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Israel Del Toro[1,2,*], Kevin Towle[3], Drew N. Morrison[1], and Shannon L. Pelini[2,4]

Abstract - We investigated ant species richness, interspecific behavioral interactions, and community composition in adjacent forested and open habitat plots in two forest types of the northeastern United States: 1) the more common hemlock-White Pine forest studied at Harvard Forest Long Term Ecological Research Station in central Massachusetts, and 2) the rare Pitch Pine barrens of Myles Standish State Forest in southeastern Massachusetts, which also provide habitat for multiple rare and endangered species. Overall, we found that species richness, behavioral interactions, and ecological traits vary between forested and adjacent open habitat plots. The number of species is five times higher per plot in the hemlock-White Pine open habitat (compared to forest habitat), but this pattern (i.e., higher species richness in open vs. forested plots) is not observed in the Pitch Pine barren site. Non-metric multidimensional scaling analyses suggest that community composition is significantly different between forest and open plots at both sites. However, community composition in open plots at both sites did not significantly differ from each other. We show that behaviorally dominant and submissive species mostly occur in open plots while neutrally interacting species are more restricted to forested plots, suggesting that interspecific competitive dynamics may be contributing to the community assembly patterns observed in open habitats. Our findings suggest that conservation and management for both open and forested habitat at either site is extremely important when attempting to maintain optimal ant biodiversity because each habitat type provides suitable conditions for different suites of ant communities.

Introduction

Communities are structured by various mechanisms including competitive dynamics, niche partitioning, biotic and abiotic environmental drivers, and evolutionary pressures on populations (Harrison and Cornell 2008, Parr and Gibb 2010). Previous studies on the community structure of ants of the northeastern US have documented species diversity gradients and suggest assembly rules based on body size across regional scales, but have not provided assembly rules for local determinants of community composition (Gotelli and Ellison 2002a, b).

In this comparative and observational study, we investigate species richness differences (i.e., the number of species per plot) in paired forested and open habitats at two sites in Massachusetts, the *Pinus rigida* Mill. (Pitch Pine) barrens of Myles Standish State Forest (MSSF), and the hemlock-*Pinus strobus* L.

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(White Pine) forests at Harvard Forest Long Term Ecological Research Station (HFLTER). The ants at both sites have been extensively sampled for nearly two decades, and the overall fauna is relatively well understood (Stefan Cover and Aaron Ellison, Harvard Forest, Petersham, MA, pers. comm.). The forests of MSSF are classified as core and critical units of conservation by the Massachusetts Department of Fish and Game and the Nature Conservancy because they are habitat for a wide variety of threatened and endangered species of birds, reptiles, amphibians, and invertebrates (Motzkin et al. 1996, Woolsey et al. 2011).The habitat at HFLTER is more common, but still considered an important forest habitat core, representative of much of the New England landscape with significantly lower species diversity (Jenkins et al. 2008, Woolsey et al. 2011). By understanding fine-scale species richness patterns at these two sites, we aim to inform management strategies required for the maintenance of ant biodiversity at sites of conservation interest. Ants are important members of most terrestrial ecosystems and mediate multiple ecosystem services and processes (e.g., seed dispersal and nutrient cycling in temperate forests) (Del Toro et al. 2012), and so conservation of the functional and biological diversity of these animals should be a research and management priority.

The overarching objective of this study is to compare species richness and density patterns in forested versus open habitat at two sites (i.e., MSSF and HFLTER). Specifically this study aims to: 1) compare species richness estimates at MSSF and HFLTER paired forested and open sites, 2) document natural history traits that are associated with species occurrence (i.e., behavioral traits and nesting microhabitat), and 3) compare the community similarity patterns between MSSF and HFLTER forested and open habitat. We conclude by synthesizing our findings and offering habitat management suggestions which can be applied to maximize ant conservation.

Methods

MSSF is located in Plymouth County in eastern Massachusetts (41.8686°N, 70.6688°W) with a mean elevation of 50 m.a.s.l. The habitat is dominated by Pitch Pine, *Quercus ilicifolia* Wangenheim (Scrub Oak), and *Quercus prinoides* Willdenow (Dwarf Chinquapin Oak) overstory, *Vaccinium* spp. (blueberries) in the understory, and extremely sandy soils. HFLTER is located in Worcester County in central Massachusetts, (42.5391°N, 72.1898°W) with a mean elevation of 300 m.a.s.l. The habitat is dominated by *Tsuga canadensis* L. (Eastern Hemlock) and White Pine overstory, *Mitchella repens* L. (Partridge Berry) in the understory, and with soils ranging from sandy to gravelly loams.

We sampled ant nests at ten 5- x 5-m plots at both MSSF and HFLTER (5 forest habitats and 5 open habitats at each site; *n* = 20 plots). The forested and open plots were paired and separated by 200–300 m, and were at least 50 m from any distinct forest edge, to minimize edge effects on richness patterns. Each pair of plots was separated from the other pairs by at least 750 m and as much as 10 km; on average, the distance between the pairs of plots was 2.85 km. We considered

forest plots as those with a closed overstory (tree canopy) and open plots as those lacking overstory vegetation with an understory dominated primarily by herbaceous vegetation and grasses. Each 5- x 5-m plot was divided into 1-m^2 grids, and each grid was exhaustively searched for ants (an average of 6 person hours per plot), which were hand collected and identified to the species level. We recorded the location of the nest within the grid system and the nesting microhabitat, which was classified into five categories (Table 1). We also collected ants using an array of 36 pitfall traps (50-ml Falcon tubes filled with 25 ml of 75% ethanol) placed at 1-m intervals across the sampling grid and left open to collect ants for 48 hours.

We evaluated interspecific ant interactions at baits using 16 Petri dishes with 2 g of tuna spaced at 3-m intervals in a 9- x 9-m grid (which included the 5-x 5-m grid where pitfall traps and hand collecting occurred). We observed each dish for 2 minutes, recorded any interspecific interactions, and collected the interacting ants for species-level identification. We observed each bait station three times during a 96-minute sampling window (up to 48 possible independent interactions during the sampling period per plot) and counted the number of aggressive and neutral interspecific interactions at the baits. The occurrences of ants at baits that were monopolized by heavy recruitment were only counted once so that each species occurrence was treated as an independent observation. Interactions were recorded as dominant, neutral, or submissive. We assigned a classification (i.e., dominant, submissive, or neutrally interacting) to species that were observed interacting a minimum of 5 times based on the majority of their interspecific interactions. The majority of species that we observed interacting were consistent in their behavioral response more than 80% of the time. A dominant interaction consisted of any competitive behavior such as attacks or defenses of resources. A submissive interaction included retreat, loss of resource allocation, or death resulting from aggression or stress. A neutral interaction was when neither species altered their behavior in the presence of the other.

We compared species richness, community composition, nesting microhabitat type, and number and type of behavioral interactions in open versus forest habitats at MSSF and HFLTER. We estimated species richness using rarefaction analyses implemented in EstimateS (Colwell 2009). We completed the analyses at the site and habitat-type levels (Appendix 1) and used two non-parametric estimators of species richness for incidence-based data: the ICE metric and the Chao2 metric, which are appropriate when analyzing species occurrences (rather than abundances) at pitfall traps (Gotelli et al. 2011). We present the mean and standard deviation of the observed interspecific interactions per sampling window ($n = 48$, unless baits were monopolized by a single heavily recruiting species; Table 1). We used the Wilcoxon rank sums test to evaluate if there were differences between forest and open habitat richness measures, as well as the number and type of behavioral interactions, and nesting microhabitat type (Table 1).

We used non-metric multidimensional scaling (NMDS) to evaluate community composition and similarity. We applied the optimal dimensionality of three

Table 1. Wilcoxon rank sums test statistics: Pair-wise comparisons between forest and open plots at Harvard Forest and Myles Standish State Forest. Total plots = 20; n = 5 per habitat type and forest. We report the mean and standard deviation for observed and estimated species richness as well as the mean and standard deviation for the counts of observed interspecific interactions (i.e., the number of interactions per observation period at a single bait station) and the mean and standard deviations of the number of nests and nesting microhabitat types per plot. * indicates significant difference ($P < 0.05$) between forest and open plots at a given site.

	Harvard Forest			Myles Standish		
	Forested plots	Open plots	W-stat (*P*-value)	Forested plots	Open plots	W-stat (*P*-value)
Diversity measures						
Species Observed	3.00 ± 1.00	9.40 ± 4.16	2.50 (0.04)*	8.20 ± 3.11	9.80 ± 2.86	7.00 (0.29)
ICE metric	3.60 ± 2.08	11.91 ± 5.53	2.50 (0.05)*	14.46 ± 5.24	12.96 ± 6.23	15.00 (0.69)
Chao 2 metric	3.19 ± 1.29	10.57 ± 4.69	2.50 (0.05)*	13.45 ± 5.20	11.11 ± 4.23	10.00 (0.69)
Behavioral interactions						
Total interactions	1.00 ± 1.25	2.80 ± 2.10	7.50 (0.33)	6.40 ± 4.73	7.20 ± 2.18	10.50 (0.75)
Aggressive interactions	0.20 ± 0.45	2.40 ± 1.10	6.50 (0.09)	0.60 ± 0.89	6.00 ± 2.99	3.50 (0.05)*
Neutral interactions	0.80 ± 0.24	0.40 ± 0.25	16.0 (0.49)	4.00 ± 1.94	1.20 ± 1.31	18.50 (0.19)
Nest density and nesting habitat						
Total nests	7.80 ± 2.17	13.40 ± 8.02	5.00 (0.14)	29.80 ± 14.38	32.60 ± 15.37	11.00 (0.77)
Nests in soil	1.40 ± 1.52	11.80 ± 6.98	2.50 (0.04)*	13.60 ± 6.23	23.80 ± 16.23	7.00 (0.29)
Nests in woody debris	0.40 ± 0.89	0.20 ± 0.45	10.00 (0.67)	4.60 ± 3.05	0.80 ± 1.30	22.5 (0.04)*
Nests in vegetation	0.00 ± 0.00	0.00 ± 0.00	NA	0.00 ± 0.00	4.80 ± 4.21	2.50 (0.02)*
Nests in leaf litter	6.00 ± 1.58	0.60 ± 0.89	25.00 (0.01)*	11.80 ± 10.21	3.00 ± 6.71	19.00 (0.18)
Nests under rocks	0.00 ± 0.00	0.80 ± 0.64	5.00 (0.07)	0.00 ± 0.00	0.20 ± 0.42	10.00 (0.42)

axes with a stress value of 0.133. The first two axes of the NMDS explained 96% of the variation observed in community composition and so are the only ones reported here. We followed the NMDS with an analysis of similarity (ANOSIM) to evaluate the overall difference in community composition between forest and open plots at the two sites. The Wilcoxon rank sums test, NMDS, and ANOSIM analyses were implemented in R (R-Development-Core-Team 2009) using the statistical package "vegan" (Oksanen et al. 2010).

Results and Discussion

Observed and estimated species richness was five times higher at HFLTER in open compared to forested plots. Species richness did not significantly differ between MSSF open and forest plots (Table 1, Appendix 1). Additionally, species richness at HFLTER open plots did not significantly differ from either forest or open plots at MSSF. The higher species richness at the HFLTER open plots conforms to a global pattern described for ants in open and warmer habitat types (Andersen 1995, 1997). We hypothesize that the open nature of the environment allows ants to be more active and less thermally constrained, as opposed to forested sites, where cool and damp conditions may be acting as a habitat filter (Lessard et al. 2009). At MSSF, the numbers of species did not differ significantly between forest and open sites but remained high (compared to HFLTER) in both forest and open plots. This finding could be an indication that additional environmental factors (e.g., the sandy soil type) might be contributing to the observed high ant abundances, which may ultimately lead to higher species richness. Another factor that can potentially explain the high richness patterns observed at MSSF is the open nature of the canopy in the Pitch Pine barren habitat, which increases habitat complexity in the understory and makes more nesting niches available, a pattern suggested for Massachusetts forests (Woolsey et al. 2011).

We observed behavioral interactions for 15 species (Appendix 2) based on 169 observed interactions at the bait stations. Based on our observations, we were able to classify 13 of the 15 species as either "dominant", "submissive", or "neutral" interacting species. The number of aggressive and neutral interactions at HFLTER did not differ between forest and open habitat. However, a larger sample size may increase support for the non-significant trend ($P = 0.09$), which may suggest that more aggressive interactions may be occurring in open habitat at HFLTER. In MSSF, there were significantly more aggressive interactions in open plots than in forest plots ($P = 0.05$; Table 1), despite there being no differences in the total number of interactions between open and forested plots. The number of observed interspecific interactions only considers a subset of the regional species pool; however, this observational study may be more reflective of the realistic interactions between ground-foraging ant species of the region, in particular when they are competing for a limited, high-quality food resource.

We found that within-site nest densities between forested and open plots did not significantly differ. However, while there were significantly fewer nests in the forested plots at HFLTER than in MSSF ($P = 0.011$), there was no significant

difference in nest densities between HFLTER and MSSF open plots (P = 0.121). The patterns of densities may partially explain why richness was significantly lower in HFLTER forest plots and than all other plots. We hypothesize that in Massachusetts forests, there exists a positive correlation between species richness patterns and local species densities. Furthermore, at HFLTER, we found significantly more nests in soil in open plots than in forest plots, and more nests in leaf litter in forest plots than in open plots (differences in these nesting microhabitats at MSSF were not significant). At MSSF, we found more nests in woody debris in forest plots than in open plots, and found more nests under rocks in open habitat than in forested habitat. These findings highlight the microhabitats in which ant nests were mostly collected and may prove to be important determinants of nesting preferences that should be further examined in subsequent studies and may provide important details about conservation and management of ants for these forests.

Nonmetric multidimensional scaling analyses show that local communities in forest and open habitat at MSSF and HFLTER are significantly different from each other. Species composition in the open sites of MSSF and HFLTER were not different from each other as indicated by the overlapping 95% confidence intervals (Fig. 1). In contrast, we found that forested-plot ant communities at HFLTER and MSSF are significantly different from each other, but still more similar to each other than to open-plot communities at either HFLTER or MSSF (Fig. 1). The ANOSIM results (R = 0.563, P = 0.001) suggest that a significant amount of variation in ant community composition is predictable based on habitat type (i.e., forest vs. open).

For the species that were observed interacting at the baits, neutrally interacting species were mainly found in forested plots, while aggressive/submissive interacting species were mainly found in open habitat plots (Fig. 1). The neutrally interacting species that were commonly collected in forested plots included *Camponotus noveboracensis* Fitch (New York Carpenter Ant), *C. pennsylvanicus* DeGeer (Eastern Carpenter Ant), *Lasius alienus* Foerster (Cornfield Ant), *Aphaenogaster picea* Wheeler (Pitch Black Ant), *Myrmica punctiventris* Roger (Punctured Ant), and *Temnothorax curvispinosus* Mayr (Bent-spined Ant). This suite of species was exclusively collected in forested plots and was not observed in open habitat. The aggressive species that dominated open habitat were *Lasius neoniger* Emery (Labor Day Ant), *Crematogaster lineolata* Say (Small-lined Ant), and *Monomorium emarginatum* DuBois (Furrowed Ant)*,* and the submissive species that were commonly collected in open habitat were *Dolichoderus pustulatus* Mayr (Common Bog Ant)*, Tapinoma sessile* Say (Odorous House Ant)*, Formica incerta* Buren (Uncertain Ant)*,* and *F. pallidefulva* Latreille (Pale Ant)*.* These species were more commonly associated with open habitat or edge habitat, but *F. pallidefulva* was occasionally collected in some of our forest pitfall traps (a total of 9 individuals from 2 pitfall traps).

Based on the observed interactions, we hypothesize that competition for food resources is also likely to contribute to the structure of communities in open habitat plots, but this is a question that remains to be tested in future studies. It is also

likely that in northern latitudes, environmental variables such as temperature can interfere with how a species behaves, such that a species may be less thermally constrained and subsequently more behaviorally aggressive in open habitats. We observed this to be the case with edge species like *Formica subsericea* Say (Silky Ant), which was predominantly neutrally interacting in forested plots but could occasionally be aggressive in open plots. Behavioral shifts have been noted to be context dependent and should be further experimentally studied in species like *F. subsericea*, which commonly occurs in both habitat types, to identify the exact mechanisms that cause behavioral shifts.

The data compiled here suggest that both forested and open habitat is necessary for maintaining ant biodiversity. The forests of HFLTER and MSSF are unique in their species composition (Fig. 1), but those of MSSF support far more species (Appendices 1, 2). Open habitat is particularly important in
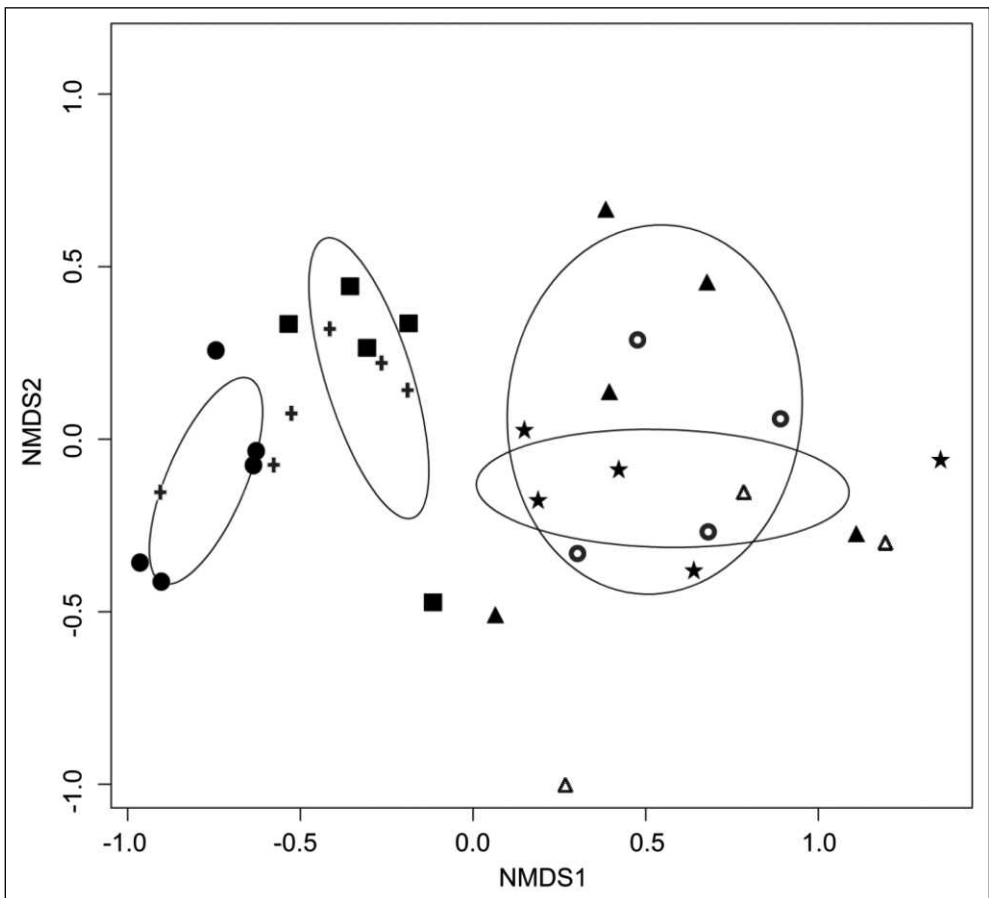
Figure 1. Nonmetric multidimensional scaling plot. Depicts plots as solid symbols (solid circles = HFLTER forested; squares = MSSF forested; stars = HFLTER open; solid triangles = MSSF open). Ellipses show 95% confidence intervals around plot symbols. Additional symbols are species scores classified based on observed behavioral interactions (hollow circles = submissive species; hollow triangles = dominant species; crosses = neutral species).

HFLTER since this habitat supports up to five times the number of species, including ecologically important species (e.g., *Aphaenogaster picea, Formica* spp.), than forested habitat (Appendix 1). Open habitat in MSSF is also important because the community structure (not species richness) is different in forest and open plots (Fig. 1), and therefore, maximizing biodiversity conservation requires the appropriate management for both habitat types. It is also important to note that the pine barren habitat of MSSF is rare in the northeastern US and is home to many species of conservation concern (Motzkin and Foster 2002, Motzkin et al. 1996, Woolsey et al. 2011). As an example, MSSF is one of few sites in the northeastern US where rare ant species like *Formica knighti* Buren (Knight's Ant)*, Monomorium viridae* Brown (Green Monomorium), and a new species of socially parasitic *Nylanderia* have been collected (Ellison et al. 2012). While the forest type at HFLTER is more common in the New England landscape, conservation efforts should consider that the maintenance of early successional open habitat is necessary for optimally managing ant biodiversity, which has been a topic considered in the conservation efforts of bird species (DeGraaf and Yamasaki 2003) but never considered from the perspective of invertebrate conservation for the region.

Acknowledgments

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Appendix 1. Rarefaction and species richness estimation (a), number of species observed (b), and Number of species estimated (c), derived from incidence-based estimators.
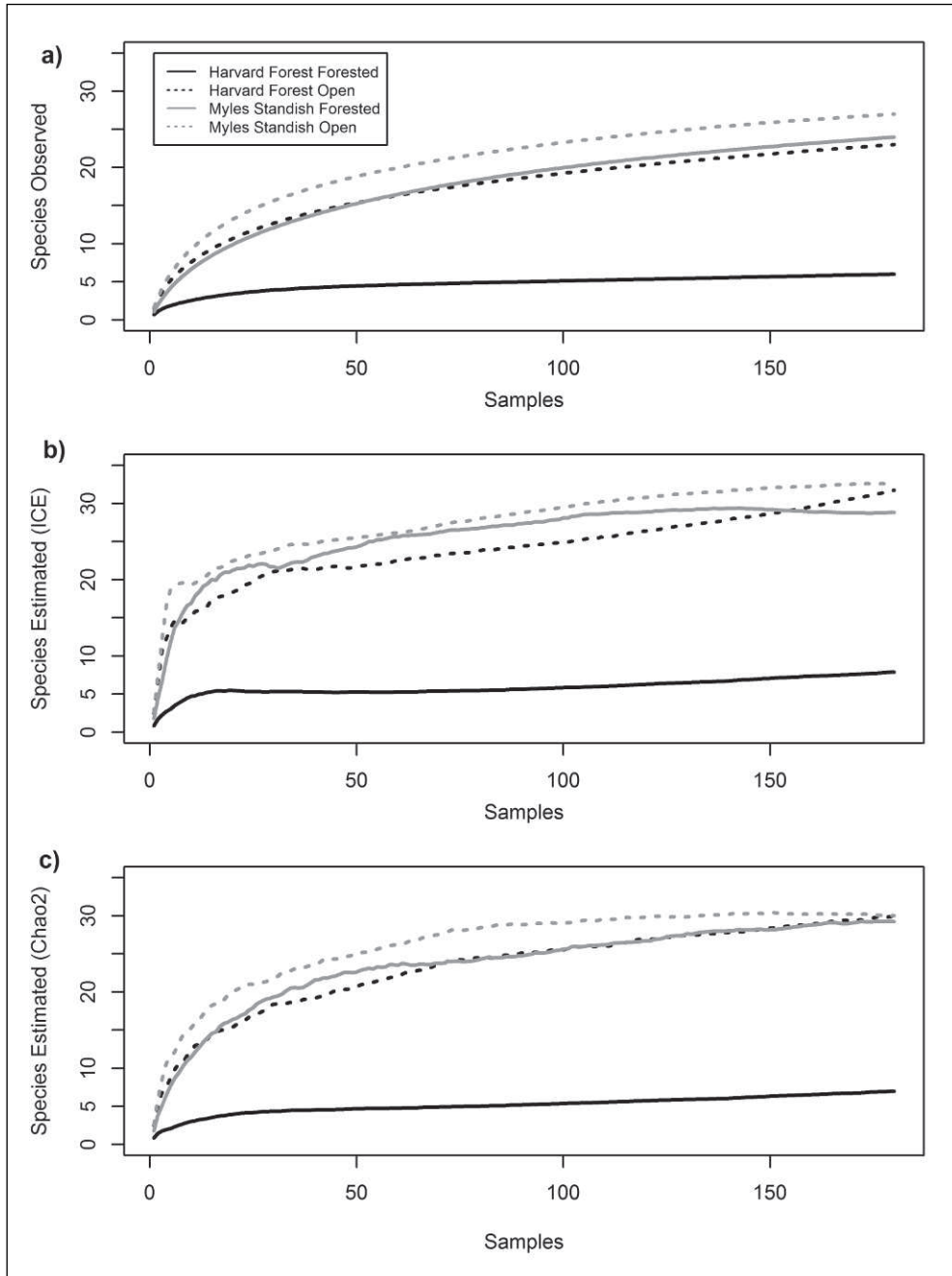
Appendix 2. Species list for HFLTER and MSSF with natural history observations. Sites: MS = Miles Standish State Forest, HF = Harvard Forest LTER, 2011 = sampled in 2011, and PC = previous collections. Behavioral interactions: D = dominant, S = submissive, N = neutral, and N/A = not applicable. Nesting habitat: S = soil, WD = woody debris, LL = leaf litter, V = vegetation, and UR = under rocks. Colony size: A = 10–100 individuals, B = 101–1000 individuals, C = 1001–10,000 individuals, and D = >10,000 individuals.

Subfamily	Genus	Species	Sites				Behavioral interactions				Nesting habitat					Colony size			
			MS	HF	2011	PC	D	S	N	N/A	S	WD	LL	V	UR	A	B	C	D
Amblyoponinae	Amblyopone	pallipes	•	•		•				•	•				•	•			
Dolichoderinae	Dolichoderus	mariae	•	•	•	•					•	•				•	•	•	
Dolichoderinae	Dolichoderus	pustulatus	•								•	•				•	•		
Dolichoderinae	Tapinoma	sessile	•	•	•	•		•			•	•	•	•	•	•	•		
Formicinae	Brachymyrmex	depilis	•	•	•	•		•			•								
Formicinae	Camponotus	americanus	•	•	•	•				•	•					•	•		
Formicinae	Camponotus	noveboracensis	•	•	•				•	•	•	•					•		
Formicinae	Camponotus	pennsylvanicus	•	•	•	•			•		•	•					•		
Formicinae	Formica	dolosa	•	•						•	•					•			
Formicinae	Formica	incerta	•	•		•		•			•			•		•	•	•	
Formicinae	Formica	knighti	•	•		•					•			•				•	
Formicinae	Formica	lasiodes	•	•		•		•		•	•	•	•	•		•	•		
Formicinae	Formica	pallidefulva	•	•		•		•			•	•		•					
Formicinae	Formica	neogagates	•			•				•	•	•					•		
Formicinae	Formica	rubicunda	•			•				•	•								
Formicinae	Formica	subsericea	•	•		•					•	•	•		•	•	•		
Formicinae	Lasius	alienus	•	•		•				•	•	•	•	•	•	•	•		
Formicinae	Lasius	claviger	•	•		•				•	•				•	•	•		
Formicinae	Lasius	flavus	•	•		•				•	•	•		•		•	•		
Formicinae	Lasius	nearcticus	•	•	•	•	•				•	•		UR					
Formicinae	Lasius	neoniger	•	•		•				•	•	•	•			•	•	•	
Formicinae	Lasius	umbratus	•	•		•				•	•	•							
Formicinae	Nylanderia	parvula	•	•	•	•				•	•	•		•		•	•		
Formicinae	Nylanderia	sp.	•	•	•						•								
Formicinae	Prenolepis	imparis	•	•	•	•				•	•					•	•		
Formicinae	Mymicinae	Aphaenogaster picea	•	•		•					•	•	•			•			

Subfamily	Genus	Species	Sites				Behavioral interactions				Nesting habitat					Colony size			
			MS	HF	2011	PC	D	S	N	N/A	S	WD	LL	V	UR	A	B	C	D
Mymicinae	Aphaenogaster	rudis	•	•		•		•			•	•	•	•		•	•		
Mymicinae	Crematogaster	cerasi	•	•	•	•		•	•			•	•	•		•	•		
Mymicinae	Crematogaster	lineolata	•	•	•		•				•			•		•	•		
Mymicinae	Monomorium	emarginatum	•	•			•			•	•				•	•			
Mymicinae	Monomorium	viridae	•						•	•									
Mymicinae	Myrmica	americana	•	•	•				•	•				•	•	•	•		
Mymicinae	Myrmica	detrinodis	•	•	•				•	•				•	•	•			
Mymicinae	Myrmica	puntiventris	•	•		•		•	•	•	•		•	•	•	•	•		
Mymicinae	Myrmica	scuptilis	•	•					•	•					•				
Mymicinae	Myrmica	smithana	•	•					•	•					•				
Mymicinae	Myrmecina	americana	•	•	•				•	•						•	•		
Mymicinae	Pheidole	pilifera	•	•	•				•	•	•							•	
Mymicinae	Solenopsis	molesta	•	•					•	•			•	•		•	•		
Mymicinae	Stenamma	brevicorne	•	•	•				•	•	•		•		•				
Mymicinae	Stenamma	schmitti	•	•	•	•			•	•	•	•							
Mymicinae	Temnothorax	curvispinosus	•	•	•			•	•	•	•	•		•	•	•	•		
Mymicinae	Temnothorax	longispinosus	•	•	•				•	•	•	•				•	•		
Mymicinae	Temnothorax	schaumii	•	•					•	•			•						
Mymicinae	Tetramorium	caespitum	•	•	•				•	•			•	•		•	•		
Ponerinae	Ponera	pennsylvanica	•	•	•	•			•	•						•			