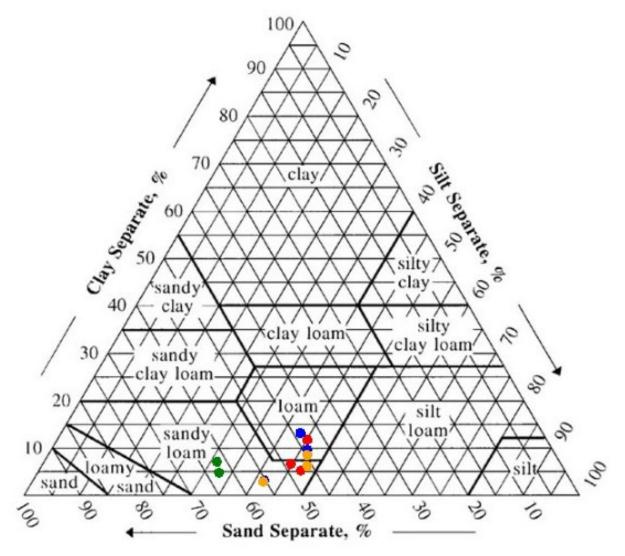


Figure 6. Soil composition triangle

Soil composition combinations following the Jeffers (2019) soil test method. Red dots correspond to composition of soils collected at Pleasant Valley sites, Blue at Jacksonville Sites, green from Anniston sites, and Orange from Oxford sites. Soil types in triangle are based on USDA soil composition grouping values. Source: NRCS Web Soil Survey.

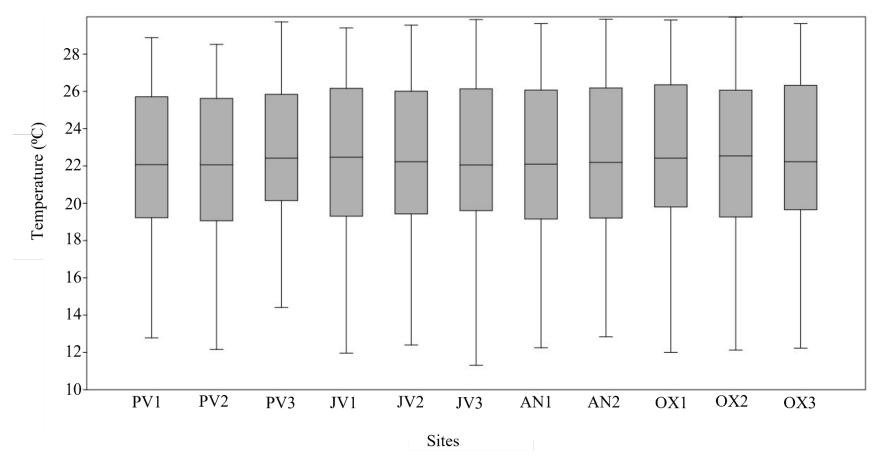


Figure 7. Boxplot of soil temperatures

Soil temperature ranges from 06 May 2022 to 10 June 22 displayed as box plots for 11 sites along the north-south corridor where sites 1-3 are in Pleasant Valley, 4-7 are in Jacksonville, 7-8 are in Anniston and 9-11 are in Oxford. The vertical line in center of each box indicates the median temperature.

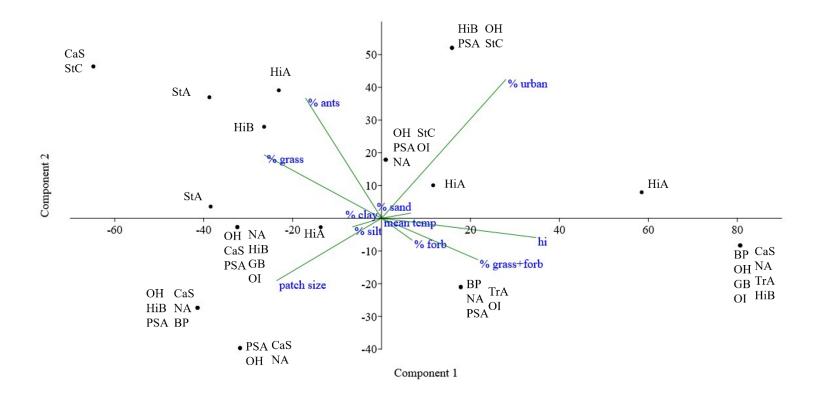


Figure 8. Principal component analysis results graph

Results from a Principal Components Analysis (PCA) for environmental conditions where each beetle and mite species were collected. Landscape variables included: % urban cover per patch, patch size, and heterogeneity index and habitat variables included: % sand, % silt, % clay, % grass, % forb, and % grass+forb. Principal Component 1 (PC1) explained 57% of the variation and Principal component 2 (PC2) explained 21% of variation. NA = *Necrophila americana*, OI = *Oiceoptoma inaequale*, BP = *Boreocanthon probus*, PP = *Phyllophaga sp.*, OH = *Onthophagus hecate*, CA = Scarab A sp., AC = *Aphonus castaneous*, MC = *Maladera castanea*, StA = Staphylinidae A sp., StB = Staphylinidae B sp., StC = Staphylinidae C sp., BR = *Belonuchus rufipennis*, OC = *Ontholestes cingulatus*, StD = Staphylinidae D sp., HiA = Hister A sp., HiB = Hister B sp., SP = *Saprinus pennsylvanicus*, TrA = Trogidae sp., EIA = Elateridae spp., ChA = Chrysomelidae sp., CaS = Carabidae sp., GB = *Galerita bicolor*, AE = *Agonum extensicolle*.

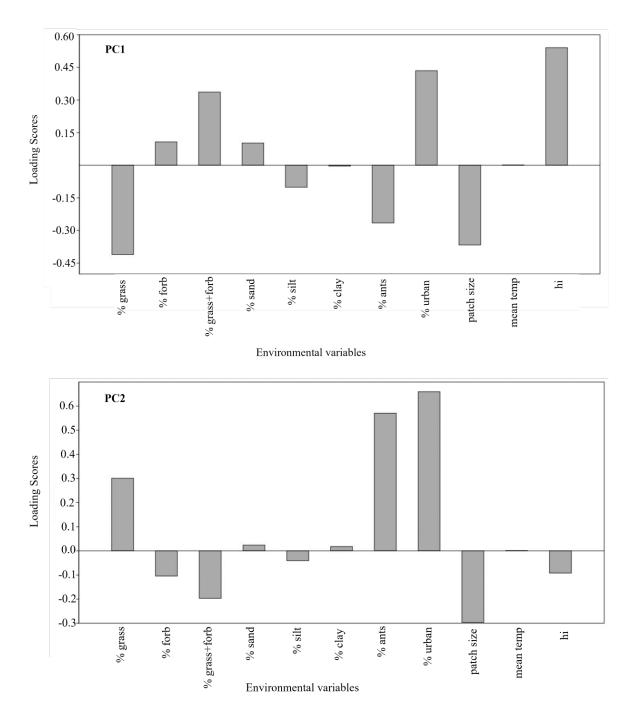


Figure 9. Principal component analysis loading scores

Loading scores of each habitat variable and each landscape variable included in the Principal Components Analyses.

APPENDICES

Appendix A. Beetle and mite collections per week

Beetle and mite collections for each trap at each site for each week during collection period (06 May 2022 to 10 June 2022). NA = *Necrophila americana*, OI = *Oiceoptoma inaequale*, BP = *Boreocanthon probus*, PP = *Phyllophaga sp.*, OH = *Onthophagus hecate*, CA = Scarab A sp., AC = *Aphonus castaneous*, MC = *Maladera castanea*, StA = Staphylinidae A sp., StB = Staphylinidae B sp., StC = Staphylinidae C sp., BR = *Belonuchus rufipennis*, OC = *Ontholestes cingulatus*, StD = Staphylinidae D sp., HiA = Hister A sp., HiB = Hister B sp., SP = *Saprinus pennsylvanicus*, TrA = Trogidae sp., EIA = Elateridae spp., ChA = Chrysomelidae sp., CaS = Carabidae sp., GB = *Galerita bicolor*, AE = *Agonum extensicolle*

						Site	es				
week 1	PV1	PV2	PV3	JV1	JV2	JV3	AN1	AN2	OX1	OX2	OX3
NA	0	0	0	1	0	0	0	0	0	0	0
Mites	0	0	0	1	0	0	0	0	0	0	0
OI	0	0	0	1	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
PP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ОН	0	0	0	4	0	1	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
CA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
MC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
Stc	0	0	0	1	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BR	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
OC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StD	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0

HiA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
SP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
TrA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ElA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ChA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
CaS	0	0	0	0	0	1	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
GB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AE	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
beetle abundance	0	0	0	7	0	2	0	0	0	0	0
taxa richness	0	0	0	4	0	2	0	0	0	0	0
mite abundance	0	0	0	1	0	0	0	0	0	0	0
week 2	PV1	PV2	PV3	JV1	JV2	JV3	AN1	AN2	OX1	OX2	OX3
NA	0	1	3	0	0	1	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
OI	0	0	0	0	0	1	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BP	0	1	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
PP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ОН	1	0	0	0	1	1	0	0	0	0	0
Mites	0	0	0	0	1	0	0	0	0	0	0
CA	0	1	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
МС	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StA	0	0	0	0	0	0	0	0	0	0	0

Mites	0	0	0	0	0	0	0	0	0	0	0
StB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StC	0	0	0	1	0	2	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BR	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
OC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StD	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiA	0	0	0	1	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiB	0	0	0	0	0	0	2	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
SP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
TrA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ElA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ChA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
CaS	0	0	0	0	0	0	2	3	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
GB	0	0	0	0	0	0	1	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AE	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
beetle abundance	0	3	3	2	1	5	5	3	0	0	0
taxa richness	0	3	1	2	1	4	3	1	0	0	0
mite abundance	0	0	0	0	1	0	0	0	0	0	0
week 3	PV1	PV2	PV3	JV1	JV2	JV3	AN1	AN2	OX1	OX2	OX3
NA	0	0	4	0	0	9	0	0	0	0	0
Mites	0	0	1	0	0	6	0	0	0	0	0
OI	0	0	2	0	0	10	1	0	0	0	0
Mites	0	0	0	0	0	6	0	0	0	0	0
BP	0	0	1	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0

PP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ОН	0	1	0	2	3	4	2	0	0	0	0
Mites	0	0	0	0	1	2	0	0	0	0	0
CA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
МС	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StA	0	0	0	1	0	2	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BR	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
OC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StD	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiA	0	0	0	0	0	1	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
SP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
TrA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ElA	0	0	0	0	0	0	1	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ChA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
CaS	1	1	0	0	0	0	3	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
GB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AE	0	0	0	0	0	0	0	0	0	0	0

Mites	0	0	0	0	0	0	0	0	0	0	0
beetle abundance	1	2	7	3	3	26	7	0	0	0	0
taxa richness	1	2	3	2	1	5	4	0	0	0	0
mite abundance	0	0	1	0	1	14	0	0	0	0	0
week 4	PV1	PV2	PV3	JV1	JV2	JV3	AN1	AN2	OX1	OX2	OX3
NA	0	0	0	0	0	0	1	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
OI	0	0	1	0	0	0	2	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BP	0	1	0	0	0	0	1	0	0	0	0
Mites	0	1	0	0	0	0	0	0	0	0	0
PP	0	0	0	0	0	0	1	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ОН	0	0	0	2	1	9	5	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
CA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
MC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StA	0	0	0	1	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StB	0	0	0	1	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BR	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
OC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StD	0	0	0	0	0	1	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiA	0	0	2	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiB	0	1	0	0	0	2	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
SP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0

TrA	0	0	1	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ElA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ChA	0	0	0	0	0	0	2	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
CaS	0	0	0	0	0	0	3	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
GB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AE	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
beetle abundance	0	2	4	4	1	12	15	0	0	0	0
taxa richness	0	2	3	2	1	3	7	0	0	0	0
mite abundance	0	1	0	0	0	0	0	0	0	0	0
week 5	PV1	PV2	PV3	JV1	JV2	JV3	AN1	AN2	OX1	OX2	OX3
NA	0	3	4	1	0	0	0	0	0	0	0
Mites	0	4	2	0	0	0	0	0	0	0	0
OI	0	0	2	0	0	0	0	0	0	0	0
Mites	0	0	1	0	0	0	0	0	0	0	0
BP	0	0	1	0	0	0	0	0	0	0	0
Mites	0	0	2	0	0	0	0	0	0	0	0
PP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ОН	0	0	0	2	14	5	1	0	0	0	0
Mites	0	0	0	0	0	1	0	0	0	0	0
CA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
MC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StC	0	0	0	0	1	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BR	0	0	0	0	1	0	0	0	0	0	0

Mites	0	0	0	0	0	0	0	0	0	0	0
OC	1	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StD	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiA	0	0	0	0	1	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiB	0	0	0	0	1	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
SP	0	0	0	0	0	1	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
TrA	0	0	0	0	0	0	1	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ElA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ChA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
CaS	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
GB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AE	0	0	0	0	0	1	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
beetle abundance	1	3	7	3	18	7	2	0	0	0	0
taxa richness	1	1	3	2	5	3	2	0	0	0	0
mite abundance	0	4	5	0	0	1	0	0	0	0	0
week 6	PV1	PV2	PV3	JV1	JV2	JV3	AN1	AN2	OX1	OX2	OX3
NA	7	0	4	0	0	0	0	0	0	0	0
Mites	6	0	3	0	0	0	0	0	0	0	0
OI	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
PP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ОН	0	0	0	8	3	11	0	0	0	0	0
Mites	0	0	0	0	1	0	0	0	0	0	0
CA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0

	0	0	0	0		0	0	0	0	0	0
AC	0	0	0	0	1	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
MC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StB	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
Stc	0	0	0	1	2	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
BR	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
OC	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
StD	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
HiB	4	0	0	0	0	1	0	0	0	0	0
Mites	5	0	0	0	0	0	0	0	0	0	0
SP	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
TrA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ElA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
ChA	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
CaS	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
GB	0	0	0	0	0	2	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
AE	0	0	0	0	0	0	0	0	0	0	0
Mites	0	0	0	0	0	0	0	0	0	0	0
beetle abundance	11	0	4	9	6	14	0	0	0	0	0
taxa richness	2	0	1	2	3	3	0	0	0	0	0
mite abundance	11	0	3	0	1	0	0	0	0	0	0

Appendix B. Ant exposure table per site

Ant exposure for each trap at each site for six weeks. 0 is absence of ants and 1 is presence of ants. Percentage of ants present was calculated to give the percentage of ant exposure (% Exposure) for each site.

Site	Trop	Week	Week	Week	Week	Week	Week	% Exposure
Sile	Trap	1	2	3	4	5	6	% Exposure
PV1	1	0	0	0	0	0	0	
PV1	2	1	1	0	0	0	0	
PV1	3	0	0	0	0	0	0	6
PV1	4	0	0	0	0	0	0	
PV1	5	0	0	0	0	0	0	
PV2	1	0	0	0	0	0	0	
PV2	2	0	0	0	0	0	0	
PV2	3	1	1	1	1	1	1	20
PV2	4	0	0	0	0	0	0	
PV2	5	0	0	0	0	0	0	
PV3	1	0	0	0	0	0	0	
PV3	2	0	0	0	0	0	0	
PV3	3	0	0	0	0	0	0	0
PV3	4	0	0	0	0	0	0	
PV3	5	0	0	0	0	0	0	
JV1	1	0	0	0	0	0	0	
JV1	2	0	0	0	0	0	0	C
JV1	3	0	0	0	1	1	0	6
JV1	4	0	0	0	0	0	0	
JV2	1	1	1	1	0	0	0	
JV2	2	1	1	1	0	0	0	
JV2	3	1	1	1	0	0	0	33
JV2	4	1	1	0	0	0	0	
JV2	5	0	0	0	0	0	0	
JV3	1	0	0	0	0	0	0	
JV3	2	0	0	0	0	0	0	
JV3	3	0	0	0	0	0	0	0
JV3	4	0	0	0	0	0	0	
JV3	5	0	0	0	0	0	0	

Site	Trap	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	% Exposure
AN1	1	0	0	0	0	0	0	
AN1	2	0	0	0	0	0	0	
AN1	3	0	0	0	0	0	0	0
AN1	4	0	0	0	0	0	0	
AN1	5	0	0	0	0	0	0	
AN2	1	1	1	1	1	1	1	
AN2	2	1	1	1	1	1	1	
AN2	3	1	1	1	1	1	1	100
AN2	4	1	1	1	1	1	1	
AN2	5	1	1	1	1	1	1	
OX1	1	1	1	1	1	1	1	
OX1	2	1	1	1	1	1	1	
OX1	3	1	1	1	1	1	1	100
OX1	4	1	1	1	1	1	1	
OX1	5	1	1	1	1	1	1	
OX2	1	1	1	1	1	1	1	
OX2	2	1	1	1	1	1	1	100
OX2	3	1	1	1	1	1	1	100
OX2	4	1	1	1	1	1	1	
OX3	1	1	1	1	1	1	1	
OX3	2	1	1	1	1	1	1	100
OX3	3	1	1	1	1	1	1	100
OX3	4	1	1	1	1	1	1	

Appendix B. (Continued)