The Ant Fauna of Inland Sand Dune Communities in Worcester County, Maryland

Jennifer A. Frye[1,*], Christopher T. Frye[1], and Theodore W. Suman[2]

Abstract - Ants inhabiting inland dune and ridge woodlands in Worcester County, MD, were surveyed in 2008 and 2009 using a combination of pitfall traps and litter samples. We employed both methods in 2008 and pitfall traps only in 2009. Thirty dune sites were targeted for survey work. We collected and identified a total of 44,930 ants representing 67 species. Data on annual and seasonal variation in the ant community are reported, as is variation in species composition based on trapping method. Expanding survey efforts to include multiple years, seasons, and trapping methodology served to increase the overall number of species encountered primarily through documenting the presence of rare or infrequent species. We provide a list of ant species collected from inland dune and ridge woodlands and discuss the significance of apparent habitat-restricted species.

Introduction

Xeric habitats are characterized by dry conditions with persistently low moisture levels. A number of specialist or habitat-restricted invertebrate species are uniquely adapted to such conditions for reasons including specialization on limited-range host plants (Litvaitis et al. 1999, Wagner et al. 2003); unique microhabitat availability for nesting, burrowing, and foraging (Droege et al. 2009, Litvaitis et al. 1999, Wagner et. al 2003); and avoidance of predators and parasitoids (Fernandes and Price 1992). There are several species of rare invertebrates restricted to xeric habitats in Maryland. *Limotettix minuendus* Hamilton (Eastern Sedge Barrens Leafhopper), an apparent Maryland endemic, is found only in serpentine barrens in the Piedmont Region (Frye and Tyndall 2010, Hamilton 1994). *Cicindela abdominalis* Fabricius (Eastern Pinebarrens Tiger Beetle) and *C. patruela* Dejean (Northern Barrens Tiger Beetle) demonstrate a state-wide and range-wide restriction to barrens and woodlands with dry, sandy soils (Knisley and Schultz 1997, Pearson et al. 2006). The butterflies of Maryland are particularly well documented. *Callophrys irus* Godart (Frosted Elfin) is currently found only in dry woodlands and pastures with sandy soils that support *Lupinus perennis* L. (Sundial Lupine) and *Baptisia tinctoria* L. (Wild Indigo) (Frye 2012, Schweitzer 1992). *Euchloe olympia* W.H. Edwards (Olympia Marble) is apparently restricted to shale-barren habitats within close proximity to woodlands in Maryland's Ridge and Valley Region and are found nowhere else in the state (MD Natural Heritage Program [NHP], Annapolis, MD, unpubl. data; Parshall 2002a); their distribution in West Virginia is limited by the

[1]Maryland Department of Natural Resources, Wildlife and Heritage Service, Natural Heritage Program, 909 Wye Mills Road, Wye Mills, MD 21601. [2]Smithsonian Institution, National Museum of Natural History, Department of Entomology, 10th and Constitution NW, Washington, DC 20560. [*]Corresponding author - jfrye@dnr.state.md.us.

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same habitat conditions (Allen 1997). *Pyrgus centaureae wyandot* W.H. Edwards (Grizzled Skipper) has been recorded from a variety of dry, early-successional situations including shale barrens, fields, glades, and power line cuts both in Maryland and in other parts of their range (Parshall 2002b). *Hesperia metea* Scudder (Cobweb Skipper) and *Hesperia leonardus* T. Harris (Leonard's Skipper), both of which utilize bluestem grasses as caterpillar host plants, are found only at a handful of xeric habitats in the state (MD Natural Heritage Program [NHP], unpubl. data). Leonard's Skipper appears to be restricted to serpentine and shale-barrens habitats; Cobweb Skipper is also found in these habitats but is distributed more broadly in dry, open woodlands with sandy soils. These findings are consistent with observations of both species by Allen (1997) in West Virginia.

Inland dune and ridge woodlands, herein referred to generally as "dunes" or "dune habitat", represent globally rare xeric habitats that occur on the Delmarva Peninsula and in southern New Jersey (NatureServe 2013). These communities are characterized by low-relief inland dunes shaped by northwest winds during the Pleistocene epoch (Newell and Dejong 2011) and are comprised of sand sheets of the Parsonsburg Formation (Denny et al. 1979, Newell and Dejong 2011). These woodlands are dominated by *Pinus echinata* Mill. (Shortleaf Pine), *P. taeda* L. (Loblolly Pine), and *Quercus* spp. (oaks), most commonly *Q. falcata* Michx. (Southern Red Oak), *Q. nigra* L. (Water Oak), and *Q. velutina* Lam. (Black Oak) (Harrison 2004), and are known to support several specialist invertebrates, some of which are found nowhere else in the state. The tenebrionid beetle *Helops cisteloides* Germar is known only from a small number of dunes on the outer coastal plain (W. Steiner, National Museum of Natural History, Washington, DC, unpubl. data) and is known generally from xeric habitats range-wide (Steiner 2009). The same is true of the tenebrionid beetle *Schoenicus puberulus* LeConte, a species that has not been encountered in Maryland since the late 1990s despite several years of targeted survey work (W. Steiner, unpubl. data). *Cicindela abdominalis* is also restricted to dune habitats on the Delmarva Peninsula where its larvae burrow beneath sandy soils (Knisley and Schultz 1997, Pearson et al. 2006).

The ant fauna of these dune habitats, however, has not been thoroughly investigated. Ants are critically important components of nearly every terrestrial ecosystem due to their services as soil engineers and their roles in various trophic level associations (e.g., Folgarait 1998, Frouz and Jilková 2008, Sanders and van Veen 2011). Their unique social structure (e.g., Hölldobler and Wilson 2009), economic impact (e.g., Lofgren 1985), and ability to dominate by invasion (e.g., Lach and Hooper-Búi 2010) only amplify their importance. In dune habitats specifically, they are of major interest because their colonies often persist in the leaf litter and beneath the soil, making the dry, sandy substrate a potentially important component in determining the presence or absence of a given ant species. This study sought to document the ant species present in this rare community type, as well as identify any known or apparent habitat-restricted species based on our own findings as well as those of local myrmecologists and from published records.

Field-site Description

The study was conducted in Worcester County, MD, on the Atlantic Coastal Plain Physiographic Province east of the Chesapeake Bay. Thirty survey sites were distributed over two adjacent United States Geological Survey (USGS) quadrangles, Snow Hill and Dividing Creek, an area known for its dune fields (Newell and Dejong 2011). Dunes are characterized by an increase in elevation as compared to the surrounding forest matrix, an elliptical shape, and well-drained soil series. To locate dunes, we used a combination of USGS quadrangle (topographic) maps and two ArcMap GIS (geographic information system) software data layers: United States Department of Agriculture Soil Survey Geographic (SSURGO) data, and Light Detection and Ranging (LIDAR) imagery. These resources allowed us to determine the locations of dune sites within the two quadrangles. All dunes were then mapped as polygons using ArcMap GIS. A total of 303 dunes were mapped. Using the natural breaks function in ArcMap (extension X-Tools Pro), the dunes were divided into three statistically determined size classes (small, medium, and large). We used ArcMap to calculate the actual range of each size class based on natural groupings inherent in the data, determining break points that "best group similar values and maximize the differences between classes" (ESRI 2012). Of the 303 dunes identified and mapped, 30 were chosen at random for sampling. We ground-truthed all sites to verify that the polygons represented dune habitat. Of these, 9 were small dunes (<1.1 ha), 14 were medium dunes (1.1–4.0 ha), and 7 were large dunes (>4.0 ha). In addition to size, sites differed in their historical management practices, in forest stand age, in vegetative composition, and in the degree of connectivity to other dunes, which were separated from the nearest neighboring dune by a range of 0.03–17 km. Dunes are typically interspersed throughout a landscape of basin swamps and lowland forests.

Methods

Ants were sampled using a modified version of the ALL (Ants of the Leaf Litter) protocol (Agosti and Alonso 2000), which employs (at a minimum) a combination of pitfall traps and litter samples intended to capture epigaeic and subterranean ants. The ALL protocol broadly recommends placing at least one 200-m transect with 20 pitfall traps (1 trap placed every 10 m) in a given sampling area. The protocol also recommends having 20 litter-sampling points within the sampling area. The ALL Protocol is intended to offer guidelines to ensure consistent sampling among different sites by different researchers. The protocols do not specify the number of transects required per unit area; this facet of the survey design must be determined by the individual researcher(s) based on the size and heterogeneity of the habitat being sampled.

In order to determine whether the use of a 200-m transect would be efficient for sampling ants in our study system, we conducted preliminary sampling in 2007 on the two largest dunes in our sample. We generated species-area curves and first-order jackknife estimates using PC-ORD (v. 3.04; MjM Software, Gleneden Beach, OR) in order to determine the minimum number of sampling units (pitfall traps and litter samples) required to capture ant species diversity and to derive area-based factors for sampling across different dune sizes.

Pitfall traps

Species accumulation curves for ants in individual pitfall traps (*n* = 120, pooled samples from both dunes) declined dramatically after 40 cups (equal to two 200-m transects), indicating that 2.4 cups per ha would be required to maximize species capture rates. This seemingly small number of cups indicated that a single 200-m transect (20 cups) as recommended by the ALL protocol would be sufficient at most dunes in our sample including all the dunes in the small and medium size class; large dunes required additional transects. Because dunes are small relative to the surrounding matrix, we employed 100-m transects as it was usually difficult to place a single 200-m transect on most dunes. The number of 100-m transects employed was based on dune size class. Small dunes (<1.1 ha) received a single 100-m transect; dunes in this size class were often too small to place more than one 100-m transect while still maintaining a distance of 10 m between each cup. We employed two 100-m transects (20 cups) at each dune in the medium size class (1.1 ha–4 ha); and three 100-m transects (30 cups) at each dune in the large size class (>4 ha) with the exception of the two largest dunes (6.9 ha and 10.7 ha), which each received four 100-m transects (40 cups). The placement of transects at each dune differed in 2008 and 2009, but the number of cups at each dune remained constant.

Pitfall traps were dug in the ground and closed one week before opening them to reduce digging-in effects as described by Greenslade (1973). Traps were filled with approximately 60 mL of a 50:50 propylene glycol and water solution and left open for a period of seven days for each spring, summer, and fall sample. Sampling dates varied slightly from year to year and between different dunes; the exact dates were dependent upon weather conditions and on available labor. We took spring samples between 29 April and 29 May, summer samples between 21 and 30 July (2009 only), and fall samples between 15 September and 7 October. To minimize by-catch of non-target invertebrates, we used relatively small 7-oz plastic cups with a 7-cm diameter (Bestelmeyer et al. 2000). Each cup was covered with a plastic lid when not in use.

Litter samples

The ALL protocol recommends collecting litter from 1-m^2 plots. However, we used an alternative method that is not currently described in the published literature but is used by some researchers due to the limitations of plot sampling (T. Schultz, National Museum of Natural History, Washington, DC, pers. comm.). A single observer walked each dune in the general vicinity of each pitfall transect collecting and sifting soil and litter until 3 L of material was collected. The goal of this method is to target areas likely to harbor ants, including rotting wood and areas of dense leaf litter, from several locations along each transect that were approximately equivalent yet subject to some variation. This method is open to potential bias—especially observer bias—as collection sites are not random, but maximizes the number of species captured. To minimize observer bias, the same observer collected litter at each transect on every dune. Litter was sifted and processed using winkler extraction techniques described in Bestelmeyer et al. (2000) and Longino and Nadkarni (1990). Due to constraints in time and manpower, we collected litter samples only in the spring and fall in 2008 and collected no litter samples in 2009.

We generated a species-area curve for litter samples (n = 12) based on the preliminary sampling data from 2007 on the two largest dunes in our sample. Although Sorenson distances between subsamples declined appreciably after four samples, the curve had a long tail with large standard deviations, characteristic of the presence of singletons in the sample. The curve indicated that minimally, 0.73 litter samples per ha were required, significantly fewer than the 20 samples recommended by the ALL protocol. Following the ALL protocol was logistically impossible given the large number of sites and the limitations in collectors and equipment. We therefore decided to collect one litter sample per 100-m pitfall trap transect (one litter sample for small dunes, two for medium dunes, three for large dunes, and four for the two largest dunes). This protocol was likely inadequate at fully capturing species diversity of litter ants given the poor refinement of the 0.73 litter samples per ha figure. However, it represented the maximum number of samples we were able to process.

Missing data

We deployed 600 pitfall traps amongst 30 sites in a given sampling period. Occasionally individual cups were "lost", most often because they'd been dug up by animals, flooded by rainwater, or trampled. Most dunes incurred significantly less than a 10% loss (i.e., retrieving 9 of 10 cups per transect) in any given sampling period. There were two instances where higher losses were incurred when entire transects were "lost" (presumably to foxes in one case and humans in another case). These transects were re-deployed in other areas of the dunes and left out for another 7-day sampling period. In all instances, there was no systematic bias and the missing values were simply excluded from the analysis. Data missing at random can be deleted with negligible impacts to the mean even when 50% of samples are missing (Scheffer 2002).

Data analysis

Although abundance data were collected at all dunes, it was not used in data analysis because it violated the rule of independent samples; due to the fact that ants live in colonies, an individual ant in a pitfall trap or litter sample cannot be considered independent of other ants of the same species in that sample (Gotelli et al. 2011). Further, if a pitfall trap or litter sample was located near a colony, that species of ant would often be over-represented in the data and skew the results. We chose to avoid log-transformed abundance data based on potential drawbacks inherent in this methodology (O'Hara and Kotze 2010). Additionally, square root transformations failed to remove statistical outliers. For these reasons, all data were converted to binary (presence–absence) format at the dune level before analysis. In addition to overall ant species diversity, we also compared diversity between the different collection methods (pitfall and litter), different seasons (spring, summer, and fall), and different years (2008 and 2009), also using binary datasets.

We used multiple-response permutation procedure (MRPP) as employed in PC-ORD, a multivariate analog of analysis of variance to test the null hypothesis of no significant differences in ant species composition between years, seasons, and trapping methods. Details of the procedure may be found in Mielke and Berry (2001). The strategy of MRPP is to compare the observed intragroup average distances with the average distances that would have resulted from all the other possible combinations of the data under the null hypothesis. The test statistic, usually symbolized with a lowercase delta (δ) is the average of the observed intragroup distances weighted by relative group size. The observed delta is compared to the possible deltas resulting from every permutation of the data. The MRPP reports a test statistic (T) describing the separation between groups, a measure of effect size (A) describing within-group agreement, and a *P*-value representing the likelihood of finding an equal or smaller delta than the observed based on all possible partitions of the dataset using the Pearson Type III distribution of deltas. We used Sorenson distance and a ranked-distance matrix following the protocols in McCune and Grace (2002). We conducted indicator species analysis (ISA) as employed in PC-ORD as a complement to MRPP to describe the value of different ant species for indicating trends in annual variation, seasonal variation, or for a particular trapping method. Indicator values range from zero (no indication) to 100 (perfect indication). Statistical significance of indicator values was evaluated by a Monte Carlo method using 1000 randomizations.

Species identification and determination of habitat-restricted species

Ants were identified in-house using multiple resources (Coovert 2005, Johnson 1988, Lynch 1987, Snelling 1988, Trager et al. 2007). Species identifications were verified by referencing Smithsonian specimens and through consultation with local entomologists. Species taxonomy follows the "working list" as described by Fisher and Cover (2007) but follows recent generic realignments (AntWeb 2013).

Based on our own findings, literature reviews, unpublished reports and data, and consultation with local myrmecologists, we attempted to broadly categorize all ant species recorded in our study into one of five categories:

1. *ubiquitous*: present or likely to be present in a variety of natural and anthropogenic habitats, and without any apparent physiographic restriction;
2. *forest species*: present in one or more types of forested situations, including both dry and mesic situations and both mature and early successional forests;
3. *open-area species*: present in a variety of open habitats including sparse woodlands, fields, meadows, and pastures, and possibly a variety of managed situations including lawns and parks;
4. *field and forest species*: present in a variety of open-area and forested habitats;
5. *habitat-restricted (xeric habitats):* found only in xeric habitats including dunes, barrens, and other dry areas often characterized by loose, sandy soils; may include a combination of natural and anthropogenic situations.

The literature we consulted emphasized seminal works, as well as papers and observations from the mid-Atlantic region and surrounding areas. Coovert (2005) had already characterized ecological field data for many of the species based on data from the Ohio Ant Survey and from existing literature. We relied heavily on his assessments, as well as on Lynch (1981, 1987), Lynch et al. (1988), and on the personal observations of John LaPolla (Towson University, Towson, MD) and Tim Foard (i2L Research USA, Inc., Baltimore, MD) for Maryland data; Carter (1962a, 1962b) for North Carolina data; and Ellison et al. (2012) for New England data.

Results

A total of 44,967 individual ants were collected representing 67 species from 25 genera. Individuals that could not be identified with reasonable certainty were excluded from the analysis, bringing the total to 44,930. Of these, 28,057 were collected in pitfall traps, and 16,873 were collected in litter samples.

Effect of trapping method

For comparisons of trapping methods, we analyzed just 2008 data, as that was the only year in which both trapping methods were employed. A total of 57 species were collected in 2008 representing 24 genera. Most species of ants were captured in both pitfall and litter samples, although MRPP analysis indicated a significant overall difference in the ant fauna between pitfall and litter samples (T = -12.904, A = 0.122, $P = 0.000$). Of the 57 species collected in 2008, pitfall traps captured 50 species while litter samples captured 52 species. Five species occurred significantly more frequently in pitfall traps, and four occurred significantly more frequently in litter samples (Table 1).

A total of 12 species occurred exclusively from only one trapping method (Table 2): 7 species occurred only in litter samples, and 5 species occurred only in pitfall traps. All 12 species represented relatively rare or infrequently encountered species that were only collected in 1 or 2 samples (i.e., a litter sample or a pitfall

Table 1. Ant species exhibiting a higher capture rate in one trapping method as compared to the other. Comparisons are based on the observed indicator values (IV) for species versus that resulting from randomized groups (1000 randomizations).

			IV from randomized groups		
Species	Max group	Observed IV	Mean	SD	*P*
Camponotus chromaiodes	Pitfall	32.0	17.7	4.18	0.020
Formica pallidefulva	Pitfall	61.3	33.9	4.83	0.002
Formica subsericea	Pitfall	38.4	19.5	4.17	0.003
Pheidole morrisii	Pitfall	36.3	20.1	4.60	0.013
Ponera pennsylvanica	Litter	69.4	34.5	4.28	0.001
Prenolepis imparis	Pitfall	60.9	42.8	4.05	0.001
Stigmatomma pallipes	Litter	27.0	12.8	3.83	0.008
Strumigenys clypeata	Litter	35.2	18.3	4.51	0.008
Strumigenys rostrata	Litter	53.4	32.9	4.38	0.004

transect) in 2008; in all but one case the total number of individuals collected was <5. All recorded species in the genus *Strumigenys* Smith appeared to be disproportionately associated with litter samples. Of the 6 *Strumigenys* species recorded in 2008, two of these, *S. clypeata* (Roger) and *S. rostrata* (Emery), occurred significantly more frequently in litter samples (Table 1). Three species, *S. pulchella* (Emery), *S. reflexa* (Wesson and Wesson), and *S. talpa* (Weber), were each represented by a single litter sample in 2008, and were not recorded at all from pitfall traps (Table 2). The remaining *Strumigenys* species, *S. ohioensis* (Kennedy and Schramm), was represented by a total of 7 samples: 6 litter samples and 1 pitfall trap transect; the pitfall record was for a single individual. This pattern was not statistically significant, likely because it was only recorded from 7 samples, too small a number to discern trends. However, it reinforces that *Strumigenys* spp. are better represented in litter samples.

Of the 7 species collected exclusively from litter samples in 2008 (Table 2), only one of those species, *Temnothorax longispinosus* (Roger), was recaptured in 2009 when only pitfall traps were used; two individuals were collected.

Annual variation

Overall annual variation was difficult to compare because sampling methods varied in 2008 and 2009. Litter samples were employed in 2008 but not in 2009. Because the trapping method used was shown to influence the species captured to some degree, annual comparisons were based on pitfall trap results only. Because summer sampling was conducted only in 2009, results from the summer sampling were also excluded from the inter-annual analysis.

A total of 53 species were collected in pitfall traps in the spring and fall of 2008 and 2009. Results of the MRPP showed that there was a significant difference between species captured in 2008 and 2009 ($T = -2.344$, $A = 0.011$, $P = 0.025$), but this result can probably be attributed to the presence of species that occur very infrequently. ISA showed that only 4 species were significantly more abundant in a given year (always 2009; Table 3). When comparing the binary results with the actual abundance

Table 2. Ant species restricted to one trapping method over the course of 60 sampling events (30 dunes surveyed in each of 2 seasons in 2008.

Species	Trapping method	Times captured	Total individuals collected
Aphaenogaster tennesseensis	Pitfall Only	1	1
Camponotus snellingi	Litter Only	1	1
Formica integra	Pitfall Only	1	2
Lasius claviger	Litter Only	2	191
Nylanderia arenivaga	Pitfall Only	3	3
Pheidole pilifera	Pitfall Only	1	1
Proceratium croceum	Litter Only	1	2
Strumigenys pulchella	Litter Only	1	1
Strumigenys reflexa	Litter Only	1	1
Strumigenys talpa	Litter Only	1	1
Temnothorax texanus	Pitfall Only	1	2
Temnothorax longispinosus	Litter Only	2	4

data, we found that 2 of the 4 species, *Camponotus castaneus* (Latreille) and *Myrmica punctiventris* Roger, always occurred at low densities, with 10 or less individuals observed at a given dune. The other two species, *Pheidole davisi* Wheeler and *Ponera pennsylvanica* Buckley, occurred frequently and often at high densities.

Fourteen species were present in one year only (Table 4). Twelve of these species were represented by a single sample. The other 2 species were captured infrequently: *Temnothorax longispinosus* occurred in only 2 samples and *Myrmica punctiventris* occurred in 6 samples.

Seasonal variation

Seasonal variation was analyzed using only pitfall trap data for 2008 and 2009. Because summer data were not collected in 2008, sample sizes were larger for both spring and fall collections.

A total of 59 species of ants were collected in pitfall traps in the spring and fall of 2008 and in the spring, summer, and fall in 2009. MRPP showed a significant difference between spring, summer, and fall collections (Table 5). The results of the

Table 3. Indicator species analysis (ISA) results for ants exhibiting significant annual variation. Comparisons are based on the observed indicator values (IV) for species versus that resulting from randomized groups (1000 randomizations).

			IV from randomized groups		
Species	Max group	Observed IV	Mean	SD	*P*
Camponotus castaneus	2009	16.6	10.0	2.36	0.036
Myrmica punctiventris	2009	10.0	4.5	1.76	0.024
Pheidole davisi	2009	13.5	6.5	2.18	0.023
Ponera pennsylvanica	2009	26.7	17.4	2.96	0.022

Table 4. List of ants found only in one survey year (2008 or 2009) based on pitfall trap data for spring and fall months over the course of 120 sampling events; a sampling event is defined as a dune surveyed in one season of one year. An asterisk indicates that when summer data and litter-sample data are considered, the species was present in both years.

Species	Year recorded	Times captured	Total individuals collected
Aphaenogaster mariae	2009	1	1
Aphaenogaster tennesseensis	2008	1	1
Camponotus caryae	2009	1	1
*Camponotus subbarbatus**	2008	1	1
Formica integra	2008	1	2
Formica querquetulana	2009	1	5
*Myrmica punctiventris**	2009	6	11
Pheidole tysoni	2009	1	2
Proceratium silaceum	2009	1	1
Strumigenys creightoni	2009	1	1
Strumigenys ohioensis	2008	1	1
Stenamma brevicorne	2008	1	1
*Temnothorax longispinosus**	2009	2	2
Temnothorax pergandei	2009	1	1

ISA showed that most individual species did not show significant variation between seasons, although many may have been observed too infrequently to discern any significant trends. Fourteen species of ants did exhibit significant seasonal variation (Table 6). In some cases, the presence of a species among the 30 sites was significantly higher in one season as compared to the others, and in other cases the presence of a species among the 30 dunes was significantly lower in one season as compared to the others. For 4 species, seasonal variation varied significantly across all three seasons. *Crematogaster ashmeadi* Mayr, for example, was encountered most frequently in the spring, but significantly decreased in frequency as the year progressed, with the lowest frequency observed in the fall. *Prenolepis imparis* (Say) was observed significantly more frequently in the fall than in the spring, although spring observations were also fairly high. The species was significantly less frequent in the summer as compared to both the spring and the fall.

Table 5. MRPP results for seasonal variation. The table reports the test statistic (T) describing the separation between groups, a measure of effect size (A) describing within-group agreement, and a *P*-value representing the likelihood of finding an equal or smaller delta than the observed based on all possible partitions of the dataset using the Pearson Type III distribution of deltas.

Groups	T	A	*P*
Overall	-18.592	0.095	<0.001
Spring vs. Summer	-9.897	0.056	<0.001
Spring vs. Fall	-14.166	0.065	<0.001
Summer vs. Fall	-14.833	0.092	<0.001

Table 6. List of ant species showing significant seasonal variation based on seasonal pitfall trap data for 2008 and 2009 as determined by ISA. The maximum number of sampling events for each season is determined by the number of dunes surveyed (30) multiplied by the number of number of years sampled; spring and fall sampling occurred in both 2008 and 2009 (Max = 60), while summer sampling occurred only in 2009 (Max = 30). The *P* value reported indicates that there was significant seasonal variation for the species. Letters denote which seasonal comparisons were significantly different. Seasons with one or more of the same letter were not significantly different. Only species for which there was significant seasonal variation are listed. For each species, the season(s) it was most frequently found in are listed.

Species	Spring	Summer	Fall	*P*	Most frequent
Camponotus castaneus	12ab	10bc	5ad	0.018	Spring and Summer
Camponotus chromaiodes	18ab	12bc	9ad	0.049	Spring and Summer
Camponotus nearcticus	8a	0b	2b	0.052	Spring
Crematogaster ashmeadi	35a	12b	9c	0.003	Spring
Dorymyrmex bureni	9b	10a	8b	0.025	Summer
Formica pallidefulva	47a	24a	20b	0.019	Spring and Summer
Formica subsericea	24a	5b	1c	0.001	Spring
Nylanderia parvula	6b	8a	7b	0.027	Summer
Pheidole dentata	6b	5b	18a	0.046	Fall
Prenolepis imparis	53b	4c	59a	0.001	Fall
Stennama impar	7a	0b	0b	0.008	Spring
Stigmatomma pallipes	1b	4a	1b	0.013	Summer
Strumigenys clypeata	1c	15a	9b	0.001	Summer
Trachymyrmex septentrionalis	32a	11b	15c	0.024	Spring

Habitat range and determination of habitat-restricted species

The results of our effort to classify all 67 ant species into five broad categories based on the range of habitat in which they most frequently occur as described in the literature or other data is presented in Appendix 1. Of the 67 species recorded in these dune and ridge woodlands, the overwhelming majority of these are likely to occur in a variety of forested habitats, or in both forested and open-area habitats. Four species likely occur primarily or exclusively in open-area habitats, and 11 species were identified as habitat-restricted, having been typically or exclusively recorded from xeric, sandy habitats, generally because they require such a substrate for nesting. Our assessments reflect a "best-fit" habitat category for each species based on the literature that we reviewed and on consultation with local myrmecologists. The habitat category assigned to each of the species was based on information reported from various observers over different parts of the species' range, and includes data on the presence of colonies as well as foraging workers. It is intended to help predict where potential habitats exist for each of these species in Maryland and the surrounding area. There may be variability based on region, and categories may change as more information becomes available.

Discussion

Our survey documents 67 ant species from inland dune habitats on Maryland's Atlantic Coastal Plain Province. Dune habitats likely contain additional species that are not documented here, including species that form small, cryptic colonies, are very rare and therefore infrequently encountered, or are better represented by trapping methods not employed in our study (or by a level of trapping effort beyond that conducted in our study). We likely would have captured more species, and in particular those in the genus *Strumigenys*, for example, had we conducted more extensive litter sampling. *Strumigenys* nest and forage primarily in the leaf litter and in topsoil, are rarely seen on the ground surface (Bolton 2000), and as our data suggest, are best captured through litter samples (Tables 1, 2). Our data likely underestimate the number of *Strumigenys* species present in these xeric dune habitats. Additionally, there may be other species present in dune habitats that were not well represented by either pitfalls or litter samples. *Aphaenogaster mariae* Forel, for example, was represented by a single individual captured in a pitfall trap in 2009; the species is more effectively sampled through hand collections of ants foraging on trees, especially oaks (Frye and Frye 2012).

Twelve species were captured exclusively in either pitfall (5 species) or litter samples (7 species) in 2008, all of which represented relatively rare or infrequently encountered species that were only recorded from one or two sampling events that year (Table 2). These species were therefore generally infrequent, supporting the assertion by Gotelli et al. (2011) that the similarity in composition of ants sampled by different methods in the same habitat is probably greater than has been appreciated since most differences are attributed to the presence of species that are rarely encountered. Even species in the genus *Strumigenys* were not entirely excluded from pitfall traps; in 2009 when only pitfall traps were utilized, an additional species of *Strumigenys*, *S. creightoni* M.R. Smith, was recorded, represented by a single individual. Despite the similarities between litter samples and pitfalls in producing rare or infrequent species, pitfall traps as employed in our study improved species representation in this dune system in a way that litter samples could not given our limitations in adhering to the ALL protocol. When the 12 species exclusive to one trapping method over another were excluded from the analysis, 32 of the remaining 44 species were found preferentially in pitfalls while only 12 of the 44 were found preferentially in litter. Oliver and Beattie (1996) found similar results when looking at ant species richness in dry forests of Australia. It must be noted, however, that researchers equipped to handle the intense amount of litter sampling required by the protocol may achieve different results.

Annual and seasonal variation did not differ for most species; however, sampling across three seasons over two years did pick up many infrequent species. Fourteen species were present in only one year, 12 of which were represented by a single sampling event. Other species may have been missed if collections were limited to a single season. *Stenamma impar* Forel, for example, was collected only in the spring. *Camponotus nearcticus* Emery was not collected at all in the summer. While both species were collected too infrequently to discern trends on seasonal variation, it is clear that expanding the sampling period led to an increased number of documented species. Variation in seasonal activity has also been documented for litter ants in Maryland by Lynch (1981). Other species showed an increase or decrease in activity in one or more seasons. For example, *P. imparis* observations declined sharply in the summer months, which is consistent with reports that *P. imparis* has a high tolerance for cooler temperatures as compared to other ant species (Wheeler 1930) and is often less active in the summer (Talbot 1943a, 1943b). These data may be useful when sampling efforts target specific species.

We were particularly interested in determining whether any of the ant species present in dune habitats were restricted to these and other xeric habitats. While the majority of species we recorded are likely to occur in a variety of habitats, 11 species were identified as habitat-restricted, associated primarily with xeric, sandy habitats. These habitats are often maintained by periodic disturbances that expose sandy soil and prevent the build up of organic matter. Not all of these areas, however, represent "natural" xeric habitats; the literature suggests that at least 6 of the 11 habitat-restricted ant species can persist in anthropogenic environments, including road shoulders, pastures, lawns, and cultivated fields, so long as the soil is sandy. Species including *Dorymyrmex bureni* (Trager), *Forelius pruinosus* (Roger), *Myrmica pinetorum* Wheeler, *Pheidole davisi*, *P. morrisii* Forel, and even *Trachymyrmex septentrionalis* (McCook)—the only species of fungus ant in Maryland—have been collected from one or more of these modified xeric habitats. *Forelius pruinosus* may be an extreme example, as this species is considered a house pest in the Gulf Coast States (Smith 1979). Even within our own study sites, many dunes are bisected by sandy roads which provide a significant portion of the loose, open sand that may be utilized for nesting by these species.

Assuming that colony longevity is equivalent in both "natural" and anthropogenic environments, it would appear unlikely that these species would be rare given the abundance and availability of these man-made habitats. However, habitat availability does not necessarily equate with habitat preference. On developed landscapes where natural habitats are fragmented and disturbance limited, organisms may persist—at least for a time—in anthropogenic habitats that mimic natural conditions. These managed areas, including mowed fields and road shoulders, are sometimes the only places on the landscape that experience routine disturbance. Many disturbance-dependent plant species, for example, are relegated to mowed roadsides or powerline rights-of way. Seedbanking species may also appear following a timber harvest or a prescribed burn. Lupine offers a good example; populations on Maryland's outer coastal plain occur on sandy road shoulders, rights-of-way, and in areas recently harvested for timber. There are also clusters of lupine that occur on the front yards of private residences constructed on the edges of sand dunes. These are not considered preferred habitats; more likely they represent relict populations struggling to persist in the now developed landscape.

Ants are similar to plants in that colonies are spatially fixed and dependent upon the resources in the immediate surrounding environment (Anderson 1991). Ants, like plants, are often found in artificial or modified environments that offer sandy conditions required for colonization, but perhaps these habitats are utilized only when natural conditions are limited or absent. *Pheidole morrissi* was the most frequent habitat-specialist encountered, recorded from 21 of the 30 dunes. Five species were recorded from 10–20 dunes, and three species were recorded from 5–9 dunes. *Formica querquetulana* Kennedy and Dennis and *Temnothorax pergandei* (Emery) were recorded from a single dune. Of the 11 habitat-restricted species, 6 were considered to be abundant on the dunes where they were collected. *Formica querquetulana*, *Myrmica pinetorum*, *Nylanderia arenivaga* (Wheeler), *T. pergandei*, and *T. texanus* Wheeler were represented by very few individuals per dune regardless of the number of dunes from which they were collected. This finding is not necessarily an indication of rarity, but rather suggestive that these 5 species were infrequently collected using the methods employed in our study. *Nylanderia arenivaga*, for example, is not considered to be rare, but because it is a nocturnal species that nests deep underground in sandy soils, it may often evade capture from litter samples and to a lesser extent pitfall traps (J. LaPolla, pers. comm.)

Modified habitats may not offer the area or structure required for long-term persistence. Habitat along sandy roads, for example, may be too small and linear to support large numbers of specialist ant colonies. Dispersal may be limited by fragmentation in anthropogenic habitats, through an increase in dispersal barriers, or through a decrease in the odds of encountering suitable habitat in a modified landscape. Species living in modified landscapes may also be subject to disturbances to which they are maladapted, including the use of pesticides and fertilizers, and the impacts of large-scale construction projects (i.e., new housing developments) that can result in the extirpation of colonies.

The available literature indicates that *F. querquetulana*, *N. arenivaga*, *N. parvula* (Mayr), *T. pergandei*, and *T. texanus* are not generally associated with common, anthropogenic habitats, but instead are typically found in rare xeric communities that have well-drained, sandy soils. *Temnothorax texanus*, for example, has been recorded from a variety of specialized xeric habitats including pine and shale barrens and *Quercus velutina* Lamb. (Black Oak) dune habitats. *Nylanderia parvula* has been associated with pine barrens and pine-dunes. While these species are likely found in other areas of the state and are not restricted to dune and ridge woodland habitats specifically, they may prove to be indicators for more natural xeric habitats. They are also noteworthy in that their distribution may be limited by the presence of rare xeric community types including dune habitats. We intend to expand our analyses to explore how dune size, historical management practices, forest stand age, and connectivity to other dunes may impact the overall diversity of ant species and the presence of habitat-restricted species within the larger dune landscape.

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Appendix 1. List of the 67 ant species collected from inland sand and dune woodland sites by range of habitat. Our assessment reflects a "best-fit" category for each species based on literature reviews and consultation with experts. The habitat category assigned to each species is based on information reported from various observers over different parts of the species range. It is intended to help predict where potential habitats exist for each of these species in Maryland and the surrounding area. There may be variability based on region, and categories may change as more information becomes available.

Species	Habitat notes	Literature consulted
	Ubiquitous	
Camponotus pennsylvanicus (DeGeer)	Various forested habitats encompassing both dry upland forests and mesic lowland forests, but also common in buildings, yards, and streets, making this a pest species in many areas. Carter (1962b) also notes it from pastures and wet meadows.	Brown 1950, Carter 1962a, Carter 1962b, Coovert 2005, Ellison et al. 2012, Lynch 1987, MES 2012, Wheeler 1910
Formica pallidefulva Latreille	A large variety of forested and open-area habitats encompassing both dry upland forests and mesic lowland forests, pine barrens, woodlots, semi-open areas, grasslands, thickets, old fields, roadsides, campuses and parks.	Beattie and Culver 1981, Carter 1962a, Carter 1962b, Coovert 2005, Creighton 1950, Ellison et al. 2012, Fellers 1987, Lynch 1981, Lynch 1987, MES 2012, Trager 1988
Lasius claviger (Roger)	Variety of forest and open-area habitats including both dry upland forests and mesic lowland forests, open woods, wood edges, semi-open areas, fields, pastures and roadsides. Smith (1979) notes that it is a common house pest.	Carter 1962a, Carter 1962b, Coovert 2005, Ellison et al. 2012, Lynch 1987, Smith 1979
Solenopsis molesta (Say)	A variety of open area habitats including grassy areas, fields, meadows and pastures, but also in various forested habitats encompassing dry uplands and mesic lowlands, typically in more open woods or in sunny clearings; can also infest buildings and homes where they may nest in woodwork and masonry (Smith 1979).	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, Lynch 1987, Smith 1979
Tapinoma sessile (Say)	A variety of forested and open-area habitats, as well as disturbed sites; recorded from various forested habitats encompassing both dry upland forests and mesic lowland forests, including mixed deciduous forests, woodlots, and woods edges, as well as open fields, meadows, lawns, and houses.	Beattie and Culver 1981, Bristow 1984, Carter 1962a, Carter 1962b, Coovert 2005, Creighton 1950, Culver and Beattie 1978, Ellison et al. 2012, Fellers 1987, Lynch 1981, Lynch 1987, Lynch et al. 1988, MES 2012, Smith 1928
	Forest	
Aphaenogaster fulva Roger	Various forested habitats encompassing both dry upland forests and mesic lowland forests including deciduous forests and semi-open woodlands.	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Culver and Beattie 1978, Ellison et al. 2012, Lynch 1987, Lynch et al. 1988

Species	Habitat notes	Literature consulted
Aphaenogaster lamellidens Mayr	Various forested habitats encompassing both dry upland forests and mesic lowland forests including deciduous forests and semi-open woodlands. Carter (1962b) notes a preference for pine forests.	Carter 1962a, Carter 1962b, references in Coovert 2005, Creighton 1950, Lynch 1987
Aphaenogaster mariae Forel	Oak and oak-hickory forests, as well as moist woods and woods edges. In maryland they are most common in dry, oak-dominated forests (T. Foard, pers. Comm.)	Carter 1962a, Carter 1962b, Coovert 2005, Ellison et al. 2012, T. Foard (pers. comm.)
Aphaenogaster rudis Enzmann	Various forested habitats encompassing both dry upland forests and mesic lowland forests including cypress swamps; Lynch (1981) has also recorded this species from old fields and Coovert (2005) has recorded it from open areas near woods.	Beattie and Culver 1981, Carter 1962a, Carter 1962b, Coovert 2005, Culver and Beattie 1978, Ellison et al. 2012, Fellers 1987, Hölldobler and Wilson 1990, Lynch 1981, Lynch 1987, Lynch et al. 1988
Aphaenogaster tennesseensis (Mayr)	Various forested habitats including hardwood forests, mixed forests, open woodlands, and semi-open areas; Carter (1962b) has also collected them from grassy pastures with scattered pines.	Beattie and Culver 1981, Carter 1962a, Carter 1962b, Coovert 2005, Ellison et al. 2012, Lynch 1987
Camponotus caryae (Fitch)	Woodlands and woods edges; Creighton (1950) considered the species to be rare and associated with hickory. Wesson and Wesson (1940) associated *C. Caryae* with oak-hickory woodlands; Florida specimens examined by Snelling (1988) were also collected from hickory.	Carter 1962b, Coovert 2005 (and references therein), Creighton 1950, Ellison et al. 2012, Snelling 1988
Camponotus chromaiodes Bolton	Moist, rich woodlands and dry hardwood forests.	Coovert 2005, Ellison et al. 2012, T. Foard (pers. comm.), Smith 1979
Camponotus nearcticus Emery	Various forested habitats encompassing dry upland forests and mesic lowland forests, woodlots, and even houses where they may nest in roofing or wooden fence posts.	Carter 1962a, Carter 1962b, Coovert 2005, Ellison et al. 2012, Fellers 1987, Lynch 1987, MES 2012, Smith 1979
Camponotus subbarbatus Emery	Various forested habitats including dry upland forests, mesic lowland forests, second growth woods, forest edges, open woodlands and woodlots; Lynch (1981) has also recorded *C. Subbarbatus* from old fields.	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, Lynch 1981, Lynch 1987, MES 2012
Crematogaster ashmeadi Mayr	Various forested habitats including pine, oak, and hardwood forests in both mesic and xeric habitats; also collected from an urban woodlot.	Carter 1962a, Carter 1962b, Fellers 1987, Johnson 1988

Species	Habitat notes	Literature consulted
Formica subsericea Say	Primarily associated with open woods, wooded areas with light gaps, or woods edges, but also from hardwood and mesic forests, woodlots, and open areas near woods. Also recorded from fields, lawns and gardens in New England (Ellison et al. 2012).	Beattie and Culver 1981, Coovert 2005, Creighton 1950, Culver and Beattie 1978, Ellison et al. 2012, Fellers 1987, Lynch 1987, MES 2012, Smith 1979
Lasius alienus (Foerster)	A variety of forested habitats encompassing both dry upland forests and mesic lowland forests, and only occasionally in fields or meadows.	Beattie and Culver 1981, Carter 1962a, Carter 1962b, Coovert 2005, Creighton 1950, Culver and Beattie 1978, Ellison et al. 2012, Fellers 1987, Lynch 1981, Lynch 1987, Lynch et al. 1988, MES 2012, Smith 1979
Myrmecina americana Emery	A variety of forested habitats including mature deciduous forests, although may be more common in mesic forests as compared to dry forests; many records refer to moist, shady habitats.	Brown 1967, Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Creighton 1950, Culver and Beattie 1978, Ellison et al. 2012, Lynch 1981, Lynch 1987, Lynch et al. 1988, MES 2012
Myrmica punctiventris Roger	A variety of forested habitats encompassing dry open forests and shady mesic forests.	Beattie and Culver 1981, Carter 1962a, Carter 1962b, , Coovert 2005 (and references therein), Culver and Beattie 1978, Ellison et al. 2012, Fellers 1987, T. Foard (pers. comm.), Lynch 1981, Lynch 1987, Lynch et al. 1988, MES 2012, Weber 1950
Ponera pennsylvanica Buckley	Various forested habitats encompassing dry upland forests and mesic lowland forests including deciduous forests. Lynch (1981) has recorded *P. pennsylvanica* from abandoned fields in addition to forested areas and Ellison et al. (2012) notes that they also occur in bogs, fens and wet fields in New England.	Carter 1962a, Carter 1962b, Coovert 2005, Ellison et al. 2012, Lynch 1981, Lynch 1987, Lynch et al. 1988, MES 2012, Smith 1979
Prenolepis imparis (Say)	Various forested habitats encompassing both dry upland forests and mesic lowland forests including both dense and open woodlands and woodlots; less frequently recorded from open area habitats including field edges and grasslands.	Carter 1962a, Carter 1962b, Clyde 1941, Coovert 2005 (and references therein), Creighton 1950, Ellison et al. 2012, Fellers 1987, Hölldobler and Wilson 1990, Lynch 1987, Lynch et al. 1988, Wheeler 1930
Proceratium croceum (Roger)	Forested habitats including deciduous forests, pine forests and wet, shaded areas of mixed hardwood forests.	Carter 1962a, Carter 1962b, references in Coovert 2005, Lynch 1987
Proceratium silaceum Roger	Forested habitats including pine, oak, and hardwood forests, as well as open woods.	Carter 1962a, Carter 1962b, references in Coovert 2005, Ellison et al. 2012, Lynch 1987

Species	Habitat notes	Literature consulted
Stenamma impar Forel	Forested habitats including moist woods and hardwood forests; they are frequently associated with oak-dominated forests in New England (Ellison et al. 2012).	Carter 1962b, Coovert 2005 (and references therein), Creighton 1950, Ellison et al. 2012, Lynch 1981, Lynch 1987, Lynch et al. 1988, Smith 1957
Stigmatomma pallipes (Haldeman)	Various forested habitats encompassing both dry upland forests and mesic lowland forests.	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Creighton 1950, Lynch 1981, Lynch 1987, Lynch et al. 1988
Strumigenys clypeata (Roger)	Forested habitats including pine, oak and hardwood forests and mixed woods; frequently in mature, mesic forests.	Bolton 2000, Brown 1953 (and references therein), Carter 1962a, Carter 1962b, Wilson 1953
Strumigenys creightoni (M.R. Smith)	Various forested habitats including pine forests, pine-hardwood forests and dry oak woods.	Carter 1962a, Carter 1962b, references in Coovert 2005, Wilson 1953
Strumigenys ohioensis (Kennedy and Schramm)	Variety of forested habitats including both mature and successional forests; recorded from dry upland forests and mesic lowland forests including dense, shady forests and deciduous woods.	Bolton 2000, Brown 1953 (and references therein), Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Lynch 1981, Lynch 1987, Lynch et al. 1988, Wilson 1953
Strumigenys pulchella (Emery)	Forested habitats including pine and oak forests and deciduous woods.	Bolton 2000, Brown 1953 (and references therein), Carter 1962a, Carter 1962b, references in Coovert 2005, Ellison et al. 2012, Wilson 1953
Strumigenys reflexa (Wesson and Wesson)	Mesic, forested habitats including wet woods; Coovert (2005) notes record taken from a shady backyard.	Reference in Carter 1962b, Coovert 2005, Wilson 1953
Strumigenys rostrata (Emery)	Various forested habitats encompassing both dry upland forests and mesic lowland forests including mature forests and woods edges.	Bolton 2000, Carter 1962a, Carter 1962b, references in Coovert 2005, Lynch 1987, Lynch et al. 1988, Smith 1931, Wilson 1953
Temnothorax curvispinosus (Mayr)	Variety of forested habitats encompassing dry upland forests and mesic lowland forests, woodlots, and woods edges.	Carter 1962a, Carter 1962b, Coovert 2005, Culver and Beattie 1978, Ellison et al. 2012, Fellers 1987, T. Foard (pers. comm.), Headley 1943, Lynch 1981, Lynch 1987, Lynch et al. 1988, Wheeler 1903
Temnothorax longispinosus (Roger)	Variety of forested habitats including mesic forests, mature deciduous forests, oak woods, open and shady woods, woodlots, and woods edges.	Carter 1962a, Carter 1962b, Coovert 2005, Culver and Beattie 1978, Ellison et al. 2012, Fellers 1987, T. Foard (pers. comm.), Headley 1943, Lynch 1987, Lynch et al. 1988, MES 2012

Species	Habitat notes	Literature consulted
Temnothorax schaumii (Roger)	Forested habitats including mixed hardwood forests, open woods, woods edges, and woodlots.	Carter 1962a, Carter 1962b, Coovert 2005, Ellison et al. 2012, Fellers 1987, Lynch 1987, Lynch et al. 1988, Wheeler 1903
	Field and forest	
Aphaenogaster treatae Forel	Generally associated with open-area habitats including fields, grasslands, heathlands and pine barrens, although Carter (1962a, b) has also recorded them from dry pine, oak, and hardwood forests.	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, Lynch 1987, Smith 1979
Brachymyrmex depilis Emery	A variety of field and forested habitats, including both dry and mesic forested habitats, meadows, fields, and road shoulders.	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, Lynch 1987, Lynch et al. 1988
Camponotus castaneus (Latreille)	A variety of forested habitats including moist and dry woods including hardwood, evergreen, and mixed forests, frequently in areas with well-drained soils; also recorded from woodlots and open area habitats including rocky barrens, open fields, and Black Oak dunes (see references within Coovert 2005).	AntWeb 2013, Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, Fellers 1987, Lynch 1987, Wheeler 1910
Camponotus snellingi Bolton	Mature swamp forests and moist thickets, but collected from oak forests and the edges of mixed woods with deep sandy soil in Maryland (T. Foard, pers. Comm.)	Antweb 2013, T. Foard (pers. comm.), Snelling 1988
Crematogaster cerasi (Fitch)	Various forested and open-area habitats including hardwood forests, mixed woods, mesic woodlands, fields and field margins, edge habitats, and generally open and semi-open areas.	Beattie and Culver 1981, Carter 1962a, Carter 1962b, Coovert 2005, Ellison et al. 2012, Johnson 1988, Lynch 1981, Lynch 1987, MES 2012
Crematogaster lineolata (Say)	A variety of habitats including pine, oak, and hardwood forests, brushy or grassy fields, power line rights-of-way, meadows and pastures; Johnson (1988) makes a distinction between northern and southern populations, with northern colonies occurring in mesic forests, overgrown fields, and disturbed areas, and southern colonies occurring in xeric upland sand hills.	Bristow 1984, Carter 1962a, Carter 1962b, Coovert 2005, Culver and Beattie 1978, Ellison et al. 2012, T. Foard (pers. comm.), Johnson 1988, Lynch 1987
Crematogaster pilosa Emery	Various forested areas including hardwood forests and mixed woods, and often noted from moist woods; Johnson (1988) asserts that they rarely occur in xeric uplands. They are also recorded from semi-open and open areas including overgrown fields. Tim Foard (pers. Comm.) Has found them to be associated with brackish marshes in Maryland.	Carter 1962a, Carter 1962b, Coovert 2005, T. Foard (pers. comm.), Johnson 1988, Lynch 1981, Lynch 1987

Species	Habitat notes	Literature consulted
Dolichoderus pustulatus Mayr	Usually associated with open-area habitats, both dry and wet, including dry grassy fields, broomsedge-pine fields, marsh edges, fens, bogs, and swamps. However, there are also records from open and mixed deciduous woods.	Bristow 1984, Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, T. Foard (pers. comm.), Hölldobler and Wilson 1990, Lynch 1987
Formica integra Nylander	Forested habitats including hardwood forests and hardwood-conifer forests, but also open woods and woods edges, old fields, open meadows, roadsides, and grassy areas.	Carter 1962b, Coovert 2005, Culver and Beattie 1978, Ellison et al. 2012, Kloft et al. 1973, Lynch 1987, Smith 1979
Hypoponera opacior (Forel)	Primarily associated with prairies, grasslands, and fields, but also recorded from open and dry woods, including pine and oak forests.	Carter 1962a, Coovert 2005 (and references therein)
Lasius subglaber Emery	Woodlands and open areas, including tree-fall gaps.	Reference in Carter 1962b, reference in Coovert 2005, Ellison et al. 2012, MES 2012, Smith 1979
Monomorium minimum (Buckley)	Primarily open and semi-open habitats with exposed soil including fields, grassy meadows, and forest clearings, but there are also records from dry pine forests and woodlots. Smith (1979) notes that it sometimes invades houses or infests woodwork.	Carter 1962a, Carter 1962b, Coovert 2005, Fellers 1987, Hölldobler and Wilson 1990, Lynch 1981, Lynch 1987, Smith 1979
Nylanderia faisonensis (Forel)	Forested and open-area habitats including deciduous forests, pine forests, woods edges, and semi-open areas including meadows and dry or exposed areas; Coovert (2005) notes that they are occasionally found in buildings.	Coovert 2005 (and references therein), Kallal and LaPolla 2012, Lynch 1987, Lynch et al. 1988, Trager 1984
Pheidole dentata Mayr	Forested and open-area habitats including pine, oak, and hardwood forests, open woodlands, fields, grasslands, and pastures.	Carter 1962a, Carter 1962b, references in Coovert 2005, Creighton 1950, Lynch 1987, Smith 1979
Pheidole tysoni Forel	Forested and open-area habitats including pine and oak forests, forest openings, grassy fields, meadows, and grazed hillside pastures.	Carter 1962a, Carter 1962b, references in Coovert 2005, Creighton 1950
Stenamma brevicorne (Mayr)	A variety of forested and open-area habitats including moist woods, both dense and open woods, field and grassland edges, old fields, and meadows.	Coovert 2005 (and references therein), Creighton 1950, Ellison et al. 2012, Lynch 1987, Smith 1957, Smith 1979
Strumigenys talpa (Weber)	Forested habitats including pine, oak, and hardwood forests, dry open woods, woods openings, field thickets, and open grassy areas.	Bolton 2000, Brown 1953 (and references therein), Carter 1962a, Carter 1962b, references in Coovert 2005, Wilson 1953

Species	Habitat notes	Literature consulted
Temnothorax ambiguus (Emery)	Forested and open area habitats including mixed deciduous forests, damp shaded woods, oak woodlands, open woods, old fields, meadows, and grasslands.	Bristow 1984, Coovert 2005 (and references therein), Ellison et al. 2012, Lynch 1981, Lynch 1987, Smith 1979, Wheeler 1903
	Open area	
Lasius neoniger Emery	Open, often disturbed sites including woods edges, grassy fields, cultivated fields, meadows, prairies, roadsides, and lawns; rarely in woods although there are records from open woods. Smith (1979) notes that it is a common lawn and house pest.	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, J. LaPolla (pers. comm.), Lynch 1987, MES 2012, Smith 1979
Myrmica americana Weber	A variety of open area habitats, often with dry, sandy soils, including woods edges, old fields, meadows, grasslands, prairies, and college campuses, although they have been collected in mixed deciduous woods (Bristow 1984) and in open woodlands (Creighton 1950).	Bristow 1984, Carter 1962a, Carter 1962b, Coovert 2005, Creighton 1950, Ellison et al. 2012, J. LaPolla (pers. comm.), Lynch 1981, Lynch 1987, Smith 1979, Weber 1950
Pheidole bicarinata Mayr	Open-area habitats, especially dry, disturbed areas including open woods, sand dune and ridge habitats, semi-open sandy areas, old fields, corn fields, grasslands, lawns, and road shoulders.	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), T. Foard (pers. comm.), Gregg 1942, Lynch 1987, Smith 1979
Pheidole pilifera (Roger)	Various open area habitats, especially disturbed sites, including open fields, open meadows, grasslands, lawns, and roadsides.	Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, Gregg 1942, J. LaPolla (pers. comm.), Lynch 1987
	Habitat-restricted (xeric habitats)	
Dorymyrmex bureni (Trager)	Open areas with sandy soils including fields, dunes, roadsides, pastures, and lawns.	Trager 1988
Forelius pruinosus (Roger)	A variety of xeric habitats including dry forests and fields (including cultivated fields), hilltops, oak and pine dunes, xerophyl scrub, shrub steppe, and grassy fields, but also on lawns and roadsides. Smith (1979) note that they are considered a house pest in the Gulf Coast states.	AntWeb 2013, Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Smith 1979
Formica querquetulana Kennedy and Dennis	Very dry, sandy habitats including dry open woods and woods edges, oak woodlands, pine barrens and shrublands, rock outcrops, shrub steppe, upland fields, and pastures.	AntWeb 2013, Coovert 2005 (and references therein), Ellison et al. 2012, Smith 1979

Species	Habitat notes	Literature consulted
Myrmica pinetorum Wheeler	Dry forested habitats with sandy soils including open woods, mixed forests, pine forests and barrens, and dry oak forests. Also occur in open-area habitats with sandy soils including woods edges, grassy fields, meadows, and pastures. Bolton (2013) notes records from "earthy or rocky" soils.	AntWeb 2013, Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, Lynch 1987, Smith 1979, Weber 1950
Nylanderia arenivaga (Wheeler)	Open, well-drained sandy areas	Kallal and LaPolla 2012, Trager 1984
Nylanderia parvula (Mayr)	Primarily open-area habitats with sandy soils including xeric forests, pine barrens, pine-dunes, deciduous forests, open woods, open areas near woods, and grassy fields.	Beattie and Culver 1981, Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Ellison et al. 2012, Kallal and LaPolla 2012, Lynch 1987, Smith 1952, Smith 1979, Trager 1984
Pheidole davisi Wheeler	Open-area habitats with sandy soils including pine barrens, old fields, and open grasslands; Carter (1962b) has records from sandy soils of grassy areas along a major highway in North Carolina.	Carter 1962b, Lynch 1987, Wheeler 1905
Pheidole morrisii Forel	Open-area habitats with sandy soils including xeric forests, open forests, Black Oak dunes, sunny glades in pine woods, dry fields and slopes, open grasslands, and cultivated fields; also lawns and road shoulders.	Carter 1962a, Carter 1962b, references in Coovert 2005, Gregg 1942, Lynch 1987
Temnothorax pergandei (Emery)	Dry, exposed habitats including open or semi-open dry barrens, xerophyl scrub, pine scrub, longleaf pine-oak sandhills, shale barrens, grassy fields, dry fields, thickets, and meadows; there are also records for both dry upland forests and mesic lowland forests.	AntWeb 2013, Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), T. Foard (pers. comm.), Lynch 1987, Wheeler 1903
Temnothorax texanus Wheeler	Open-area habitats with sandy soils including pine barrens, shale barrens, Black Oak dunes, sand dunes, and oak woods clearings; also occur in dry, open woodlands.	Carter 1962a, Carter 1962b, references in Coovert 2005, Creighton 1950, Ellison et al. 2012, T. Foard (pers. comm.), Lynch 1987, Smith 1952, Smith 1979, Wheeler 1903
Trachymyrmex septentrionalis (McCook)	Open-area and dry forested habitats with sandy soils including dry oak or pine forests, open woods, dry shale hillsides, and sandy loam slides; also in sandy road shoulders and paths.	Carter 1962a, Carter 1962b, Coovert 2005 (and references therein), Lynch 1987