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Asian needle ant (*Brachyponera chinensis*) and woodland ant responses to repeated applications of fuel reduction methods

Joshua W. Campbell,[1,]† Steven M. Grodsky,[2] Dale A. Halbritter,[3] Patrick A. Vigueira,[4] Cynthia C. Vigueira,[4] Oliver Keller,[5] and Cathryn H. Greenberg[6]

[1]*Department of Entomology and Plant Pathology, Auburn University, 301 Funchess Hall, Auburn, Alabama 36849 USA*
[2]*Department of Land, Air & Water Resources, University of California, Davis, California 95616 USA*
[3]*USDA-ARS Invasive Plant Research Laboratory, 3225 College Avenue, Fort Lauderdale, Florida 33314 USA*
[4]*Biology Department, High Point University, One University Parkway, High Point, North Carolina 27268 USA*
[5]*Entomology and Nematology Department, University of Florida, 1881 Natural Area Drive, Gainesville, Florida 32611 USA*
[6]*USDA Forest Service, Southern Research Station, 1577 Brevard Road, Asheville, North Carolina 28806 USA*

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Abstract. Ants (Formicidae: Hymenoptera) are important components of forest ecosystems and can be affected by fuel reduction forest management practices. We assessed the impact of repeated applications of fuel reduction treatments on abundance and diversity of ants within upland mixed-hardwood forests in the Southern Appalachian Mountains in North Carolina, USA. We established three replicate blocks (~56 ha each) and split each block into four fuel reduction treatments, which included prescribed burning (B), mechanical felling (M), a combination of prescribed burning and mechanical felling (MB), and a control (C; i.e., no treatment). We implemented treatments multiple times (two mechanical thinnings and four prescribed burns) over the course of a 15-yr period. Due to tree mortality and resultant canopy gaps from high-severity burns, forest structure was dramatically altered in MB. Over a 3-yr period (2014–2016), we captured 54,219 ants comprised of 23 genera using pitfall and colored pan traps. *Prenolepis imparis* was the most common ant species collected, and it was significantly lower in abundance in MB than all other treatments. However, the non-native species *Brachyponera chinensis* was more abundant in MB than all other treatments. Thus, some fuel reduction treatments may have consequences for invasive ant colonization in forests. Most ant taxa did not differ in abundance among treatments, suggesting that some fuel reduction practices may affect some, but not all ant species. Our results indicate that some fuel reduction treatments can alter forest ant communities, thus contributing to changing forest ecosystem dynamics. Monitoring of ants and other bioindicators after repeated rounds of fuel reduction treatments could provide useful knowledge that can be used to help balance forest management and biological diversity.

Key words: Asian needle ant; Formicidae; fuel reduction; *Prenolepis imparis;* prescribed burns; understory thinning.

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† **E-mail:** joshw.campbell@gmail.com

Introduction

Invertebrates are often used to monitor ecosystem health and impacts of land management practices. Ants (Hymenoptera: Formicidae) have been used as ecological indicators in agroecosystems (Peck et al. 1998), rangelands (Andersen et al. 2004), and forested habitats (Stephens and Wagner 2006). Ants are particularly well suited for this purpose because they are ubiquitous, diverse, and respond to environmental changes (Majer 1983, Andersen 1990). Ant communities can be used to

detect immediate, short-term responses to modifications of an ecosystem as well as long-term ecological changes (Bisevac and Majer 1999, York 2000). Ants have been used to examine impacts of logging (Vasconcelos et al. 2000), prescribed fire (York 2000, Izhaki et al. 2003, Houdeshell et al. 2011), land conversion (Roth et al. 1994, Perfecto and Snelling 1995), forest fragmentation (Carvalho and Vasconcelos 1999), livestock grazing (Hutchinson and King 1980), and mining (Andersen et al. 2003). Additionally, ants occupy multiple trophic levels (Alonso 2000) and can contribute to various ecosystem services, such as, but not limited to, nutrient cycling (Lal 1988), seed dispersal (Ashton 1979), pollination services (Abbate and Campbell 2013), and food for wildlife (Große et al. 2003, Grodsky et al. 2015). Finally, ants can also be collected or monitored with ease in numerous ways (see Underwood and Fisher 2006). When all of these criteria are considered together, ants have the ability to provide researchers with robust ecological information about how anthropogenic and natural changes affect habitat quality and ecosystems.

Unmanaged forest fuel loads can increase wildfire risk and limit game animal abundance (Waldrop et al. 1987). Therefore, modern forest management practices, including prescribed burns and understory thinning, are commonly employed to lessen fuel loads on forest floors. In the Southern Appalachian Mountains, Native Americans historically used fire to increase food availability and provide conditions for unencumbered travel (Greenberg and Collins 2016). Early European settlers also utilized fire in the Southeastern United States to maintain grazing land for livestock (Brose et al. 2001). Today, primary goals of fuel reduction techniques are to minimize wildfire risk and increase game animal forage (Masters et al. 1993, Fernandes and Botelho 2003).

Invertebrates can be impacted by fuel reduction techniques through habitat alteration or direct mortality (McCullough et al. 1998, Swengel 2001). Numerous invertebrates have been used in previous research to monitor ecological responses to various forest management practices, including ants (York 2000, Izhaki et al. 2003, Houdeshell et al. 2011), spiders (Vickers and Culin 2014), beetles (Pearce and Venier 2006, Campbell et al. 2018*a*), pollinating insects (Campbell et al. 2007, 2018*b*), as well as the overall invertebrate communities (Schowalter et al. 2003, Greenberg et al. 2010, Grodsky et al. 2018*a*).

Colonization of non-native or invasive species also can be affected (e.g., facilitated, encumbered) by forest management practices. Many forest management practices can promote non-native species by altering habitat structure, making it suitable for their colonization (Keeley 2006). Most non-native ants prefer disturbed habitats, but *Brachyponera chinensis* Emery (Asian needle ant)—a non-native ant—has been invading mature hardwood forests of the Southeastern United States (Guénard and Dunn 2010). Little is known regarding effects of forest management on Asian needle ant colonization, and how fuel reduction practices affect Asian needle ant abundance or spread effectively is unknown.

We studied ant abundances, including abundance of non-native *B. chinensis*, and ant taxa richness with pitfall and colored pan traps over a 3-yr period on experimental plots that we treated with repeated fuel reduction techniques (e.g., prescribed burns and/or understory thinnings) applied over a 15-yr timespan. We hypothesized that changes in understory fuel composition over the 15-yr period would affect ant community structure. We predicted that ant species and ant functional groups that depend on duff and other debris for nesting structure would decrease in abundance in fuel reduction treatments that removed duff. How coarse woody debris affects ants is largely under researched; however, interactions between forest ants and coarse woody debris in the Southeastern United States have been shown to alter forest ecology (Warren and Bradford 2011, Grodsky et al. 2018*b*). Therefore, we predicted that ants that depend on dead trees or coarse woody debris for nesting structure would increase in abundance in fuel reduction treatments with heavy overstory tree mortality.

Methods

Study sites and design

We used the Green River Game Land (GRGL) as our research site. The GRGL comprises 5841 ha within the Blue Ridge Physiographic Province (35°17′0900″ N, 82°19′42″ W and 35°15′42″ N, 82°17′27″ W) in Polk County, North Carolina, USA (Fig. 1). The average annual temperature is 17.6°C, and annual average precipitation is 164 cm within the region. Soils consisted

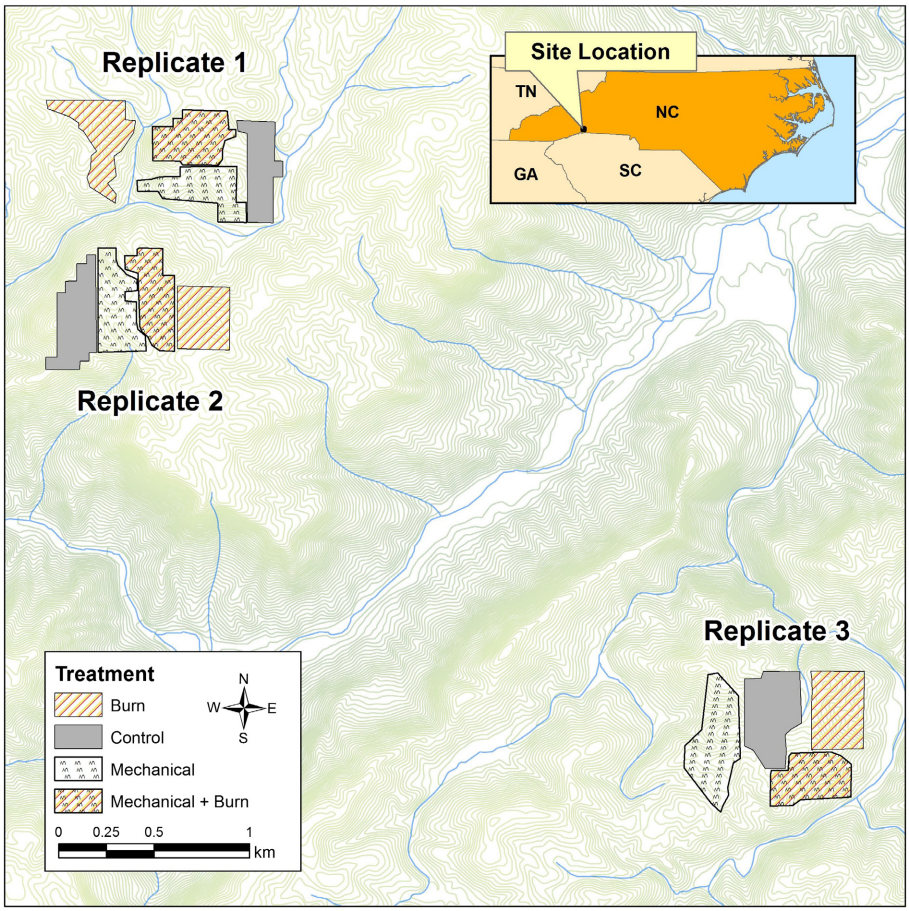

Fig. 1. Map of Green River Game Land (Polk County, North Carolina, USA) in which experimental plots of three forest management treatments and controls were applied to three blocks.

primarily of the Evard series (i.e., fine-loamy, oxidic, mesic, Typic Hapludults); they are very deep (>1 m) and well-drained in these mountain uplands (Keenan 1998). Elevation ranges from approximately 366 to 793 m. Oaks (*Quercus* spp.) and hickories (*Carya* spp.) are the primary trees in the upland hardwood forest, whereas shortleaf pine (*Pinus echinata* Mill.) and Virginia pine (*P. virginiana* Mill.) are dominant ridgetop species and white pine (*P. strobus*) occurs in moist coves. The predominant shrub along ridgetops and upper southwest-facing slopes is mountain laurel (*Kalmia latifolia* L.), and rhododendron (*Rhododendron maximum* L.) is the most common shrub in mesic habitats. Forest age within our experimental units ranges from ~85 to 125 yr old. Prior to our study, no forest management had occurred within the study area for a minimum of 20 yr.

Within the GRGL, we selected three replicate study areas (hereafter "blocks"; Fig. 1). All three blocks were similar in forest age, cover type, and management history, and each had the spatial capacity to accommodate four experimental units. Perennial streams bordered or traversed each of the three blocks. Experimental units within blocks were a minimum of 14 ha, so that we could establish 10-ha treatment plots with 20 m wide buffers. We randomly assigned three fuel reduction treatments and an untreated control within each block (12 experimental units total; Fig. 1). We implemented the following treatments: (1) B, repeated prescribed burns (four times; February or March 2003, 2006, 2012, and 2015); (2) M, repeated mechanical felling of all shrubs and small trees >1.4 m tall and <10.2 cm in diameter at breast height (dbh) with a chainsaw (twice; winters

2001–2002 and 2011–2012); (3) MB, initial mechanical cutting of the understory (winter 2001–2002), followed by four prescribed burns (as for B above); and (4) C, untreated controls. Debris (cut trees and shrubs) were left scattered on the forest floor in MB and M plots.

Hand-ignition using spot fire and strip-head fire techniques, as well as helicopter-assisted spot fire ignition, was used to conduct prescribed burns within B and MB plots. The initial prescribed burns conducted in March 2003 had flame heights of 1–2 m throughout all burn units. However, topography and intersecting flame fronts contributed to localized areas of erratic fire behavior in which flame heights reached up to 5 m (Waldrop et al. 2010). Mechanical felling of the shrub layer on MB plots contributed volumes of woody debris on the forest floor that was approximately twice as large as in B plots. Consequently, average fire temperature at 30 cm aboveground was much hotter in MB than B plots (370°C and 180°C, respectively; Waldrop et al. 2010). Subsequent burns of MB plots produced lower-intensity fires than the initial burn (Waldrop et al. 2010); the second burn (March 2006) produced flame heights generally <1.5 m; and the average temperature 30 cm aboveground was 155°C in B and 222°C in MB plots (Waldrop et al. 2016). The third and fourth burns were low-intensity, producing flame lengths <2 m; however, measurements of fire temperature were not collected. Numerous trees were killed in MB plots from the initial high-severity burns, resulting in a dramatic alteration of forest structure (e.g., canopy openings).

Sampling procedure

Within each treatment unit, we established two trap arrays spaced >50 m apart (six traps per sampling period per treatment unit; 72 traps per sampling period for all treatment units combined). Each trap array consisted of one pitfall trap, one set of four colored pan traps located on the ground, and one set of four colored pan traps located within the canopy. Pitfalls were a 4-oz (118 mL) cup filled half-way with soapy water, with three 30 cm long aluminum flashing drift fences trenched into the ground that radiated from the center of the cup to increase trapping efficiency. We oriented drift fences at 120° to the neighboring drift fence. Colored pan traps filled with soapy water were used, both in the midstory and on the ground, to capture ants that may not be commonly captured in pitfall traps. For the colored pan traps, we attached blue, red, white, and yellow bowls at each corner of a 66 cm square metal remesh (Nucoar) with binder clips (Campbell et al. 2018*b*). Although pan traps are usually used to capture flying insects, they have been successfully used to sample ants (Nicklen and Wagner 2006). At each of the two trapping locations within each treatment unit, we hoisted one pan trap set (one square wire remesh with four bowls) into the midstory (mean height 9.1 ± 0.3 m) and placed another set on the forest floor. At a given trapping site, the pitfall trap array, midstory pan trap set, and forest floor pan trap set were spaced <10 m (horizontal distance) apart. We sampled monthly for a 72-h period during spring and summer (4 months; May/June through September/October) each year, from 2014 to 2016. We chose to sample during these months because they coincided with the primary growing season in the region and because most ants would be active during this time period. During collecting periods, colored bowls were pooled from each trap set (four bowls per trap set). The 2014 trapping occurred prior to the fourth burn and the 2015 and 2016 insect trapping ensued after the fourth burn and second mechanical treatment. Ants were strained from the traps and stored in ethanol until they could be identified and counted in the laboratory.

Ant identification

We used Fisher and Cover (2007) for genus-level identification and MacGown (2014) for species identification. Ecological background information was taken from a variety of sources (e.g., Fisher and Cover 2007, MacGown 2014, and others). We assigned ant functional groups based on Stephens and Wagner (2006) and Bednar and Silverman (2011).

Statistical analysis

We plotted abundances of all captured ants and visually binned them into one of the following three abundance levels: (1) superabundant; (2) abundant; and (3) rare (see Grodsky et al. 2018*a*). We set the cutoff for inclusion of individual ants in analyses at the break between abundant and rare ant groups, thereby excluding all rare ants

with relatively low abundances from analyses. For example, we documented a significant reduction in abundance between *Myrmecina americana* Emery (n = 125) and *Brachymyrmex depilis* Emery (n = 56) on the plot, which constituted the sample size cutoff (i.e., n = <125) for our data set.

We conducted repeated-measures analysis of variances (RMANOVAs) to test response of the ant community and individual ant taxon to fuel reduction treatments. We employed a repeated-measures approach in the statistical analysis to account for potential issues with temporal pseudoreplication associated with sampling the same sites in sequential years. We considered a sampling station as the collection of traps in each trap array—two pitfall traps on the ground, two sets of four pan traps on ground, and two sets of four pan traps in the midstory—in each treatment plot (n = 6 traps/sampling station). We used number of captured individuals of all ants, ants in each functional group, and ants in each ant taxon and ant taxa richness pooled over all traps in each sampling station in each treatment plot for all sampling periods (i.e., months) in each year as dependent variables. For each RMANOVA, we included treatment, block, year, and a treatment × year interaction term as dependent variables. We used the generalized least squares technique (gls function in R package nlme; Pinheiro et al. 2018) and fitted models under the assumption of a temporal autocorrelation structure of order one (i.e., AR1) using the restricted maximum-likelihood method. To determine differences among treatments and treatment × year interactions, we performed post hoc Tukey's pairwise comparisons of estimated marginal means in the R package emmeans (Searle et al. 1980, Lenth 2018). We set $\alpha = 0.05$.

Results

We collected a total of 54,219 ants comprised of 23 different genera during the 3-yr study (Table 1). *Prenolepis imparis* Say was the most

Table 1. Total ants from each genus/species captured with pitfall and colored pan in three fuel reduction treatments and a control, Green River Game Land in Polk County, North Carolina, USA (2014–2016).

Genus/species	C	M	B	MB	Total	Functional group
Aphaenogaster (*rudis* complex)	393	336	287	183	1199	Opportunists
Brachyponera chinensis	3	21	8	629	661	Specialized predators
Brachymyrmex depilis	2	15	13	26	56	Cryptic species
Camponotus chromaiodes	1315	797	1402	808	4322	Subordinate Camponotini
Camponotus americanus	318	386	585	312	1601	Subordinate Camponotini
Crematogaster lineolata	8	289	576	496	1369	Generalized Myrmicinae
Forelius pruinosus	0	1	0	3	4	Dominant Dolichoderinae
Formica	489	32	328	13	862	Opportunists
Lasius	6	74	2	2	84	Cold climate specialists
Monomorium minimum	3	10	18	814	845	Generalized Myrmicinae
Myrmecina americana	45	30	35	17	127	Cold climate specialists
Neivamyrmex	8	25	49	3	85	Tropical climate specialists
Nylanderia	55	104	93	27	279	Opportunists
Pheidole	3	2	0	105	110	Generalized Myrmicinae
Ponera pennsylvanica	18	5	4	10	37	Cryptic species
Prenolepis imparis	15,652	9321	15,221	1887	42,081	Cold climate specialists
Proceratium	1	2	1	0	4	Cryptic species
Solenopsis	71	32	46	43	192	Cryptic species
Stenamma	10	10	11	34	65	Cold climate specialists
Stigmatomma	2	5	1	0	8	Specialized predators
Strumigenys louisianae	1	1	3	1	6	Cryptic species
Tapinoma sessile	4	7	16	4	31	Opportunists
Temnothorax	12	9	3	3	27	Cryptic species
Tetramorium bicarinatum	51	42	54	17	164	Opportunists
Total	18,470	11,556	18,756	5437	54,219	

Notes: C, control; M, mechanical; B, burn; MB, mechanical + burn. Functional groups are based on Stephens and Wagner (2006) and Bednar and Silverman (2011).

common ant species, comprising 77.6% of the total ant captures, followed by the genera *Camponotus* (10.9%), *Aphaenogaster* (2.2%), *Formica* (1.6%), and *Monomorium* (1.6%). Colored pan traps placed on the ground collected 59.8% of the ants, followed by pitfalls (36.9%) and colored pan traps hoisted into the midstory (3.3%). Pitfall traps collected all 23 genera, followed by colored pan traps placed on the ground (21 genera; *Stigmatomma* and *Strumigenys* not collected) and colored pan traps within the midstory (15 genera; *Forelius*, *Neivamyrmex*, *Pheidole*, *Proceratium*, *Solenopsis*, *Stigmatomma*, *Strumigenys*, *Temnothorax* not collected).

Overall ant abundance differed among treatments ($F_{3,26}$ = 5.83, P_{trt} = 0.01; Table 2) and was greater in C and B compared to MB (Table 3). *Prenolepis imparis*—the most commonly collected ant in the study—abundance differed among treatments ($F_{3,26}$ = 8.29, P_{trt} = 0.01) and was more abundant in C and B compared to MB (Fig. 2). Therefore, treatment-level response of the overall ant community likely was driven by treatment-level response of *Prenolepis imparis*. Although not statistically significant, *Tetramorium bicarinatum* Nylander and *Aphaenogaster* (*rudis* complex) also were found in lower abundances within MB compared to all other treatments (Table 3). Conversely, *Monomorium minimum* Buckley and Asian needle ant (*Brachyponera chinensis*) were more abundant in MB than other treatments (Table 3). We detected a treatment × year interaction for *B. chinensis* abundance ($F_{3,26}$ = 5.15, $P_{trt \times year}$ = 0.001); the species had significantly greater abundance in MB than any other treatments in 2015 and 2016 (Fig. 3). *Crematogaster lineolata* Say were more abundant in all fuel reduction

Table 2. Treatment and treatment × year effects on number of total ants, ant taxon richness, and number of individual ant genera and species sampled during 2014, 2015, and 2016 based on results of repeated-measures ANOVAs.

Ant taxa	Repeated-measures ANOVA								Treatment effects
	$F_{3,26}$	P_{trt}	$F_{2,26}$	P_{block}	$F_{1,26}$	P_{year}	$F_{3,26}$	$P_{trt \times year}$	
Ant community									
All ants	5.83	0.01	4.02	0.03	1.25	0.27	0.01	0.99	C^a, B^a, M^{ab}, MB^b
Richness	0.68	0.57	2.84	0.08	38.72	<0.001	0.55	0.65	
Functional groups									
Cold climate specialists	8.28	0.01	5.14	0.01	0.28	0.60	0.02	0.99	C^a, B^a, M^{ab}, MB^b
Cryptic species	0.21	0.89	0.93	0.41	0.60	0.45	1.33	0.29	
Generalized Myrmicinae	0.59	0.63	1.18	0.33	5.27	0.03	1.86	0.16	
Opportunists	1.13	0.36	0.25	0.78	4.89	0.04	0.69	0.56	
Specialized predators	1.25	0.32	0.70	0.51	5.62	0.03	5.11	0.006	2015 – MB^a, C^b, M^b, B^b 2016 – MB^a, C^b, M^b, B^b
Subordinate Camponotini	0.35	0.79	0.71	0.50	5.86	0.02	0.19	0.90	
Genera and species									
Aphaenogaster (*rudis* complex)	1.62	0.21	0.40	0.68	7.63	0.01	0.89	0.46	
Brachyponera chinensis	1.26	0.31	0.71	0.52	5.49	0.03	5.15	0.001	2015 – MB^a, C^b, M^b, B^b 2016 – MB^a, C^b, M^b, B^b
Camponotus americanus	0.36	0.78	2.28	0.12	6.82	0.01	0.14	0.94	
Camponotus chromaiodes	0.41	0.74	0.32	0.73	4.76	0.04	0.30	0.83	
Crematogaster lineolata	0.92	0.45	2.36	0.11	3.51	0.07	0.66	0.58	
Formica	0.80	0.50	0.59	0.56	0.94	0.34	0.22	0.88	
Myrmecina americana	1.54	0.23	0.93	0.41	7.34	0.01	0.84	0.49	
Nylanderia	2.23	0.11	5.21	0.01	7.73	0.01	1.96	0.14	
Prenolepis imparis	8.29	0.01	5.18	0.01	0.27	0.61	0.01	0.99	C^a, B^a, M^{ab}, MB^b
Solenopsis	0.18	0.91	0.80	0.46	0.01	0.92	1.53	0.23	
Monomorium minimum	0.70	0.56	0.69	0.51	2.63	0.12	2.59	0.07	
Tetramorium bicarinatum	1.51	0.24	0.89	0.42	17.96	<0.001	2.73	0.06	

Note: Different letters indicate significant differences among individual treatments based on Tukey's pairwise comparisons with significance levels set at α = 0.05.

Table 3. Mean (SE in parentheses) number of ants (n = 54,219) captured in three fuel reduction treatments and controls between 2014 and 2016, Green River Game Land, Polk County, North Carolina, USA.

Ant taxa	Treatments			
	Control	Mechanical	Burn	Mechanical + Burn
Ant community				
All ants	6390.67[a] (1491.13)	3852.00[a,b] (1323.38)	6018.00[a] (1698.86)	1812.33[b] (343.26)
Richness	174.00 (26.76)	186.00 (20.21)	186.33 (7.54)	161.67 (6.39)
Functional groups				
Cold climate specialists	5090.33[a] (1661.29)	3144.00[a,b] (1084.48)	5233.67[a] (1312.90)	637.00[b] (152.88)
Cryptic species	22.00 (13.87)	21.33 (6.89)	36.33 (22.84)	27.68 (12.35)
Generalized Myrmicinae	3.67 (1.86)	100.33 (25.69)	199.00 (146.00)	471.67 (419.70)
Opportunists	339.33 (183.46)	173.67 (40.67)	249.33 (126.19)	46.67 (14.24)
Specialized predators†	1.33 (0.88)	8.67 (5.78)	3.33 (0.67)	209.67 (159.95)
2014	0.00 (0.00)	0.00 (0.00)	0.33 (0.33)	4.33 (4.33)
2015	0.00[b] (0.00)	6.67[b] (5.17)	1.00[b] (0.57)	62.33[a] (55.44)
2016	1.33[b] (0.88)	2.00[b] (1.00)	2.00[b] (1.00)	143.00[a] (100.98)
Subordinate Camponotini	544.33 (208.44)	394.33 (167.38)	662.33 (331.06)	373.33 (172.33)
Genera and species				
Aphaenogaster (*rudis* complex)	131.00 (40.28)	112.00 (46.18)	94.33 (27.86)	26.00 (14.57)
Brachyponera chinensis†				
2014	0.00 (0.00)	0.00 (0.00)	0.33 (0.33)	4.33 (4.33)
2015	0.00[b] (0.00)	6.00[b] (5.51)	0.67[b] (0.33)	62.33[a] (55.44)
2016	1.00[b] (1.00)	1.00[b] (1.00)	1.67[b] (1.21)	143.00[a] (100.98)
Camponotus chromaiodes	438.33 (155.03)	265.67 (111.27)	467.33 (225.75)	269.33 (144.81)
Camponotus americanus	106.00 (55.65)	128.67 (67.15)	195.00 (111.02)	104.00 (62.75)
Crematogaster lineolata	2.67 (1.45)	96.33 (24.88)	192.00 (141.51)	165.33 (138.50)
Formica	163.00 (133.21)	10.67 (2.33)	109.33 (107.34)	4.33 (3.38)
Myrmecina americana	11.67 (3.93)	9.67 (4.81)	15.00 (1.00)	5.33 (2.91)
Nylanderia	31.00 (14.01)	34.67 (15.38)	18.33 (8.84)	9.00 (3.46)
Prenolepis imparis	5073.67[a] (1659.19)	3107.00[a,b] (1091.14)	5217.33[a] (1313.18)	629.00[b] (151.53)
Solenopsis	15.33 (15.33)	10.67 (6.89)	23.67 (23.67)	14.33 (4.18)
Monomorium minimum	1.00 (1.00)	3.33 (1.20)	6.00 (5.03)	271.33 (246.45)
Tetramorium bicarinatum	17.00 (5.69)	14.00 (5.29)	18.00 (5.03)	5.67 (1.76)

Note: Different letters indicate significant differences among treatments based on Tukey's pairwise comparisons with significance levels set at $\alpha = 0.05$.

† Indicates a significant treatment × year interaction at $\alpha = 0.05$ (see Table 2).

treatments compared to C, but the relationship was not statistically significant (Table 3).

Other ant genera showed variable responses to the treatments. For example, *Formica* had higher abundances in C compared to M and MB (Table 3), although this result was not statistically significant. Other genera, such as *Solenopsis* and *Camponotus* species, did not exhibit any preference for fuel reduction treatments over C (Table 3). Overall richness of ant genera/species did not exhibit treatment-level differences ($F_{3,26} = 0.68$, $P_{trt} = 0.57$). See Table 2 for detailed results for treatment and treatment × year effects on total ants, ant taxon richness, and abundance of various ant genera and species.

For ant functional groups, cold climate specialists differed among treatments ($F_{3,26} = 8.28$, $P_{trt} = 0.01$) and were more abundant in the C and B compared to all MB (Table 3); the cold climate specialist trend was largely driven by *P. imparis* (see Fig. 2). Specialized predators exhibited a treatment × year interaction ($F_{3,26} = 5.11$, $P_{trt \times year} = 0.006$) and were more abundant in MB compared to all other treatments in 2015 and 2016, but not 2014 (Table 3). Subordinate Camponotini ($F_{3,26} = 0.35$, $P_{trt} = 0.79$), opportunists ($F_{3,26} = 1.13$, $P_{trt} = 0.36$), and generalized Myrmicinae ($F_{3,26} = 0.59$, $P_{trt} = 0.63$) showed no treatment-level response. See Table 2 for detailed results for treatment and treatment × year effects on ant functional groups.

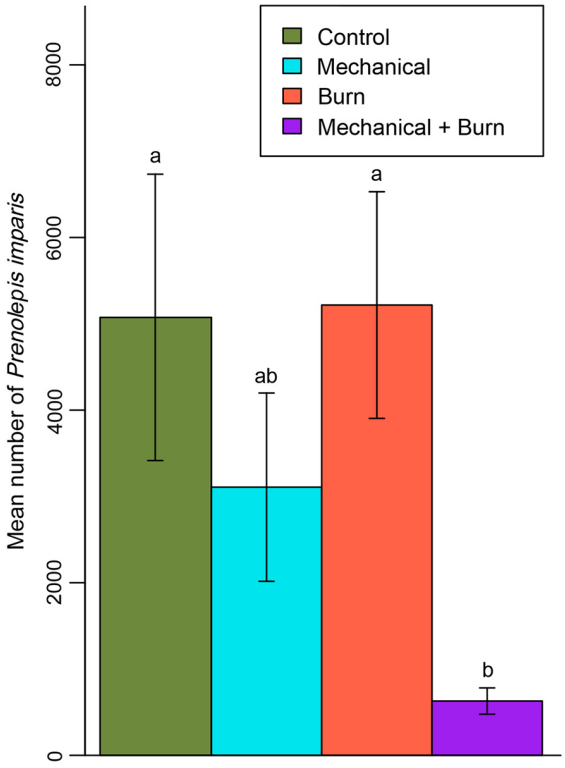

Fig. 2. Mean number (95% CI) of *Prenolepis imparis* captured in three fuel reduction treatments and controls between 2014 and 2016, Green River Game Lands, Polk County, North Carolina. Different letters indicate significant differences among treatments based on Tukey's pairwise comparisons with significance levels set at $\alpha = 0.05$.

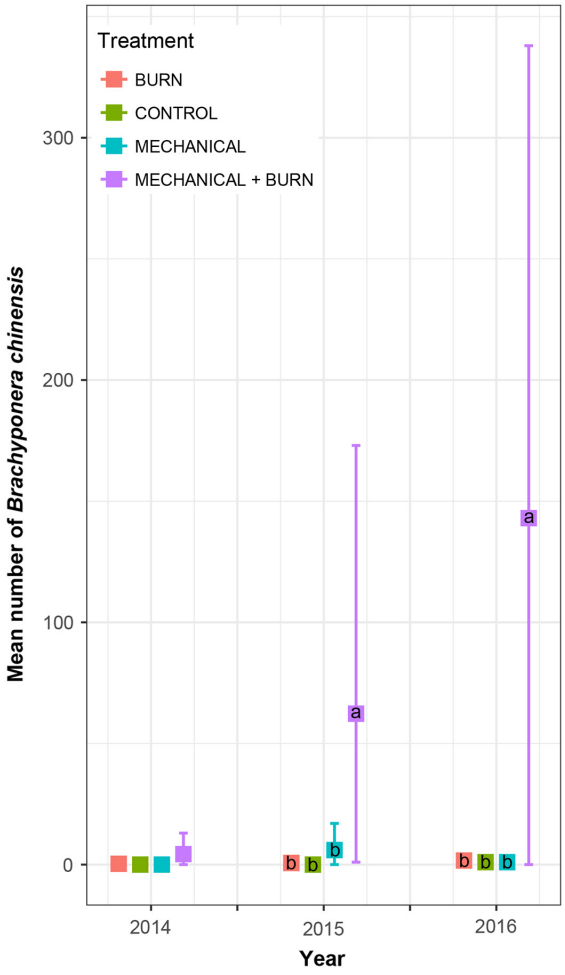

Fig. 3. Interaction plot illustrating mean number of *Brachyponera chinensis* for each treatment (i.e., three fuel reduction treatments and controls) × year combination, with 95% confidence intervals calculated by the percentile method, in the Green River Game Lands, Polk County, North Carolina (2014–2016). Different letters indicate significant differences among treatments based on Tukey's pairwise comparisons with significance levels set at $\alpha = 0.05$.

Discussion

Ants are important components of forested ecosystems, where they assist with nutrient cycling, seed dispersal, act as the primary predators of defoliating insects, and comprise a significant portion of the overall food chain (Petal 1978, Handel et al. 1981, Folgarait 1998). Our results showed that changes in the structure of the forest understory affected ant communities. Due to the diversity of niches occupied by different ant species, impacts varied across ant taxa and functional groups. Additionally, we determined that a non-native ant (*B. chinensis*) was more abundant in the most disturbed treatment, highlighting potential ramifications of fuel reduction treatments for invasive species colonization in forests.

Brachyponera chinensis is a non-native ant from Asia that was first documented in the United States in the 1930s (Smith 1934); however, others suggest it was already established in the late 1800s (Zungoli et al. 2005). Most documented non-native ant invasions have occurred in disturbed habitats, but *B. chinensis* has been found to colonize mature forests of the Southeastern United States (Guénard and Dunn 2010). Additionally, Grodsky et al.

(2018*b*) found higher abundances of *B. chinensis* in recently logged areas in North Carolina where coarse woody debris piles were left on-site compared to sites that had all coarse woody debris removed. Although some researchers suggested *B. chinensis* may outcompete native ants and other insects for food and nesting sites (Guénard and Dunn 2010, Warren et al. 2015), we found no decrease in ant taxa richness within MB, where *B. chinensis* was most abundant. Additionally, some ant species (e.g., *Crematogaster lineolata* and *Monomorium minimum*) did not exhibit any declines within MB and were relatively more common within MB, despite the higher abundance of their potential competitor *B. chinensis*. In its native habitat and introduced areas, *B. chinensis* primarily feeds on termites (Bednar and Silverman 2011), and therefore, it has a niche overlap with *Aphaenogaster* (*rudis*) complex (Warren et al. 2015). Potentially, competitive exclusion by *B. chinensis* could explain the relatively lower abundance of *Aphaenogaster* (*rudis*) complex in MB; however, this trend was not statistically significant. Displacement of *Aphaenogaster* (*rudis*) complex by *B. chinensis* could have important implications for the greater forest ecosystem because, unlike *Aphaenogaster* (*rudis*) complex, *B. chinensis* is not an efficient disperser of seeds (Warren et al. 2015). Additionally, the increase in *B. chinensis* in the MB occurred after the last round of fuel reduction treatments were implemented at the end of 2014, suggesting that heavily disturbed forests could aid the spread of *B. chinensis*.

In our study, *Aphaenogaster* (*rudis*) complex, *Myrmecina americana*, *Tetramorium bicarinatum*, *Nylanderia*, and *Prenolepis imparis* generally had lower abundances in MB than all other treatments, although only *P. imparis*' trend was statistically significant. These ants mostly nest in soil and are scavengers that will also tend honeydew-producing Hemiptera, an important food source (Fisher and Cover 2007). The MB treatments resulted in a decrease in duff and leaf litter (Waldrop et al. 2016, Greenberg et al. 2018*a*,*b*), possibly resulting in suboptimal nesting habitat for these ants, especially *P. imparis*. Additionally, honeydew-producing Hemiptera may have been less common in the MB plots due to the increased tree mortality and reduced canopy cover. Indeed, honeydew is more abundant within forest canopies (Moran and Southwood 1982), which became highly reduced in MB treatments during the application of prescribed fire and mechanical cutting of the understory over a 15-yr period (Waldrop et al. 2016). Therefore, ants dependent on honeydew would have also decreased or moved to an area with increased canopy cover and honeydew-producing Hemiptera.

The drastic decrease in *P. imparis* in the MB treatments could alter nutrient cycling and impact overall food chains within forested ecosystems. Greenberg et al. (2010) sampled ants and other arthropods from the same treatment units after the first application of treatments (2003) and found no differences in total ant abundance among treatments. However, they did not examine individual genera or species. Additionally, some changes to forest and understory structure did not become apparent until after several rounds of the fuel reduction treatments (Waldrop et al. 2016), stressing the importance of studying ant response to repeated applications of fuel reduction treatments. Our data suggested that repeated applications of fuel reduction treatments can cause pronounced changes to overall ant abundance and among various ant genera/species and functional groups. Repeated application of prescribed burns and mechanical removal may prevent *P. imparis* and other ant taxa from rebounding quickly from forest management, as we continued to observe decreased abundance two years after the last round of treatments were applied.

Neither *Camponotus americanus* Mayr nor *Camponotus chromaiodes* Bolton showed any preference for any fuel reduction treatments. *Camponotus chromaiodes* primarily nests within stumps, rotting logs, and dead trees, whereas *C. americanus* nests primarily in soil. Although changes in nesting structure availability among the treatments did not seem to alter their abundance, these species are omnivorous and food could have been similar across fuel reduction treatments, thus allowing them to establish colonies throughout treatment plots.

Temporally, ant taxa that exhibited increased abundance after a disturbance have been shown to follow a classic bell-shaped curve (Hoffmann and Andersen 2003). In theory, intermediate disturbances should result in increased species richness due to establishment of more microhabitats (Graham et al. 2009). However, we only found significant responses in abundance by *P. imparis* and *B. chinensis* and no difference among

treatments for ant taxa richness. With the exception of *B. chinensis*, no other ant genera/species exhibited yearly abundance differences from 2014 (shortly before the final round of treatments were applied) to 2016 (2 yr after last round of fuel reduction treatments). This suggests that disturbance effects on *P. imparis* within the Southern Appalachian Mountains could be maintained or prolonged due to the repeated application of fuel reduction treatments. It is unknown whether *B. chinensis* was present when the first treatments were implemented or whether they have recently colonized this portion of North Carolina following treatments. Therefore, we are uncertain whether their abundance would decrease if fuel reduction treatments ceased within the MB.

Overall, ants can be successfully used to make inferences about forest condition within the Southern Appalachian Mountains and other ecosystems. In our study, a native ant and nonnative ant exhibited opposite differences in abundance among the fuel reduction treatments. Multiple rounds of fuel reduction applications conducted over time may be required in order to detect impacts on some ant taxa. Most studies that examined forest management practices have been conducted immediately after application of treatments (Greenberg et al. 2010). This study demonstrates that continued monitoring of ants and other organisms after multiple, repeated rounds of fuel reduction treatments could provide invaluable and insightful guidance to forest managers who are looking to balance forest management and biological diversity.

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