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The effects of prescribed fire on ant community composition in a temperate deciduous forest

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23 **Abstract**

24 Prescribed fire is a tool commonly used in land management to decrease wildfire
25 frequency and promote plant diversity. However, the effects of prescribed fire on
26 invertebrate communities, especially those within temperate deciduous forest, are
27 poorly understood. I measured the response of epigeic ant communities in mixed
28 mesophytic forest in Berea, Kentucky following prescribed burning. I used pitfall traps
29 to repeatedly sample epigeic ants in replicate burned and unburned plots for up to 21
30 months postburn following two separate (2021 and 2022) prescribed fires. Ant species
31 richness was similar between treatments (burn vs. control) and by burn year. Ant
32 community composition generally differed between treatments and across years but was
33 similar between the paired 2022 burned and unburned plots, probably due to the low
34 intensity of that burn. The results of this study indicate that epigeic ant communities in
35 an eastern deciduous forest are altered by prescribed burning, and do not return to
36 normal activity levels after 1-year post-burn. Additional experimental studies are needed
37 to determine the effects of fire intensity and frequency on ant assemblages in this
38 setting.

39

40 **Introduction**

41 Ecological disturbance is any relatively discrete event in time that disrupts
42 ecosystem, community, or population structure and alters resources or habitat (Pickett
43 and White 1985). Fire is a natural disturbance in many terrestrial ecosystems and can
44 vary widely in intensity and frequency (Swetnam and Betancourt 1990, Delcourt and
45 Delcourt 1997). Fire in forested ecosystems often promotes plant biodiversity (Richter et
46 al. 1982, Mitchell et al. 2006), which generates a bottom-up effect for organisms at
47 higher trophic levels (Scherber et al. 2010). Historical suppression of wildfires in
48 temperate forest of North America altered natural forest turnover (Ryan et al. 2013),
49 leading to a decrease in biodiversity and habitat heterogeneity (Baker 1992, 1993).
50 Consequently, intentional burning (i.e., “prescribed burning”) of forests has become
51 increasingly common in forestry management operations to promote biodiversity,
52 create habitat heterogeneity, and mitigate extreme wildfire events. (Agee and Skinner
53 2005, Finney et al. 2005, Prichard et al. 2010, Cochrane et al. 2012).

54 Fire regimes can vary in frequency (i.e., number of fires per unit time) and burn
55 intensity (i.e., heat transfer per unit duration of fire, Hiers et al. 2009, Perry et al.
56 2011.). Most studies evaluating how different fire regimes influence forest components
57 focus on plant communities (Pausas 1999, Franklin et al. 2001, Bond et al. 2004, Keeley
58 2006, Miller et al. 2019), but data on ecologically important groups, like epigeic (i.e.,
59 ground dwelling) arthropods, are lacking.

60 Ants are ecologically important components of forested ecosystems. They
61 function as ecosystem engineers (Folgarait 1998, Jouquet et al. 2006), keystone seed
62 dispersers (Lengyel et al. 2010, Gorb and Gorb 2013, Warren and Giladi 2014), and
63 predators of many primary consumers (Folgarait 1998, Philpott and Armbrecht 2006).
64 Fire can negatively impact ants directly through mortality and indirectly by reducing
65 available nesting sites (Graham et al. 2009). Given that ants are numerically abundant,
66 good bioindicators of disturbance (Anderson et al. 2002), and easily sampled, they may
67 provide insight on how similar epigeic arthropods respond to prescribed fire in
68 temperate deciduous forests.

69 Previous studies have examined the effect of prescribed fire on ant species
70 richness and community composition in a variety of ecosystems, including prairies
71 (Underwood and Christian 2009, Menke et al. 2015, Bonoan and McCarthy 2022),
72 eucalypt forests (Andersen et al. 2009, Beaumont et al. 2012), and savannas (Izhaki et
73 al. 2003, Houdeshell et al. 2011). Temperate deciduous forest cover 7.8 million km²
74 worldwide and dominate most of the eastern United States (Allaby 2006). The few
75 studies that were conducted in temperate deciduous forest habitats tended to examine
76 only the short-term effects of prescribed burning on epigeic ant communities (Verble
77 and Yanoviak 2013) or analyzed a general response of soil invertebrates to prescribed
78 burning (Kalisz and Powell 2000).

79 Here, I investigate the effects of prescribed fire on the structure of epigeic ant
80 assemblages (species composition and species richness) up to 1 year following a burn in
81 an eastern deciduous forest in Kentucky, USA. I expected ant species richness to be
82 lower in burned forest (Underwood and Quinn 2010, Verble and Yanoviak 2013). I also
83 expected ant species composition in burned forest to be distinct from that of unburned
84 forest (Beaumont et al. 2012).

85 **Methods**

86 *Study Site*

87 Field work was conducted at Berea College Forest, a 3642-hectare mixed
88 mesophytic forest in Berea, Kentucky (37.5687° N, 84.2963° W). Berea Forest is
89 managed in part via an annual prescribed burn program (Patterson and Singleton
90 2019). This study focused on the effects of two annual burns conducted in April (2021
91 and 2022). In each case, only one section of forest was burned, an adjacent unburned
92 section of equal area was used as a control site and burn, and control sites did not
93 overlap between years.

94 *Experimental Design*

95 Following each prescribed burn, I established three transects in the burned site
96 and three similar transects in the adjacent control site. Each transect was 10 m long and

97 separated from other transects by > 100 m. Hereafter, *treatment* refers to burned vs.
98 unburned (control) forest and *year* refers to 2021 vs. 2022.

99 I used pitfall traps to sample epigeic ants along each transect. Each trap
100 consisted of a 475 ml plastic cup (model No. S-22770, Uline, Pleasant Prairie, WI, USA),
101 buried such that the cup opening was flush with the soil surface. A second cup was
102 placed inside the buried cup to facilitate sample collection. Each buried cup assembly
103 was sheltered with a roof of acrylic sheeting (ca. 0.6 x 15.2 x 15.2 cm) suspended 2.5 cm
104 above the cup opening with landscape staples (Amagabeli, Beijing, China). A small
105 amount of antifreeze (Model: RV and Marine antifreeze -50 °F, Splash, St. Paul, MN,
106 USA) mixed with dish soap added to each trap served as the killing agent (Fig. 1).

107 In 2021, pitfalls traps were placed every meter on alternating sides of the transect
108 for all six transects (Fig. 2). I placed 30 pitfall traps in burned forest and 30 pitfall traps
109 in unburned forest, which were sampled weekly. In 2022, I sampled burned and
110 unburned plots of forest following the 2022 burn along with the burned and unburned
111 plots established in 2021. I reduced sampling intensity to 10 pitfalls (3, 3, and 4 traps for
112 each transect) in each plot, resulting in a total of 40 pitfalls across 4 different plots in
113 2022 (Fig. 2), which were sampled monthly.

114 *Statistical Analyses*

115 Analyses include only trap data where at least one ant was present. I did not use
116 raw abundance as a response due to the social nature of ants (Wilson and Hölldobler
117 2005). Instead, I used the total number of unique occurrences (i.e., the number of times
118 a species was recorded in a pitfall trap through the entire sampling period.) The total
119 number of unique occurrences for each species was pooled over time for each pitfall
120 trap.

121 To determine whether the number of unique ant occurrences differed between
122 treatments and year, I constructed a generalized linear mixed effect model (GLMM)
123 with a negative binomial distribution to account for the extreme right-skew in the data. I
124 included the interaction term between the main effects of treatment and year and
125 included plot as a random effect (Table 1). I did not include days post-fire as an
126 explanatory effect because pitfall data were pooled across samples within a year.

127 I used non-metric multidimensional scaling (NMDS) ordination to determine
128 whether ant assemblages in burned forest were compositionally distinct from those in
129 unburned forest (Fig. 3; PRIMER Software Version 7.0.21). I created a Bray-Curtis
130 dissimilarity matrix using the number of unique occurrences for each species within
131 each pitfall trap as the response. To determine whether forest status, year, and their
132 interactions had a significant effect on ant communities, I used permutational
133 multivariate analysis of variance (PERMANOVA; Table 2). I then ran a permutational
134 test of dispersion (PERMDISP) to determine whether the potential differences were
135 attributable to the main effects or to dispersion within the data (Table 3).

136 I conducted a post-hoc test to determine which treatment and year combinations
137 were significantly different from each other (Table 4). I used Bonferroni adjusted p-
138 values to account for multiple comparisons.

139 **Results**

140 I collected 4,947 ants comprised of 23 species and 13 genera over the 21 months
141 of sampling. The total number of ants collected was distributed among 100 trap
142 occurrences, for an average of 49.5 ants per trap collection over the course of the study.
143 In most cases, each trap contained relatively few species. The most frequently collected
144 species was *Aphaenogaster carolinensis* (n = 986 occurrences), and many species were
145 represented by a single individual (e.g., *Camponotus castaneus*, *Formica pallidefulva*,
146 *Proceratium chickasaw*, *Strumigenys ohioensis*, *Temnothorax curvispinosus*, and
147 *Temnothorax schaumii*; Fig. 4)

148 Most species were collected in both burned and unburned plots. *Aphaenogaster*
149 *carolinensis*, the most abundant species, was collected approximately equally between
150 burned and unburned plots. However, some “common” species (those represented by >
151 1 occurrence) were collected exclusively from one treatment (e.g., *Lasius aphidicola* was
152 collected only in unburned plots, while *Formica subcericea* was collected only in burned
153 plots).

154 The sampling year had a significant effect on ant species richness (p-value = <
155 0.001; Table 1; Fig. 5.), with the first year of sampling yielding a greater number of
156 unique occurrences than a second year of sampling of a plot. However, treatment did

157 not have a significant effect on unique occurrences ($p = 0.46$; Fig. 6) and there was no
158 treatment x year interaction ($p = 0.27$; Table 1).

159 Ant communities in burned plots were significantly different from communities
160 in unburned plots ($F = 23.94$, $df = 1$, $P = 0.001$ and $F = 2.25$, $df = 1$, $P = 0.001$,
161 respectively; Table 2; Fig. 3). Sampling year also resulted in a distinction between
162 communities that were sampled during the first year of collection and communities
163 sampled a year following the initial burn (Table 2; Fig. 3). Year and treatment had no
164 significant effect in the PERMDISP test ($F = 0.22$, $P = 0.66$; $F = 0.12$, $P = 0.72$; Table 3),
165 indicating that observed differences were attributable to the main effects, not dispersion
166 within the data.

167 Ant community composition in the burned plot was significantly different from
168 control site in 2021, but there was no treatment effect on composition in 2022 (Table 4).
169 Ant composition also differed between the two burn plots (Table 4). Ant composition
170 also differed between the 2021 and 2022 samples from a site that was burned in 2021,
171 and between its associated control samples (Table 4).

172 **Discussion**

173 The result of this study generally agrees with those of similar studies, specifically,
174 that prescribed fire alters epigeic ant communities (Izhaki 2003, Underwood and Quinn
175 2010). However, it contrasts with other studies indicating that ant species composition
176 does not differ between burned and unburned plots (Verble and Yanoviak 2013). Pitfall
177 traps measure ant activity, so these results can also be explained by a decrease in ant
178 activity, not necessarily extermination of local species.

179 I suspect that the differences in year are due to differences in burn intensity
180 between 2021 and 2022 (Table 4). The 2022 burn appeared to be of a much lower
181 intensity. Specifically, the vegetation appeared less burnt and there was more leaf litter
182 present following the 2022 burn in vs. the 2021 burn. However, these differences in
183 anecdotal and speculative at this point because supporting data regarding fire intensity
184 are lacking. Previous studies determined that prescribed burn intensity influences ant
185 ecology (Underwood and Quinn 2010, Verble 2012).

186 The overall negative effect of prescribed burning on ant species richness has been
187 illustrated in similar systems (Izhaki et al. 2003, Underwood and Quinn 2010).
188 Contrasting studies, however, indicate that prescribed burning can increase ant
189 occurrences and species richness (Beaumont et al. 2012, Banschbach and Ogilvy 2014)
190 or have temporary effects on ant species composition (Verble and Yanoviak 2013). The
191 variety of responses of epigeic ants to prescribed fire might reflect ecosystem-level
192 differences (Vasconcelos et al. 2016). The results of this study suggest that most ant
193 species are resilient to prescribed burns. However, pitfall traps do not provide a
194 complete picture on the effects of fire on ants, thus further study of individual species
195 responses is needed to clarify the short- and long-term ecological effects of fire.

196 The differences between communities at the 2021 burned and unburned plots
197 one year after the initial burn suggest that ant assemblages require more than a year to
198 recover from fire. Communities within the 2021 burn plot are not resilient enough to
199 rebound within a year. This finding contrasts with a similar study that suggests epigeic
200 ant communities in deciduous forest are relatively resilient and can return to normal
201 activity levels less than a year after the initial prescribed burn (Verble and Yanoviak
202 2013). The significant difference in the 2021 control plot from 2021 to 2022 could be
203 due to a variety of factors, including source/sink dynamics from the adjacent burn plots,
204 natural turnover, or environmental differences between the years (Crist 2009).

205 In summary, fire intensity likely influences ant activity levels, but future
206 measurements of the intensity of prescribed burns is necessary to confirm this. As
207 prescribed burning is increasingly being added to forestry management to promote
208 plant diversity (Richter et al. 1982, Mitchell et al. 2006), it is important to document its
209 effects on common consumer taxa like ants. Although the effect of prescribed burning
210 on ants has been studied in many other ecosystems (Izhaki et al. 2003, Andersen et al.
211 2009, Underwood and Christian 2009, Houdeshell et al. 2011, Beaumont et al. 2012,
212 Menke et al. 2015, Bonoan and McCarthy 2022), additional data are needed for
213 temperate deciduous forests, as they are expansive but steadily declining ecosystems
214 (Loucks 1998).

215

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- 366

367 **Tables**

368 **Table 1.** Output of generalized linear mixed effect model with a negative binomial
 369 distribution.

Effect	Term	Estimate	Std. Error	Z-value	p-value
Intercept	Fixed	2.21	0.19	11.36	< 0.001
Year	Fixed	-0.52	0.15	-3.52	< 0.001
Status	Fixed	0.20	0.27	0.75	0.46
Year:Status	Interaction	-0.23	0.21	-1.11	0.27
Site	Random	0.04	NA	NA	NA

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373 **Table 2.** Permutational multivariate analysis of variance (PERMANOVA) output.

Effect	Term	df	Sums Squares	F-value	P(perm)
Year	Fixed	1	2.83	23.94	0.001
Status	Fixed	1	0.27	2.25	0.001
Year:Status	Interaction	1	0.14	1.16	0.25
Site	Random	NA	NA	NA	NA
Residuals	NA	95	11.22	NA	NA
Total	NA	98	14.45	NA	NA

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377 **Table 3.** Permutational multivariate analysis of dispersion (PERMDISP) output.

Effect	Term	Sums Squares	F-value	P(perm)
Year	Fixed	0.005	0.22	0.66
Residuals	NA	2.04	NA	NA
Status	Fixed	0.002	0.12	0.72
Residuals	NA	0.02	NA	NA

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380 **Table 4.** Output of post-hoc test with a Bonferroni correction comparing burned and
 381 unburned communities with the 2021 and 2022 prescribed burns. B1 refers to the 2021
 382 burn and B2 refers to the 2022 burn. Yr1 refers to the first sampling period and Yr2
 383 refers to the second sampling period. B refers to burned forest and U refers to unburned
 384 forest.

Pairs	df	Sums Squares	F-value	R ²	p-value	adjusted p-value
B1_Yr1_B vs. B1_Yr2_B	1	2.36	34.05	0.47	0.001	0.005
B1_Yr1_B vs. B2_Yr1_B	1	1.87	27.41	0.42	0.001	0.005
B1_Yr1_B vs. B1_Yr1_U	1	0.31	5.58	0.09	0.001	0.005
B2_Yr1_B vs. B2_Yr1_U	1	0.25	2.58	0.13	0.034	0.17
B1_Yr1_U vs. B1_Yr2_U	1	2.25	33.84	0.47	0.001	0.005

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387 **Table 5.** Summary of taxa collected and their corresponding occurrences in pitfall traps
 388 in burned or unburned forest.

Taxon	Burned	Unburned
Amblyoponinae		
Amblyoponini		
<i>Stigmatomma pallipes</i>	4	3
Formicinae		
Camponotini		
Camponotus americanus	129	54
Camponotus pennsylvanicus	78	127
Camponotus chromaiodes	124	81
Camponotus subbarbatus	8	16
Camponotus castaneus	1	0
Formicini		
Formica pallidefulva	1	0

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404	<i>Formica subsericea</i>	33	2
405	<i>Formica subintegra</i>	1	0
406			
407	Lasiini		
408	<i>Lasius aphidicola</i>	0	19
409	<i>Prenolepis imparis</i>	2	0
410			
411	Plagiolepidini		
412	<i>Brachymyrmex depilis</i>	2	7
413			
414	Myrmicinae		
415	Attini		
416	<i>Strumigenys ohioensis</i>	0	1
417	<i>Strumigenys talpa</i>	1	1
418			
419	Crematogastrini		
420	<i>Crematogaster cerasi</i>	60	52
421	<i>Crematogaster pilosa</i>	25	19
422			
423	Formicoxenini		
424	<i>Temnothorax curvispinosus</i>	1	0
425	<i>Temnothorax schaumii</i>	0	1
426			
427	Stenammini		
428	<i>Aphaenogaster carolinensis</i>	497	487
429	<i>Aphaenogaster fulva</i>	24	43
430			
431	Ponerinae		

432	Ponerini		
433	<i>Ponera pennsylvanica</i>	7	6
434			
435	Proceratiinae		
436	Proceratiinae		
437	<i>Proceratium chickasaw</i>	1	0
438			
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443 **Figures**

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450 **Fig. 1.** Pitfall trap placed in burned portion of forest.

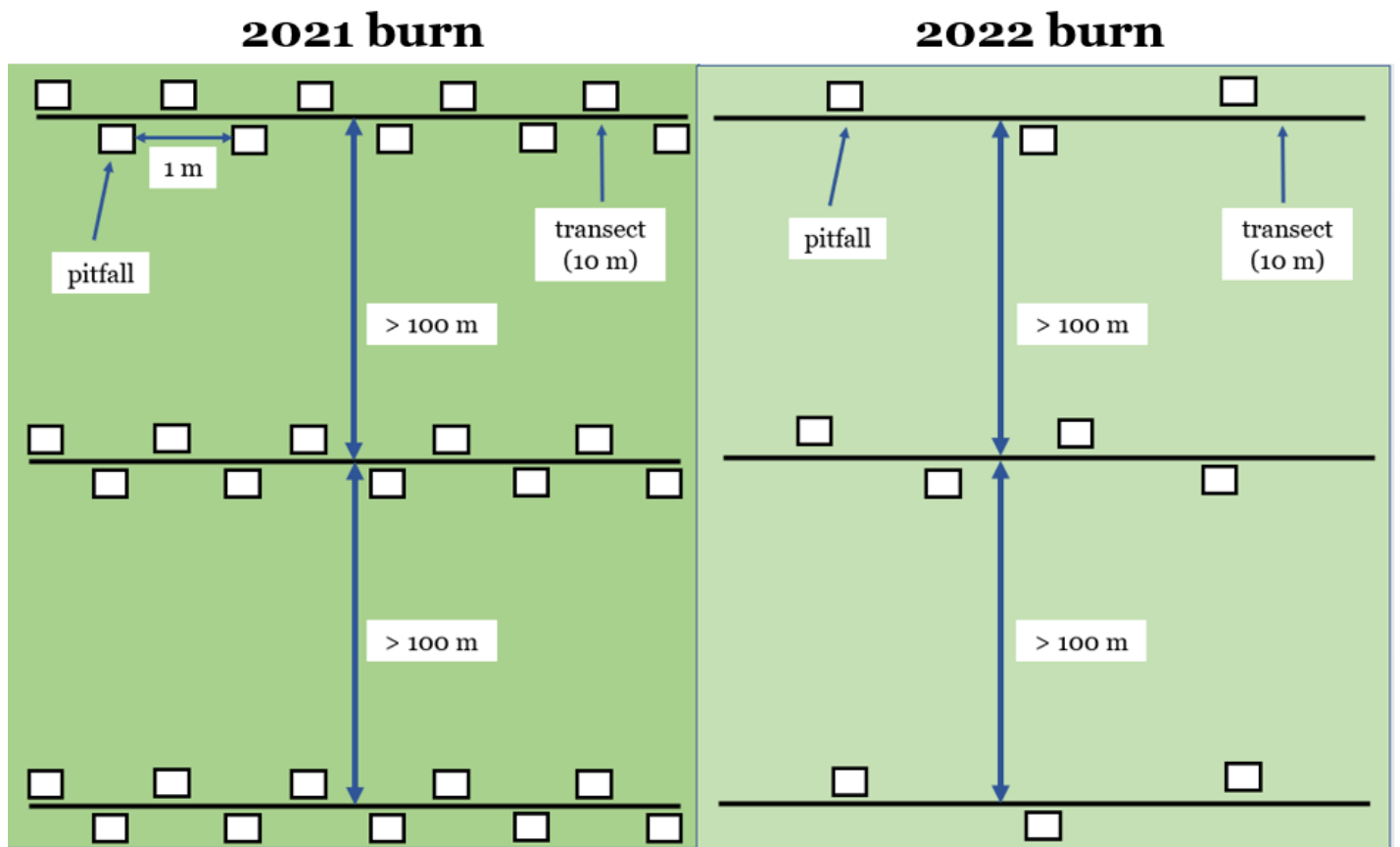
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462 **Fig. 2.** Pitfall setup for both forest treatments (burned vs. unburned). The first panel
463 symbolizes the layout of pitfall traps during sampling of the 2021 burn among burned
464 and unburned plots. The second panel symbolizes the layout during 2022 sampling of
465 the burned and unburned 2022 burn plots, and continued sampling of burned and
466 unburned 2021 burn plots. White rectangles represent individual pitfall traps and black
467 lines represent 10 m transects.

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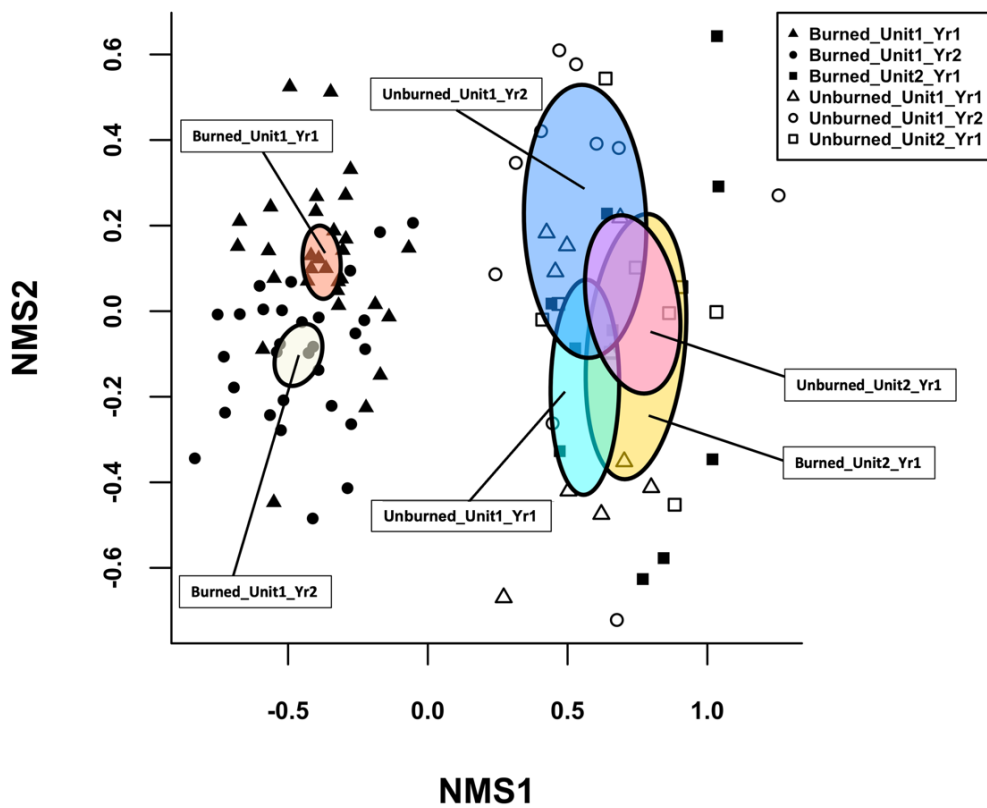
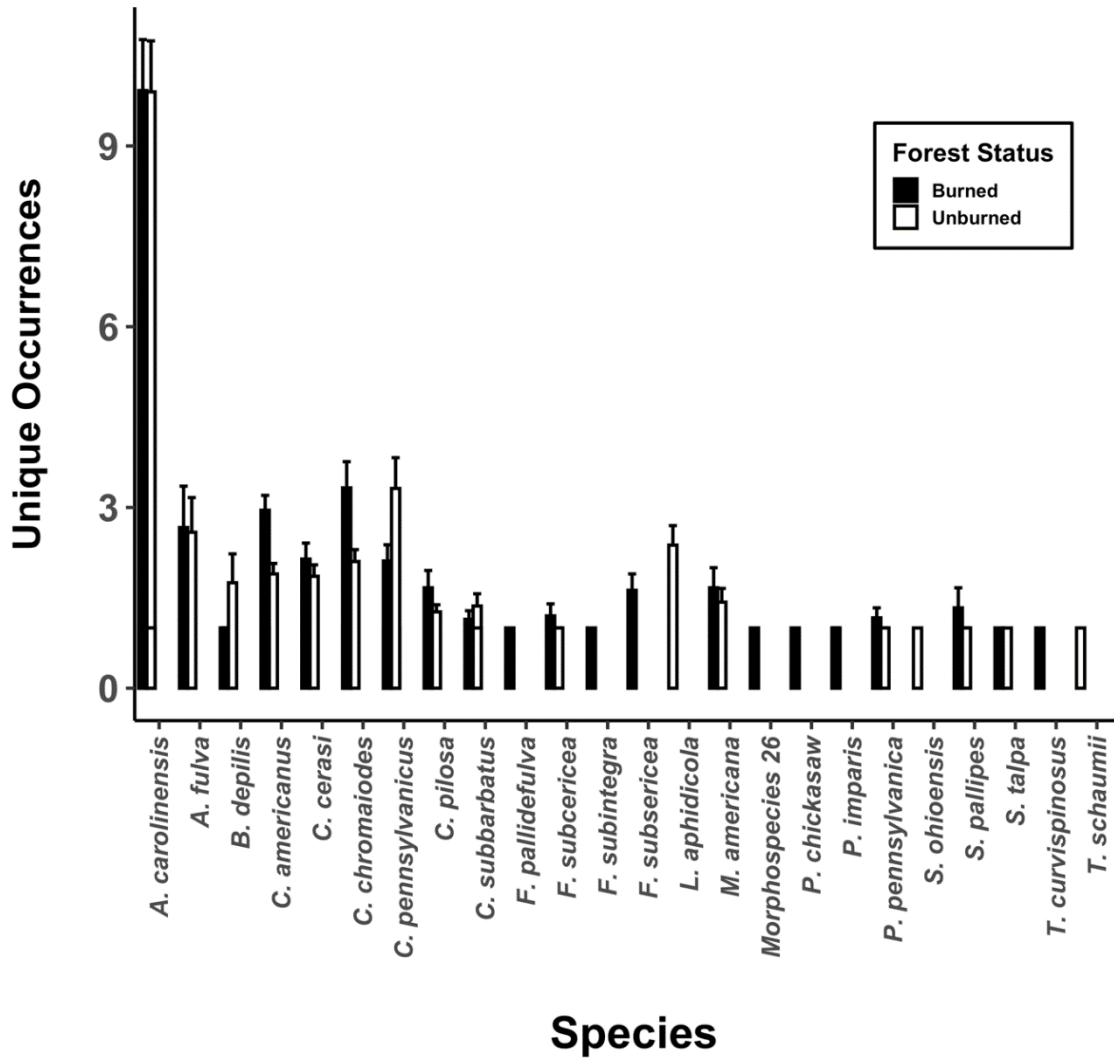


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination plot illustrating differences in ant species composition between forest treatment (burned vs. unburned) and collection year (2021 vs. 2022).

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495 **Fig. 4.** The number of unique species occurrences (± 1 SE error bars) by each ant
496 species collected in this study.

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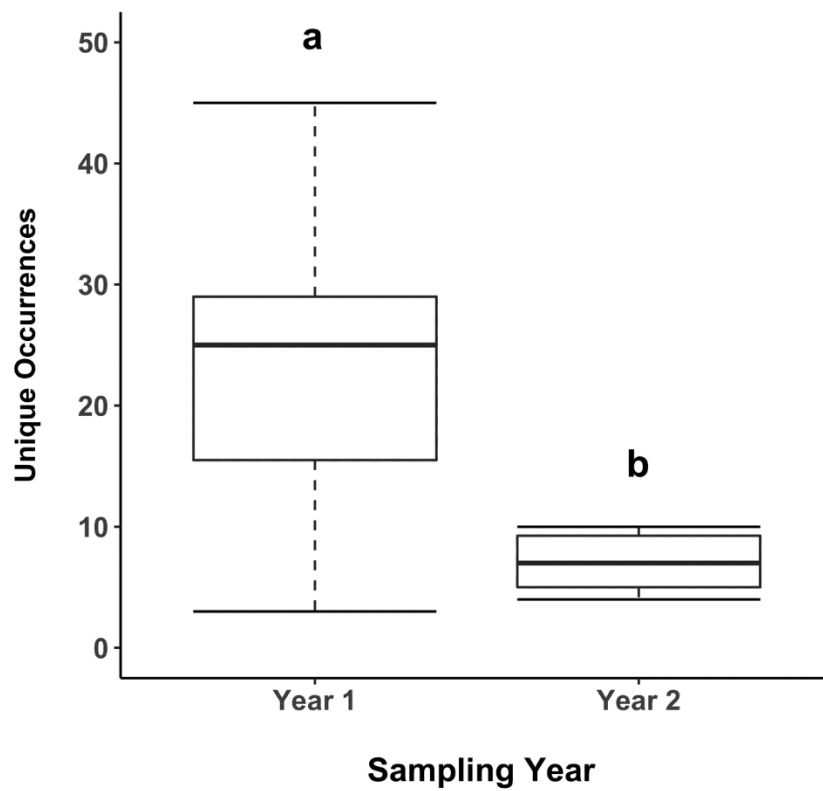


Fig. 5. Box and whisker plot illustrating the pooled data for each pitfall trap and the unique occurrences across sampling years.

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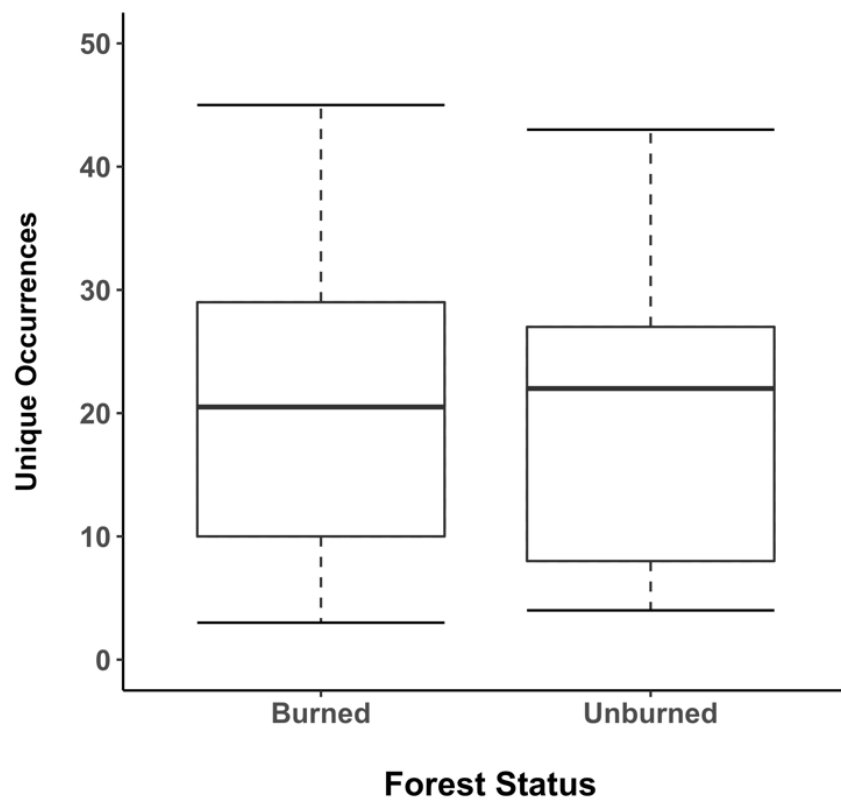


Fig. 6. Box and whisker plot illustrating the pooled data for each pitfall trap and the unique occurrences in burned and unburned forest traps.