Ant Diversity and Distribution in Acadia National Park, Maine

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ABSTRACT Exotic ant species are a primary threat to ant biological diversity, posing a negative impact to native ant communities. In this study, we examine species richness of ants (family Formicidae) in Acadia National Park, ME, as a fundamental step toward understanding the present impact of the exotic species *Myrmica rubra* on native ant species. Twelve habitat types were sampled, along six transects, with pitfall traps, visual searching, bait traps, and leaf litter extraction, and the aid of 34 volunteers. We report 42 species of ants in Acadia National Park, comprising five subfamilies (Amblyoponinae, Dolichoderinae, Formicinae, Myrmicinae, and Ponerinae) and 15 genera; the cataloged species represents 75% of the species originally recorded in the area by Procter (1946). Our findings suggest *M. rubra* is currently not a dominant species throughout the entire island. However, where this species has invaded locally, few competing native species coexist. The species *Lasius alienus*, *Formica subsericea*, *Myrmica detritinodis*, *Camponotus herculeanus*, *Formica argentea*, *Formica aserva*, and *Tapinoma sessile* occurred most often in our survey. We report the ant species *Amblyopone pallipes* and *Dolichoderus mariae* as two new records for the state of Maine.

KEY WORDS Formicidae, survey, Acadia National Park, species, *Myrmica rubra*

The importance of ants (family Formicidae) in the terrestrial environment cannot be underestimated. Ants are arguably one of the most successful organisms on earth and account for 15–20% of terrestrial animal biomass (Hölldobler and Wilson 1990). Currently, there are ≈11,000 described species (Wilson and Hölldobler 2005), with members of Formicidae ranging as far south as Tasmania, Tierra del Fuego, and southern Africa to as far north as the Arctic Circle (Hölldobler and Wilson 1990). Ants constitute an important faunal group by acting as scavengers (Lenoir et al. 2003), serving as primary predators of invertebrates (Hölldobler and Wilson 1990), and altering the terrestrial environment through the movement of soil, the transportation of plant and animal materials (Folgarait 1998), and the dispersal of seeds (Beattie 1985). The Formicidae are dominant numerically, geographically, and ecologically; yet, the status of species richness in most bioregions is largely unknown (Hölldobler and Wilson 1990). Thus, it is necessary that we gain extensive knowledge about this family to better understand both ecological functions and biological diversity in terrestrial ecosystems throughout the world.

The exotic ant *Myrmica rubra* has exhibited invasive characteristics throughout the northeastern United States, specifically along the coast of Maine and throughout Acadia National Park (Groden et al. 2005, Garnas et al. 2007, McPhee 2008). Nest densities throughout the introduced range are high and workers inflict a painful sting when disturbed (Groden et al. 2005). *M. rubra* is an ant native to the Palearctic north temperate region ranging from Ireland and Great Britain, through northern Europe to western Siberia (Groden et al. 2005). It was first reported in North America by W. M. Wheeler in 1908 (Wheeler 1908a). Populations of a stinging red ant, *M. rubra,* were first observed on Mount Desert Island circa the late 1960s to early 1970s. Reports were rare throughout the 1980s; however, in 1993, there was a drastic increase in the number of complaints on the island and in other coastal communities (Groden et al. 2005).

Once established, exotic species may rapidly dominate a habitat (Passera 1994, Tsutsui and Suarez 2003). Exotic species often outcompete natives for space and resources (Hölldobler and Wilson 1990), a characteristic *M. rubra* is reported to exhibit throughout Acadia National Park (Garnas 2004). Aggression assays demonstrated that *M. rubra* recruits to food sources more quickly and effectively displaces most native ant species from baits (Garnas 2004). Furthermore, research indicates that *M. rubra* reduces species richness and diversity (Garnas 2004), a result that threatens the current ant community, potentially leading to substantial changes in the ecology of this area. Thus, Acadia National Park is of special interest to those concerned with protecting habitats from invasive species.

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Previous research suggests that exotic ant species negatively impact native ant communities. The threat to ant diversity as a result of invasive species is considered second only to that of habitat destruction (Wilson 1992). With the prospect of continued expansion of *M. rubra* and subsequent displacement of native ant species through competition and predation, it is essential that we learn more about the ant fauna in Acadia National Park and on Mount Desert Island. Despite the demonstrated importance of Formicidae throughout terrestrial ecosystems, relatively little is known about the ant fauna of the park, and more specifically Maine. Our current understanding is garnered from a single manuscript published by Procter (1946), who conducted a fairly exhaustive survey between 1935 and 1945 on Mount Desert Island, ME, of areas that mostly lie within the current boundaries of Acadia National Park (Procter 1946). The objective of the current study was to characterize local patterns of ant diversity throughout various habitats and microhabitats in Acadia National Park, resulting in a comprehensive list of the ant species. Results from our study will provide a foundation for future research concerning the impact of *M. rubra* on native species, as well as a basis for various ecological studies and assessments.

Materials and Methods

Study Area. A survey of Formicidae was conducted between 18 and 22 June 2003 on Mount Desert Island, Acadia National Park, in the northeastern United States (44°21′N, 68°13′W). The park is characterized by several typical Maine coastal habitats, including upland and riparian deciduous forests, coniferous forests, and peatlands (Bank et al. 2006). We established and sampled ants along six transects in the park (Fig. 1). Transects were selected from a spatially referenced map, and each maximized habitat diversity from the following delineated habitats: riparian zones, pond and lake shorelines, wetlands, coniferous forest, deciduous forest, succession/old field, scrub/shrub, granitic high elevation rock outcrop, and coastal rock shoreline. Because preliminary studies suggested that *M. rubra* infestations were dramatically decreasing native ant diversity in affected areas, and this study was aimed at describing native ant diversity in the absence of *M. rubra*, efforts were made to select transects removed from known infested areas. Linear transects usually followed one of Acadia National Park's hiking trails and were typically set along an elevation gradient.

An attempt was made to provide equal sampling effort along each transect. Thirty-four volunteers were divided into survey teams consisting of five to seven individuals. To facilitate sampling, we divided equally the expertise in ant taxonomy and biology among teams by requesting all volunteers to self-rank themselves on a scale of 1–5. Each team had representatives of all expertise rankings and was assigned to a single transect. Collecting started at 10:00 a.m. and ended at 3:00 p.m., Eastern Standard Time (22 June).

Sampling Techniques. Our primary goal was to detect the majority of ant species at each site. In this survey, we employed four standard ant-collecting techniques, as recommended by Agosti et al. (2000). General collecting (visual search), litter samples, pitfall traps, and baits were used for cataloging ant biodiversity. A teaching laboratory in the Arts and Sciences Building, College of the Atlantic (Bar Harbor, ME), was used for sorting, initial identification, preservation, and preparation of museum vouchers.

One pitfall trap was dug into the following habitats: wetlands, coniferous forest, deciduous forest, succession/old field, and scrub/shrub habitat (three sites of each habitat, total traps = 15). Pitfall traps were constructed from white plastic, 1-lb cottage cheese containers (11.25 cm diameter × 7.5 cm deep) and embedded into the soil such that the lip of the container set flush with the soil surface. Traps were partially filled with a 50:50 mixture of water and propylene glycol, and deployed on 19 June and collected on 22 June. Trap contents were then transferred to 70% ethanol until identification.

Bait traps consisted of shaded 25 ml scintillation vials containing either a 1-cm^2 gauze soaked in a 25% sucrose solution or 1-cm^3 piece of drained, canned tuna fish. These baits are frequently used to explore ant community structure and represent carbohydrate and protein sources, respectively (Holloway 1999). Pairs of the baited vials were placed horizontally in each habitat and offered for approximately a 1-h period (22 June). Baits were collected, sealed with a screw top cap, and brought back to the laboratory for processing.

Leaf litter was also sampled along each transect in the deciduous and coniferous forest habitats. Litter was collected in three 1-m^2 quadrats using a hand rake. Samples were placed in black plastic trash bags, labeled, and then transported to the laboratory. In the laboratory, litter samples were divided and Berlese extractions were performed over a 24-h period.

Visual sampling was conducted by all volunteers in a team to supplement pitfall traps, baited traps, and litter sampling. On 22 June 2003, intensive visual surveys were conducted in all habitat types along each transect; ants were collected using either forceps or aspirators. When possible, a series of workers and gynes were collected to facilitate taxonomic determinations. Within each habitat, microhabitat (e.g., under a leaf, rock, within downed woody debris, or climbing on a tree branch) was recorded when an ant specimen(s) was collected. Ants were placed in vials containing 70% ethanol; appropriately labeled with transect, habitat, and microhabitat; and then brought to the laboratory for processing.

Representatives of all ant species collected were pinned and identified, with verifications provided by A. Francoeur (Université du Québec á Chicoutini, Quebec, Canada). Voucher specimens were deposited at the William Otis Sawtelle Collections and Research Center in Acadia National Park. Detailed maps, location data, and ant specimens are also archived at the park.

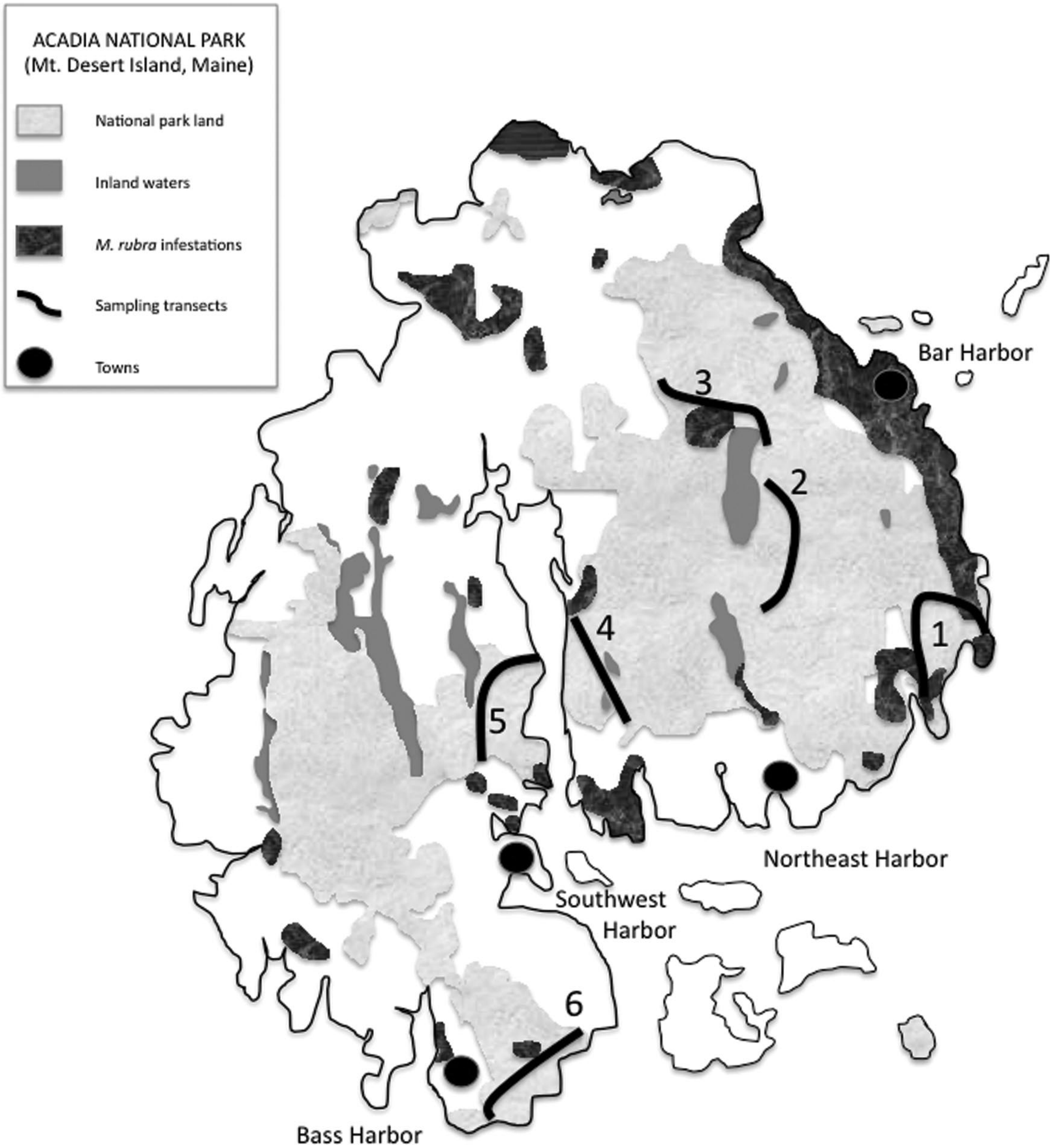

Fig. 1. Transects for ant biodiversity survey conducted in Acadia National Park. Heavy solid lines denote transects; bold numbers refer to transect numbers. Light gray areas demarcate National Park Lands, and black areas demarcate *M. rubra*-infested areas at the time of the "Ant Blitz."

Statistical Analysis. Data analysis was based upon summary statistics, linear correlation, and visual inspection of graphs of catch as a function of transect, habitat, microhabitat, and collection technique. Species richness (S) was the biodiversity metric of choice, because abundance was affected by the subjective decision of each volunteer as to the number of ants collected at a given location. To assess relative abundance and make determinations on which species are common in each habitat, we calculated the number of separate instances for which a species was recorded as the measure of occurrence. For each habitat, we applied the Pielou evenness (J′) to obtain statistics about the distribution of ant species. Linear correlation was used to examine the relationships between spatial distribution and habitat ubiquity; habitat ubiquity and species occurrences; species richness and microhabitats; microhabitats and habitats; and collection method and microhabitats. Nonmetric multidimensional scaling (Clarke 1993, McCune and Grace 2002) was used to qualitatively assess habitat and ant community associations. The software PC-ORD (McCune and Mefford 1999) was used for the ordination analysis relying upon the Sorensen distance metric with the autopilot option to select the dimensionality of the model.

Results

Species Diversity. We identified 42 ant species representing 15 genera and five subfamilies (Amblyoponinae, Dolichoderinae, Formicinae, Myrmicinae, and Ponerinae) during the 2003 survey of Acadia National Park (Table 1). Of those collected, 19 species were not reported on Mount Desert Island by Procter (1946) (Table 1). Of those previously unreported species, *Amblyopone pallipes* and *Dolichoderus mariae* represent new records for Maine (G.D.O., unpublished data). Of the 42 taxa analyzed, seven were recorded in all six transects and represented the most abundantly observed (independent collections) species. *Lasius alienus* was observed most often, with 54 recorded independent occurrences (Table 1). *Formica subsericea, Myrmica detritinodis, Camponotus herculeanus, Formica argentea, Formica aserva,* and *Tapinoma sessile* were recorded with ≥28 occurrences throughout all six transects (Table 1). *Lasius pallitarsis* was also present in all six transects; however, it only occurred 18 times throughout the survey, suggesting that this species is ubiquitous throughout the park, but in low abundance. Seven of the 42 species identified were spatially rare, being observed only once throughout the study (Table 1).

Of those species collected, 42 occurred during visual observation (Fig. 2). Tuna baits yielded 22 ant species, and all other collection methods, pitfalls, sugar bait, and litter samples, yielded 15 species or less (Fig. 2). Only visual observations and tuna baits yielded species that were not detected with at least one of the other sampling methods. Ten species were unique to visual sampling, and one to tuna baiting. Of these unique species, five were only detected in one sample. *A. pallipes* was recovered in a single tuna bait sample, and *Formica reflexa, Lasius minutus, Myrmica incompleta,* and *Stenamma diecki* were each detected in a single visual sample.

Habitat. Twelve habitat types were sampled throughout Acadia National Park. The greatest species richness (S) was observed in habitats designated rocky outcrop (S = 26), old field/meadow (S = 24), and wetlands (S = 25); moderate species richness was observed in deciduous forest (S = 16), coniferous forest (S = 11), scrub/shrub (S = 14), shoreline (S = 12), jack pine high elevation (S = 9), and high elevation scrub/shrub (S = 10), and the lowest species richness was observed in parking lot/roadside areas (S = 3), on rocky peninsulas (S = 4), and in heath and bog habitats (S = 4). Overall, the Pielou evenness values (J′) ranged from 0.294 to 0.799. The habitats with the greatest degree of evenness (not dominated by few or single species) were the rocky outcrop (J′ = 0.788), old field/meadow (J′ = 0.799), and wetlands (J′ = 0.759) habitats. The deciduous forest (J′ = 0.654), coniferous forest (J′ = 0.562), scrub/shrub (J′ = 0.637), shoreline (J′ = 0.604), jack pine high elevation (J′ = 0.545), and high-elevation scrub/shrub (J′ = 0.600) had moderate evenness, and the lowest diversity and more dominated communities were found in the parking lot/roadside (J′ = 0.294), rocky peninsula (J′ = 0.356), and heath-and-bog (J′ = 0.371) habitats.

To determine whether there were unique species/habitat associations, national multidimensional scaling (NMS) ordination of habitats and species was performed. A three-dimension solution was optimal with a final stress of 16.533 (considered adequate for ecological studies; Jongman et al. 1995). The variation explained by the three axes was 33.2, 23.2, and 12.8%, for axes 1–3, respectively. Therefore, axes 1 and 2 explained 56.4% of the total community variation. Axis 1 represents (as defined by habitat loadings) a gradient of forested/wetland habitats to road and rocky outcrop habitats. Axis 2 is characterized by disturbed temporary habitats, such as arid coastal and meadow grasslands transitioning into later succession scrub/shrub and then heath habitats on the other end of the axis. Fig. 3 shows ordination of the habitats and suggests that the ant community in Acadia National Park is using forests (coniferous and deciduous), wetlands, scrub/shrub habitats, meadows, rocky outcrops, and coastline habitats in a similar manner. The more unique habitats, as defined by the ant community, were revealed to be jack pine stands; disturbed habitats, such as road edges, heaths, and bogs; and rocky coastal narrow peninsulas.

Fig. 4 depicts the NMS ordination of the 42 ant species within habitat space. The top of the main cluster of ant species represents those that tend to be found in wetter habitats, such as *M. rubra* and *Lasius neoniger*, whereas the bottom of the cluster represents species that appear to be in drier conifer forest and meadow/old field specialists, such as *Myrmica americana, Tetramorium caespitum,* and *Formica exsectoides.* The center of the cluster tends to represent the more numerically dominant species. The cluster of five species (*D. mariae, Dolichoderus pustulatus, F. reflexa, L. minutus,* and *M. incompleta*) in the top left-hand corner of the ordination space depicts more spatially rare species that are associated with bogs, wetlands, and heath habitat. The lower left-hand part of the ordination is occupied by another spatially rare species collected in deciduous forests, *S. diecki.* The recent invading species, *M. rubra*, is in the center of the ordination cluster representing habitats that are used by most of the overall ant community, many of which are native species. This suggests that competition for resources, as *M. rubra* populations increase, will affect much of the existing ant community in Acadia National Park.

To facilitate comparisons of community structure, the most common three or four species (four species in cases in which two species were observed in equal numbers) in a habitat were recorded to determine whether certain species dominate a particular habitat (Table 1). The two most abundant species, *L. alienus* and *F. subsericea*, were each dominant throughout

Table 1. Annotated list of all ant species identified in Acadia National Park, distribution and dominance in sampled habitats

	Total No. occurrences	Deciduous Forest	Coniferous Forest	Wetland	Old field/ meadow	Scrub-shrub	Rocky outcrop	Shoreline	Jack pine-high elev.	High elev. Scrub-shrub	Parking Lot/ Roadside	Rocky peninsula	Heath and Bog
Amblyoponinae													
Amblyopone pallipes (Haldeman)[a,b]	1						X						
Dolichoderinae													
Dolichoderus mariae Forel[a,b]	2			X									**X**
Dolichoderus plagiatus (Mayr)	5						X	X	**X**				
Dolichoderus pustulatus Mayr[a]	13			**X**									**X**
Dolichoderus taschenbergi (Mayr)	7			X			X			X			
Tapinoma sessile (Say)	30	X	X	**X**	X		X	X	X	X			
Formicinae													
Brachymyrmex depilis Emery[a]	3				X		X						
Camponotus caryae (Fitch)[c]													
Camponotus herculeanus (Linn.)	32	X	X	X		**X**	X	**X**		**X**			
Camponotus noveboracensis (Fitch)	8			X	X	X	X						
Camponotus pennsylvanicus (De Geer)	19	**X**	**X**	X	X					X			
Formica argentea Wheeler[a]	29			X	X	X	X	**X**					
Formica aserva Forel	28		X	**X**	**X**		X			**X**			X
Formica cf. *fossaceps* Buren[a]	2						X						
Formica cf. *integra* Nylander[a]	3	X					X		X				
Formica exsectoides Forel[a]	4				X								
Formica fusca Linn.	1	X											
Formica lasioides (Emery)[a]	13			X	X	X	X			X	**X**	**X**	
Formica neogates Viereck[c]													
Formica neorufibarbis Emery[c]													
Formica obscuriventris Mayr[c]													
Formica reflexa Buren[a]	1			X									
Formica subsericea Say	40	X	X	X	**X**	X	X	**X**	**X**	X		**X**	**X**
Lasius alienus (Foerster)	54	**X**	**X**	X	X	**X**	**X**	X	**X**				
Lasius (Acanthomyops) claviger (Roger)[c]													
Lasius flavus (Fabricius)[a]	12	X	X		X	X	X						
Lasius (Acanthomyops) interjectus (Mayr)[c]													
Lasius minutus Emery[a]	1			X									
Lasius neoniger Emery	6			X	X			X			**X**		
Lasius pallitarsis (Provancher)	18	**X**	X	X	X	X						**X**	
Lasius subumbratus Viereck	6				X	X	X			X			
Lasius umbratus Nylander	5	X		X			X						
Myrmicinae													
Aphaenogaster rudis complex (cf. *picea* Wheeler)[a]	3	X			X	X							
Crematogaster cerasi Fitch[a]	14	X		X	X	X	**X**	X	X				
Crematogaster lineolata (Say)	11	X			X		**X**		X				
Leptothorax muscorum cmplx Nylander	7	X		X			X	X				**X**	
Myrmica americana Weber	4				X								
Myrmica detritinodis Emery	39	**X**	**X**	X	X	**X**	**X**				**X**		
Myrmica fracticornis Forel	10			X	X			X					
Myrmica incompleta Provancher	1			X									
Myrmica latrifrons Strcke[c]													
Myrmica rubra Linn.[a]	13			X		X	X	X					
Myrmica sabuleti Mein[c]													
Myrmica sculptilis Francoeur[a]	5			X			X		X	**X**			
Stenamma brevicorne (Mayr)	3				X		X						
Stenamma dieckiEmerya Emery[a]	1		X										
Temnothorax ambiguous (Emery)	1				X								
Temnothorax longispinosus (Roger)[a]	16	X	X	X		X	X	X	X	**X**			
Tetramorium caespitum (Linn.)[a]	4				X								
Ponerinae													
Ponera pennsylvanica Buckley	2				X		X						

[a]Not reported in 1946; new Acadia National Park record.
[b]Not reported in 1946; new Maine record.
[c]Reported in 1946; not found in 2003 survey.
Bold denotes dominant species.

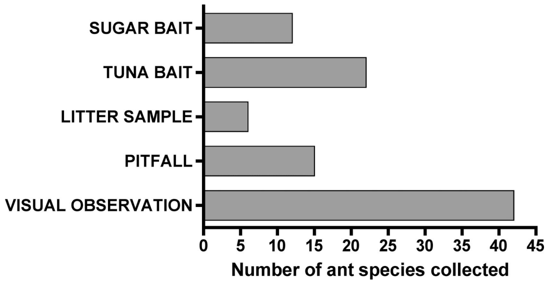

Fig. 2. Number of species collected with each collection method used during ant biodiversity survey conducted in Acadia National Park.

five habitats, yet the two species were codominant in only one shared habitat, jack pine high elevation (Table 1). *L. alienus* and *M. detritinodis* codominated throughout the deciduous and coniferous forest, scrub/shrub, and rocky outcrop habitats. Both *F. argentea* and *T. sessile* were dominant in a single habitat, yet they were among the most commonly observed species (Table 1).

A visual representation of diversity was provided for the two most species-rich habitats by graphing species occurrences (Fig. 5). Of the 42 species recorded in this survey, eight species were not collected in rocky outcrops or wetland habitats. Nineteen of the 35 species reported in these two habitats did not co-occur. Thirteen species varied in abundance between habitats,

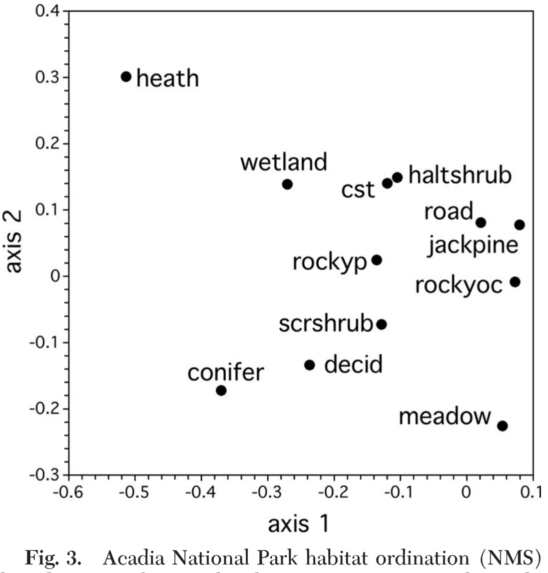

Fig. 3. Acadia National Park habitat ordination (NMS) based upon utilization by the ant community. Habitat abbreviations are for the habitats listed in Table 1: conifer = conifer forest, cst = shoreline, decid = deciduous forest, heath = heath and bog, haltshrub = high elevation scrub/shrub, jackpine = jack pine high elevation, meadow = old field/meadow, road = parking lot/roadside, rockyoc = rocky outcrop, rockyp = rocky peninsula, scrshrub = scrub/shrub. Details of ordination: percentage of variance explained and definition of axes are given in text.

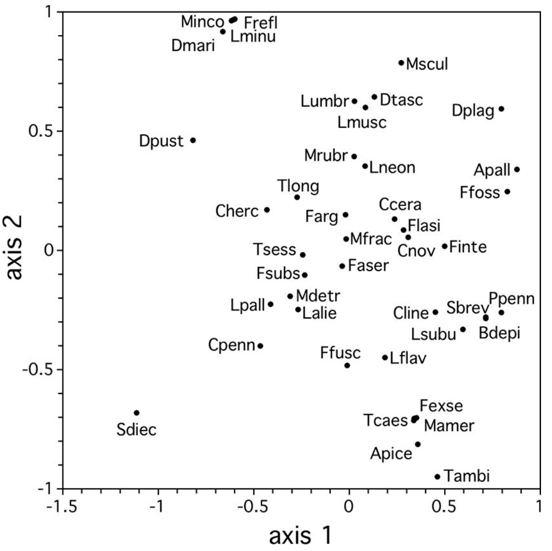

Fig. 4. Ant species ordination (NMS) based upon ant community structure within habitats. Species codes are comprised of the first letter of the genus (capitalized) and the first four to six letters of the species name. Details of ordination: percentage of variance explained and definition of axes are given in text.

whereas *Camponotus noveboracensis, Dolichoderus taschenbergi,* and *Myrmica sculptilis* were equally distributed throughout the two habitats.

Uniformity of spatial distribution across the entire landscape and habitat ubiquity was highly correlated ($r = +0.877$, $P < 0.0001$); thus, ant species associated with a higher number of transects (more distributed throughout the park) were also associated with a greater number of habitats. Habitat ubiquity was also highly correlated with the total number of occurrences (relative abundance) during the survey ($r = +0.873$, $P < 0.0001$). This might be expected, but does not always occur.

Ant species richness and occurrence were positively correlated in the 17 microhabitats identified ($r = +0.944$, $P < 0.0001$). The majority of species occurred under rocks and logs (Fig. 6), both of which often serve as nesting sites for ant colonies in this landscape. Other studies suggest that leaf litter sampling is a sufficient method to assess species richness (Fisher 1999, Ellison et al. 2007); however, the small number of ant occurrences in leaf litter (Fig. 6) most likely reflects the sample size of litter samples. In the current study, sampling effort was primarily focused on visual observation. The number of ant species collected in microhabitats and habitats was highly correlated ($r = +0.883$, $P < 0.0001$), demonstrating that the ant species that were abundant throughout many habitats were also abundant throughout many microhabitats within the habitats. The number of collection methods with which ant species were captured was also positively correlated with the number of microhabitats in which ant species were collected ($r = +0.755$, $P = 0.0001$).

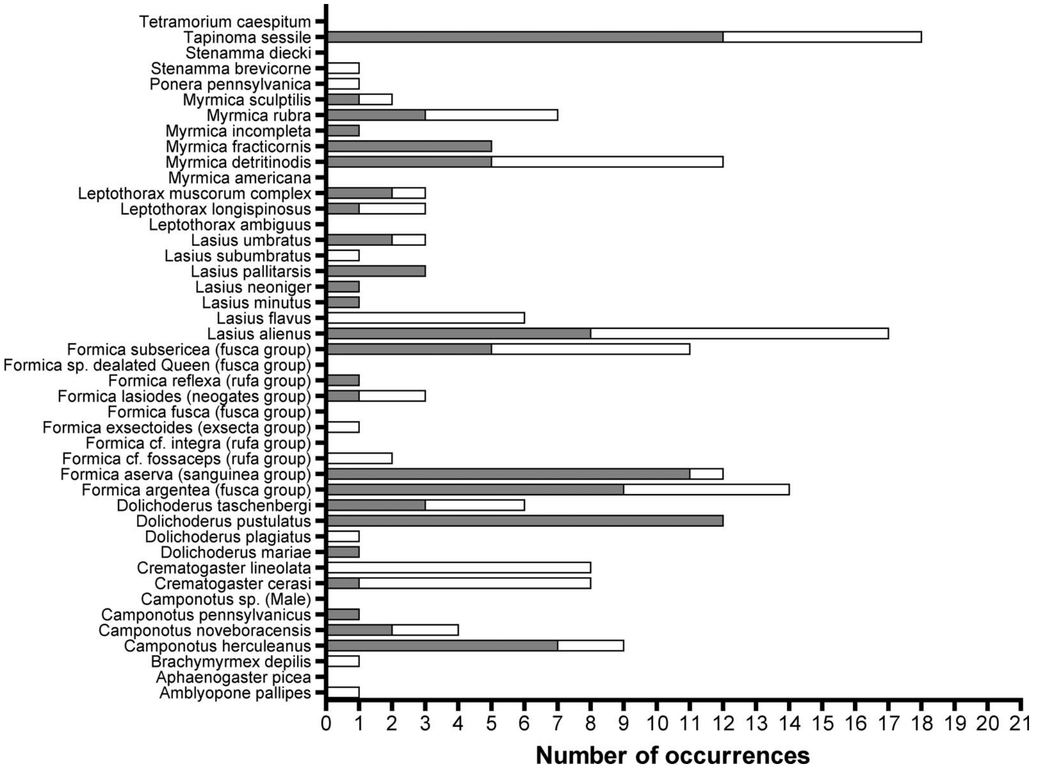

Fig. 5. Ant species richness in wetland (▩) and rocky outcrop (□) habitats in Acadia National Park.

Discussion

Biological diversity is declining worldwide, due chiefly to habitat destruction and impact from exotic and invasive species. As a result, efforts to document species composition are paramount for understanding fundamental temporal ecosystem changes. Vital to this effort are local faunal studies conducted over long periods of time. Studies have demonstrated that regional comparisons, derived from these local faunal lists, are important measures of biological diversity (Bartlett et al. 1999). Overall, our understanding of the Maine ant fauna, and more specifically the Acadia National Park fauna, is hampered by a paucity of biological surveys. Procter (1946) provided the most comprehensive species list as a result of his multiple year survey. However, since Procter's initial work, the influence of two important ecological factors has potentially altered the documented ant fauna: 1) in 1947, a forest fire burned ≈6,880 ha on Mount Desert Island, giving rise to major changes in the primary plant communities (Bank et al. 2006), and 2) the introduction and impact from the nonnative species *M. rubra* (Groden et al. 2005).

The species reported in this work probably represents the majority of ant species present in Acadia National Park. This richness estimate is based upon observed captures. King and Porter (2005), in a study of ant species richness in Florida, showed that estimates of observed richness were intermediate compared with estimates calculated with six different methods; thus, our estimate of richness might be considered a reasonable one, albeit less than estimates that take into account spatially rare species. Reassessment of Procter's collection of insects on Mount Desert Island indicates that Procter cataloged 32 modern species representing 11 genera and four subfamilies (Procter 1946) (G.D.O., unpublished data). Of those originally cataloged, we recorded 75% in the present survey (Table 1). Furthermore, from published records, 71% of all species previously identified throughout the state of Maine were collected during this survey (Wheeler 1908b, Wing 1939, Procter 1946, Gregg 1963) (G.D.O., unpublished data). We report in

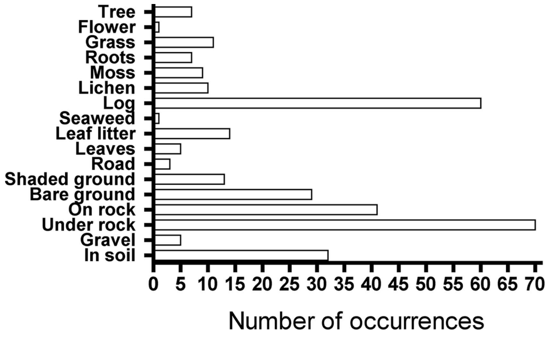

Fig. 6. Relative abundance of ant species throughout various microhabitats in Acadia National Park.

this study two new species records for Maine. The species, *A. pallipes* and *D. mariae,* were not previously recorded by Procter (1946) or during any other survey of the Maine ant fauna (Wheeler 1908b, Wing 1939) (G.D.O., unpublished data). From published records, these species exist as far north as Massachusetts (Wheeler 1906, Creighton 1950, Traniello 1982, MacKay 1993, Fisher 2002).

This survey was conducted in areas thought to be devoid of *M. rubra* to characterize ant diversity in the absence of this invasive species. Our results do confirm that there are many areas through Acadia National Park in which *M. rubra* does not yet occur. However, we did recover this ant in 14 occurrences in two transects. Whether its occurrence along these two transects represents the early stages of its spread into these areas or its inability to dominate at these sites is not known. *M. rubra* is a generalist in habitat preference and reported common throughout wooded habitats, lawns, and recreational parks (Garnas et al. 2007, Groden et al. 2005). This exotic species is competitively superior to native ants, presenting a great potential for it to dominate habitats (Garnas 2004). Where it has become established on Mount Desert Island, it has resulted in the local extirpation of the native ant fauna (Groden et al. 2005). It is therefore important to develop control methods before populations reach peak levels and cause irreversible damage to the native ant fauna. Thus, the data presented in this study will be useful when decisions are made concerning the impact of *M. rubra* on the current ant fauna throughout Acadia National Park.

Of interest was the recovery of another ant species introduced to North America from Europe, *T. caespitum,* in Acadia National Park. Although this species was introduced in the 1700s and is broadly distributed throughout North America, it is frequently identified as a pest in urban areas. However, in its native range it is considered a semixerophilous species commonly found in open habitats with dry soils (Radchenko et al. 1998). This species was recovered in dry, open meadow habitat in Acadia National Park, but was not a dominant species.

King and Porter (2005) stress the importance of sampling a variety of macro- and microhabitats within a landscape. Our results indicate the most common species recorded in this survey show varying preferences for both open habitats and specialized sheltered microhabitats. The habitats in which these species were most abundant do not necessarily reflect the documented general habitats. *M. detritinodis* and *C. herculeanus* are reported common throughout Maine in strip-clearcut and dense spruce-fir forest habitats, often nesting within rotting conifer logs and stumps (Krombein et al. 1979, Jennings et al. 1986, Lough 1997, Fisher 2002). In support of these reports, we observed *M. detritinodis* was common throughout forested areas under rocks, whereas *C. herculeanus* was collected primarily along the shoreline under rotting logs. We found the ants *L. alienus* and *T. sessile* equally common in rotting logs and stumps, as well as under stones. Likewise, Krombein et al. (1979) reported similar microhabitat preferences for these species. Wheeler and Wheeler (1963) also report locating nests of *T. sessile* in boggy or swampy areas and along the coast; thus, this species' prevalence throughout Acadia National Park wetlands does not come as a surprising result.

The three most common *Formica* species in this survey were all recorded in sheltered microhabitats. *F. subsericea* and *F. argentea* often nest in soil, under stones, rocks, wood, or leaf litter; however, they show a general habitat preference for open deciduous woodlands (Krombein 1979). We found that both were common species along the shoreline, with *F. subsericea* also occurring throughout old field and meadow habitats. *F. aserva* is reported common throughout open, sunny habitats and is considered a generalist species (Fisher 2002, Lafleur et al. 2006). During our study, this species was most commonly collected in old field and meadow habitats, as well as wetland and bog areas. We found logs and rocks were the two microhabitats in which the greatest number of ants occurred (Fig. 6). These results are not surprising because four of the seven most abundant species were recorded within these microhabitats.

A comparison of the collecting techniques shows that the vast majority of species and all but one of the unique species were collected by the general collecting/visual search method (Fig. 2). Similar findings have been reported in other studies. Ellison et al. (2007) surveyed the ant assemblage in temperate hardwood forests in New York using pitfall traps, sieved litter, hand collecting, and two types of baits. In their study, 94% of the species were collected by litter sampling and hand collections combined; thus, the authors suggest these collection methods are sufficient to determine species richness in northern temperate forests (Ellison et al. 2007). Our results are in line with those reported by Ellison et al. (2007). The general collecting method (visual search) is synonymous to the hand collection technique used by Ellison et al. (2007), and in this study, we report that 95% of species in Acadia National Park were collected using this technique. In contrast, litter samples were the least successful collection method in our survey, with only 14% of species collected in these samples (Fig. 2). Because subterranean species would primarily be observed through litter samples, it is possible that the present survey may have underestimated the number of subterranean species throughout the park. Thus, the fact that low numbers of subterranean species were collected may not be truly indicative of their rarity. However, in contrast with our study, King and Porter (2005) in Florida showed that hand collecting was the least efficient method for estimating an index of combined abundance and richness, whereas baiting was the most efficient sampling method. It should be noted that in our study, with the number of volunteers involved and the high level of expertise in myrmecology of several individuals, considerably more effort was allocated to visual search relative to other sampling methods. Any future research on ant communities in the park should include an increased number of litter samples to provide a confident estimate of subterranean species.

Sixty-two years after William Procter's initial survey, this study reflects renewed interest in understanding the biological diversity on Mount Desert Island and specifically Acadia National Park. The results presented above are the first comprehensive published listing of ants in this area since Procter (1946). Although it is possible that subterranean species were not fully represented in this survey, all other data suggest that the current study represents a comprehensive base on which future ant biodiversity studies can build. Overall, this compilation provides insight into the ecological processes that are occurring throughout the park, a baseline for examining the species richness, and a fundamental step in understanding the important role of the Formicidae throughout Acadia National Park and all the surrounding environs.

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