

Associations of Ants (Hymenoptera: Formicidae) on Oaks and Pines in Inland Dune and Ridge Woodlands in Worcester County, Maryland

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ABSTRACT: Inland dune and ridge woodlands represent a rare community type largely restricted to the Delmarva Peninsula. Shortleaf pine (*Pinus echinata* Mill.) exhibits a restricted distribution in Maryland and is often a dominant component of these woodlands. It is also likely to represent one of the geologically oldest tree components in these communities. We compared the overall species composition of ants (Hymenoptera: Formicidae) on shortleaf pine, loblolly pine (*P. taeda* L.), and various species of oaks (*Quercus* L. spp.) to determine whether there were any ant species restricted to or preferentially associated with shortleaf pine. Ants were sampled using hand collection methods from 241 trees representing a mix of these three groups. Multiple-response permutation procedure (MRPP) revealed a marginal difference between the three groups. Systematic group exclusion revealed a marginally significant difference between oaks and loblolly pine, a non-significant difference between loblolly and shortleaf pines, and a significant difference between oaks and shortleaf pine. Indicator species analysis (ISA) showed that three ant species were associated with oaks while one species was associated with loblolly pine. Of the 35 species that were collected, none showed an association with shortleaf pine.

INTRODUCTION

Inland dune and ridge woodlands (Figure 1) are globally rare natural communities occurring only on the Delmarva Peninsula and in southern New Jersey (NatureServe 2012). These communities feature low-relief inland dunes shaped by northwest winds during the Pleistocene epoch (Newell and Dejong 2011) and are comprised of dry sandy soils of the Parsonsburg Formation (Denny et al. 1979; Newell and Dejong 2011). They are dominated by shortleaf pine (*Pinus echinata* Mill.), loblolly pine (*P. taeda* L.) and oaks (*Quercus* L. spp.), most commonly southern red oak (*Q. falcata* Michx.), water oak (*Q. nigra* L.), and black oak (*Q. velutina* Lam.) (Harrison 2004). Shortleaf pine exhibits a restricted distribution in Maryland growing only in areas with well-drained, nutrient-poor soils (Little 1971) and achieving dominance only in dune and ridge woodlands on the Delmarva Peninsula. On the Delmarva, however, it has been largely or completely displaced in many dune and ridge woodland sites by loblolly pine, a preferred species for commercial timber production. Some loblolly-dominated stands result from natural regeneration of previously harvested stands while others were planted for commercial timber production, many over a century ago (Maryland Department of Natural Resources – Forest Service, unpublished site data). Shortleaf pine stands result from natural regeneration and remain a key component of dune and ridge woodlands.



Figure 1: Typical dune and ridge woodland, Worcester County, Maryland. Location near Snow Hill, 26 October 2009.

Shortleaf pine is considered to be the most cold-hardy species of the southern pines and likely existed in a continuous distribution across the continental shelf, whereas loblolly pine persisted in southern Texas and northern Mexico refugia during the Pleistocene, expanding its range north only after the glaciers receded (Schmidtling 2007). Shortleaf pine was therefore likely persistent in Maryland long before other pine species migrated there or were planted, and is probably one of the geologically oldest tree components of dune and ridge woodlands on the Delmarva Peninsula. Its historical distribution and persistence may have allowed for the evolution of specialized relationships between shortleaf pine and invertebrates, many of which are dependent on trees for nesting, foraging, and for temporary refuge (Büchs 1990; Simon 1991; Hanula and Franzreb 1998; Majer et al. 2003). In addition to its long-term presence in these communities, specific characteristics of the bark and the presence or absence of potential competitors or predators on shortleaf pine may also impact the invertebrate assemblage it supports. Characteristics such as these have been demonstrated to influence the invertebrate fauna supported by different tree species in other studies (Nicolai 1993; Majer et al. 2003; Verble and Stephen 2009). To our knowledge, there are no published studies on the associations of ants (Hymenoptera: Formicidae) and shortleaf pine, even in the southern United States where shortleaf pine is more abundant.

Our study sought to determine whether there were any ant species in dune and ridge woodlands on the Delmarva Peninsula that were restricted to or preferentially associated with shortleaf pine. We also compared the overall species composition of ants on shortleaf pine, loblolly pine, and oak and compiled a list of ants associated with pines and oaks in this natural community.

METHODS

The study area encompassed 30 dune and ridge woodland sites in Worcester County, Maryland. All 30 sites were within two adjacent United States Geological Survey (USGS) quadrangles, Snow Hill and Dividing Creek. Sites differed in their historical management practices, in forest stand age, and in tree species composition.

To locate dune and ridge woodland sites, which are typically interspersed throughout a landscape of basin swamp and lowland forest, we used a combination of USGS quadrangle (topographic) maps and two ArcMap GIS (geographic information system) software data layers: United States Department of Agriculture (USDA) Soil Survey Geographic (SSURGO) data, and LIDAR (Light Detection and Ranging) imagery. Characteristics of dune and ridge woodlands include an increase in elevation as compared to the surrounding forest matrix, an elliptical shape, and well-drained soil series, each of which can usually be ascertained using these resources. Potential dune and ridge woodlands were mapped as polygons in both quadrangles using ArcMap, and then 30 of those sites were chosen at random for this study. All sites were ground-truthed to verify that the polygons did indeed represent dune and ridge woodland habitat.

Surveys of ants were conducted in June and August in 2008 and 2009 from trees at all 30 sites. Since we could not control for differences in management, stand age, or tree species composition, we sampled a consistent number of pines and oaks from all 30 sites. Each site fell into one of three habitat size classes (i.e., dune area): small (< 1.1 ha [2.7 ac]), medium (1.1 – 4.0 ha [2.7-9.9 ac]) and large (> 4.0 ha [9.9 ac]). Six trees were sampled at each small site, 9 trees at each medium site, and 12 trees at each large site. All trees were selected at random, with the condition that they have a minimum diameter of 6 cm (2.4 in) and be a minimum distance of 10 m (32.8 ft) from any other surveyed tree. In most cases, an equal number of shortleaf pines, loblolly pines, and oaks were sampled at each dune. When this was not possible (i.e., if no shortleaf pine was represented at a site), the same number of trees was sampled given the size class of the site but the ratio of tree species was adjusted.

We surveyed for ants using 15-minute sampling periods per tree, between 1000 and 1600 hours. Investigators collected all ants observed within that time period with an aspirator. Each tree was sampled only once and all collections were made from the lower 2 m (6.6 ft) of the trunk. Multiple investigators sampled trees at each dune and ridge woodland site. In order to reduce collector bias, investigators were required to survey multiple tree species at each site (so that one person wasn't continuously sampling the same tree species).

Ants were identified in-house using multiple resources (Lynch 1987; Johnson 1988; Snelling 1988; Coovert 2005; Trager et al. 2007; LaPolla et al. 2010). Species identifications were verified by referencing specimens at the Smithsonian Institution's National Museum of Natural History (USNM) and through consultation with local entomologists. Taxonomy follows the "working list" as described by Fisher and Cover (2007).

We used multiple-response permutation procedure (MRPP), a nonparametric analog of analysis of variance, to test the null hypothesis of no significant differences in ant species composition between shortleaf pine, loblolly pine, and oaks. Details of the method may be found in Mielke and Berry (2001); the program we used is employed in PC-ORD (v. 3.04, MjM Software, Gleneden Beach, Oregon). 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 among 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 data set 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 used indicator species analysis (ISA) as a complement to MRPP to describe the value of different ant species for indicating each group of trees. Indicator values range from zero (no indication) to 100 (perfect indication). We evaluate statistical significance of indicator values by a Monte Carlo method using 1000 randomizations. The null hypothesis is that the observed maximum indicator value IV_{max} is no larger than would be expected by chance. Species that occurred fewer than three times were excluded from the analysis. A Spearman's correlation was conducted using an online calculator (Wessa 2012) to determine whether tree diameter had any influence on the results of the ISA.

RESULTS

A total of 241 trees were surveyed at the 30 sites: 77 shortleaf pines, 83 loblolly pines, and 81 oaks. The breakdown of oaks sampled is as follows: 12 *Quercus alba* L. (white oak), 21 *Q. velutina*, 23 *Q. falcata*, 16 *Q. nigra*, and 7 *Q. stellata* Wangenh. (post oak). For two trees the species of oak was not recorded.

Ten species of ants were excluded from the analysis because they occurred fewer than three times. These were *Aphaenogaster treatae* Forel, *Camponotus caryae* (Fitch), *Camponotus subbarbatus* Emery, *Crematogaster pilosa* Emery, *Forelius pruinosus* (Roger), *Myrmecina americana* Emery, *Myrmica punctiventris* Roger, *Pyramica rostrata* (Emery), *Temnothorax ambiguus* (Emery), and *Trachymyrmex septentrionalis* (McCook).

The final MRPP data matrix comprises 25 ant taxa x 241 trees. The results indicate an overall marginal difference between the three groups ($p = 0.067$). The results of systematic group exclusion are illustrated in Table 1 and show no difference between

loblolly and shortleaf pine ($p = 0.749$), a marginal difference between oak and shortleaf pine ($p = 0.052$) and a significant difference between oak and loblolly pine ($p = 0.026$).

Table 1. Results of Multi-Response Permutation Procedures (MRPP) for ant species on trees. The first line is the overall multivariate comparison; subsequent lines compare pairs of groups. Analysis is based on a rank-transformed Sorenson distance matrix comprising 25 ant taxa x 241 trees. (T) describes the separation among groups, (A) is a measure of effect size describing within-group agreement, and (p) is the probability of finding a higher value of T in all permutations of the data. Significant p values are in bold.

Groups	T	A	p
Overall	-1.640	0.006	0.067
Oak vs. Shortleaf	-1.860	0.008	0.052
Oak vs. Loblolly	-2.425	0.010	0.026
Shortleaf vs. Loblolly	0.732	-0.003	0.749

Indicator species analysis (Tables 2 and 3) detected four ant species as indicators. *Aphaenogaster mariae* Forel ($p = 0.003$), *Camponotus pennsylvanicus* (DeGeer) ($p = 0.005$), and *Prenolepis imparis* (Say) ($p = 0.017$) all occurred with greater abundance and frequency on oaks, while *Crematogaster ashmeadi* Mayr ($p = 0.018$) occurred with greater abundance and frequency on loblolly pine.

Spearman's correlation showed no relationship between tree diameter and the number of ants collected per tree ($r = 0.06$, $df = 236$) or between tree diameter and the number of ant species collected per tree ($r = 0.08$, $df = 236$). Three trees were excluded from the analysis because the diameter was not recorded.

DISCUSSION

The MRPP analysis suggests that different tree species support different suites of ant species. The overall p-value ($p = 0.067$) approaches but does not support rejecting the null hypothesis at the traditional $p < 0.05$ level. While the difference between oaks and pines is apparent, no significant differences were detected between the different pine species. We found no evidence that the arboreal or trunk-using ants in our dune and ridge woodland sites have evolved a preferential relationship with shortleaf pine. In the few cases where an ant species demonstrated a higher occurrence on one species group over another, the preference was usually for oak. Since a pool of five oak species was sampled for ants, there could be additional partitioning of the ants per oak species, but that association was not investigated. Only *C. ashmeadi* showed a preference for loblolly pine, although it was also found on both shortleaf pine and on oak (Table 2).

Results of the ISA should be viewed with caution, as some of the significant results are based on the presence of a species with low numbers of observations (from sometimes very few trees). *Camponotus pennsylvanicus*, for example, was observed only six times on a total of five trees (Table 2). While it can nest in rotted tree cavities and is known to forage on tree trunks, it is not truly arboreal (Coovert 2005) and may be better sampled

using alternate survey techniques. In general, *Camponotus* species were collected very infrequently using timed hand collection methods. Therefore, despite the p-value, the inferred preference for oak may not be reliable. The same is probably true of *P. imparis*, known soil nesters that often forage on trees (Lynch 1987, Coovert 2005). Large numbers of workers have been observed to concentrate at food sources, including sap running from tree wounds (Lynch 1987). This could impact our results, as it may be available food resources that influence its presence and not necessarily tree species. We may also have underestimated the presence of this ant, as both Lynch (1987) and Coovert (2005) indicate a lull in activity during the summer months, when we conducted our surveys.

Table 2. Results of the Indicator Species Analysis (ISA) showing the relative abundance of ants found on the three different tree groups. Values range from 0% (no indication) to 100% (perfect indication). The table also shows the total number of ants collected for each species (Individuals Collected), and the number of individual trees from which each species was collected (Trees with Ants). (Because relative abundance values are rounded to whole numbers, the sum per individual species may range from 99 to 101.)

Species	Individuals Collected	Trees with Ants	Relative Ant Abundance (%)		
			Oak (N=81)	Loblolly (N=83)	Shortleaf (N=77)
<i>Aphaenogaster fulva</i> Roger	46	11	11	56	34
<i>Aphaenogaster lamellidens</i> Mayr	205	77	40	36	24
<i>Aphaenogaster mariae</i> Forel	58	10	83	17	0
<i>Aphaenogaster rudis</i> Enzmann	121	72	35	22	43
<i>Camponotus castaneus</i> (Latreille)	6	6	50	33	18
<i>Camponotus chromaioides</i> Bolton	11	7	18	26	56
<i>Camponotus nearcticus</i> Emery	14	13	36	42	23
<i>Camponotus pennsylvanicus</i> (DeGeer)	6	5	100	0	0
<i>Camponotus snellingi</i> Bolton	8	6	62	12	26
<i>Crematogaster ashmeadi</i> Mayr	452	68	13	57	30
<i>Crematogaster cerasi</i> (Fitch)	4	3	49	0	51
<i>Crematogaster lineolata</i> (Say)	96	45	33	30	37
<i>Formica pallidefulva</i> Latreille	11	9	36	26	38
<i>Formica subsericea</i> Say	16	6	69	18	13
<i>Lasius alienus</i> (Foerster)	31	3	73	0	27
<i>Monomorium minimum</i> (Buckley)	30	5	0	22	78
<i>Myrmica americana</i> Weber	4	3	75	25	0
<i>Nylanderia faisonensis</i> (Forel)	30	26	26	35	38
<i>Pheidole bicarinata</i> Mayr	6	6	49	16	35
<i>Pheidole morrisii</i> Forel	5	2	0	19	81
<i>Prenolepis imparis</i> (Say)	47	7	79	21	0
<i>Tapinoma sessile</i> (Say)	61	12	46	35	19
<i>Temnothorax curvispinosus</i> (Mayr)	8	5	75	25	0
<i>Temnothorax longispinosus</i> (Roger)	4	2	100	0	0
<i>Temnothorax schaumii</i> (Roger)	11	6	46	54	0

Table 3. Results of the Monte Carlo test evaluating the statistical significance of indicator values based on 1000 randomizations. For each ant species, the table shows the dominant tree species (Max Group) based on a combination of relative abundance and relative frequency, the observed indicator value (Observed IV), and the mean and standard deviation for each indicator value from the randomized groups. Significant p values are in bold.

Species	Max Group	Observed IV	IV Randomized Groups		
			Mean	SD	p
<i>Aphaenogaster fulva</i>	Loblolly	2.7	3.1	1.28	0.548
<i>Aphaenogaster lamellidens</i>	Oak	13.8	14.1	2.33	0.475
<i>Aphaenogaster mariae</i>	Oak	8.2	3.1	1.22	0.003
<i>Aphaenogaster rudis</i>	Oak	12.8	13.6	2.49	0.582
<i>Camponotus castaneus</i>	Oak	1.9	2.3	1.05	0.633
<i>Camponotus chromaiodes</i>	Shortleaf	1.5	2.6	1.20	0.844
<i>Camponotus nearcticus</i>	Loblolly	2.5	3.7	1.30	0.814
<i>Camponotus pennsylvanicus</i>	Oak	6.2	2.0	0.95	0.005
<i>Camponotus snellingi</i>	Oak	2.3	2.4	1.15	0.512
<i>Crematogaster ashmeadi</i>	Loblolly	19.3	12.1	2.52	0.018
<i>Crematogaster cerasi</i>	Oak	1.2	1.7	0.89	0.698
<i>Crematogaster lineolata</i>	Oak	7.3	9.5	2.14	0.871
<i>Formica pallidefulva</i>	Oak	1.8	2.9	1.21	0.868
<i>Formica subsericea</i>	Oak	3.4	2.4	1.16	0.173
<i>Lasius alienus</i>	Oak	1.8	1.6	0.88	0.249
<i>Monomorium minimum</i>	Shortleaf	3.0	2.2	1.12	0.220
<i>Myrmica americana</i>	Oak	1.9	1.6	0.89	0.323
<i>Nylanderia faisonensis</i>	Shortleaf	5.5	6.0	1.59	0.527
<i>Pheidole bicarinata</i>	Oak	1.8	2.3	1.08	0.702
<i>Pheidole morrisii</i>	Shortleaf	1.1	1.5	0.70	0.434
<i>Prenolepis imparis</i>	Oak	5.9	2.8	1.25	0.017
<i>Tapinoma sessile</i>	Oak	2.3	3.9	1.56	0.876
<i>Temnothorax curvispinosus</i>	Oak	2.8	2.2	1.09	0.211
<i>Temnothorax longispinosus</i>	Oak	2.5	1.4	0.73	0.210
<i>Temnothorax schaumii</i>	Loblolly	2.6	2.3	1.05	0.302

We are more confident in the significant p-values for *A. mariae* and *C. ashmeadi*, because they were collected from a greater number of trees with greater abundances (Table 2), and because their life history suggests a strong association with trees. *Aphaenogaster mariae* was a significant indicator for oak; 48 individuals were collected on eight oaks (found at least once on all five species of oak surveyed), as compared to ten individuals collected from two loblolly pines. It was not collected from shortleaf pine. *Aphaenogaster mariae* nests under oak bark and in rotted tree cavities, and has also been observed foraging on oaks (Coovert 2005). This is consistent with our observations, as it was rarely discovered on pine. It is also noteworthy that despite extensive pitfall trapping and litter sampling at the same sites in 2008 and 2009, *A. mariae* was only found in a single pitfall trap and was never collected from the litter (J. A. Frye, unpublished data). This indicates that hand collection may be the best way to capture this species, and that

its absence from pitfall traps or litter samples does not necessarily indicate its absence from a site.

Crematogaster ashmeadi may also be well represented from direct hand collection from tree trunks as it is a true arboreal species. In Florida Coastal Plain pine forests, for example, it is considered to be the most dominant arboreal species (Tschinkel 2002). It showed a significant preference for loblolly pine followed by shortleaf pine, but was also found on oak (Table 2). Johnson (1988) described two morphs in the east, a black-bodied morph typically found on hardwoods and a bicolored morph typically found on pines, noting that in mixed hardwood and pine forests both morphs occur. None of the individuals that we collected were distinctly black-bodied, and the few that tended toward a darker morph were found just as often on pine as they were on oak.

Our ISA results could also indicate inadequate sampling. Even tree trunk surveys using bait have shown that the rate of detection of a species can be significantly lowered, especially if colonies are small, unless the tree is surveyed on multiple occasions. Tschinkel (2002) found that single-baited studies substantially underestimated the number of trees occupied by *C. ashmeadi*. Ants may have also gone undetected if they were using a part of the tree other than the lower trunk, which was the only part of the tree that we sampled, or if they preferentially foraged at night, since all of our surveys took place during the day. Despite this limitation, we were able to analyze data from 241 trees in 30 different dune and ridge woodland sites spanning two quadrangles, which should serve to document the species of ants present on pines and oaks in this rare community.

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