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DIVERSITY AND ABUNDANCE OF ANTS AT FOREST EDGES

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DIVERSITY AND ABUNDANCE OF ANTS AT FOREST EDGES
IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

A Dissertation
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy
Entomology

by
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Accepted by:
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ABSTRACT

Fragmented habitats are a common result of human activities that involve the clearing of native vegetation for various land uses. Habitat fragmentation has two primary and inseparable components: habitat loss and insularization. Landscape-level connectivity in fragmented habitats is diminished for many species, and edge characteristics become more important as the edge-to-interior ratio increases. The study of the effects of edges on biodiversity has compelled ecologists to study them for over a century and has influenced the design and management of natural preserves. Invasion of habitats by non-native species is a phenomenon that coincides with the increased human activity typical of fragmented habitats. Biological invasions are second only to habitat loss in terms of effects on native biota and synergistically compound the impacts of habitat fragmentation. The primary goal of this research was to describe the effects of habitat boundaries between undisturbed forests and artificially maintained grasslands on ant communities. A secondary goal was to ecologically assess the invasive potential of *Pachycondyla chinensis* (Emery), a little-studied adventive species in North America.

Ant communities were sampled across the forest-grassland habitat boundary in the Great Smoky Mountains National Park (GSMNP), North Carolina and Tennessee, USA. Different ant communities were found on either side of this boundary. The native forest-ant community is intact within 15 m of edge zones. Twenty-seven significant indicator species were identified within four

distinct ant assemblages. Ecotonal effects were observed only in forests when individual species abundance was compared at different distances into undisturbed forest habitat. Analysis of variance revealed differential abundance, with respect to habitat boundaries, of significant indicator species in both grassland and forest habitats. Differences in rarely collected species as visualized with rank abundance plots, occurred in the forest only. Total species richness was greatest near edge zones in both forest and grassland habitats. However, within-habitat ecotonal effects were not found in analysis of averaged, per sample species richness or diversity across distances from edges. Analysis of averaged per sample ant abundance revealed an ecotonal effect in the grassland where values increased with distance from the forest edge. Several biotic and abiotic habitat characteristics were identified that correspond with patterns in habitats and ant distributions. These characteristics have not been causally linked with trends in ant communities and should be interpreted as starting points for future hypothesis testing.

Pachycondyla chinensis (Emery), native to southeastern Asia, was detected in the United States more than 70 years ago. Basic knowledge regarding the biology and ecology of this species is lacking, especially in its expanded range in North America. This work documents the first collection of *P. chinensis* within the forests of GSMNP. In South Carolina, USA, habitats were surveyed, colonies were excavated, and ant communities were sampled along transects to determine the nest characteristics and formicid-community ecology of *P. chinensis*. Colonies of *P. chinensis* were found just beneath the soil under stones, logs, and stumps, and ranged in size from thirty-nine to several thousand individuals, most with multiple dealated females per nest. In forest

habitats sampled in South Carolina, *P. chinensis* is a dominant ant in the community in terms of abundance and frequency. *Pachycondyla chinensis* and *Paratrechina faisonensis* (Forel), the two ants with the highest relative importance values and similar nesting habits, had a significant negative association. *Pachycondyla chinensis* was not found in open-field habitats. Although *P. chinensis* is not well established in GSMNP, the forests are similar, in terms of ant assemblage composition, to heavily infested forests in South Carolina. The future establishment of dense populations of *P. chinensis* within the GSMNP is likely. Following a substantial lag phase since the original introduction to North America, *P. chinensis* has become well established in urban habitats, where it reaches high population densities and is a true invasive species able to dominate naturally forested habitats. The known range of the species is summarized from published and unpublished sources, with significant range expansion noted in the United States and unpublished records from the Australasian and Oriental zoogeographic regions.

To validate sampling techniques for ground-foraging ants in temperate North America, capture data were compared for Winkler litter extraction and pitfall trapping at three periods in the calendar year. Sampling was conducted in the forests and grasslands of GSMNP. Individual species were biased towards capture with both collection techniques, and as expected their combined use generated more comprehensive species lists than did the use of either technique alone. These findings agree with literature, citing Winkler litter extraction and pitfall trapping as complementary techniques. However, ecological studies often use a single collection technique due to resource limitations. In forest habitats, Winkler litter extraction is recommended if a single technique will be

used. The majority of species showing bias in forests were captured more frequently with Winkler litter extraction across all subsample sizes. However, *Camponotus* species, an ecologically important genus, were biased towards pitfall trapping. In grassland habitats, an equal number of species showing bias was divided between sampling techniques. Pitfall trapping captured more total species in the grassland. However, at small sample sizes (< 40), Winkler litter extraction performed better. Additionally, species of Ponerinae were biased towards Winkler litter extraction in both forest and grassland habitats. Seasonal sampling revealed that the majority of species were captured in July-August versus December-January or March-April and that the reduced species assemblages of the latter two pairs were perfectly nested subsets of summer sampling with one exception. *Stenamamma meridionale* Smith was not present in July-August sampling and had peak frequency in December-January.

DEDICATION

This work is dedicated to my wife, friends, and colleagues who have made these years the best of my life.

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TABLE OF CONTENTS

	Page
TITLE PAGE	i
ABSTRACT	ii
DEDICATION	vi
ACKNOWLEDGMENTS	vii
LIST OF TABLES	xiv
LIST OF FIGURES	xvii
INTRODUCTION	1
Goal 1	3
Goal 2	4
Goal 3	5
CHAPTER	
1. LITERATURE REVIEW	6
Mountain Ants of Southeastern North America	6
Formicid Diversity of the Great Smoky Mountains National Park	8
Ants and Ecosystems	19
The Influence of Habitat Characteristics on Formicid Communities	27
Nesting Sites	34
Anthropogenic Disturbance of Forests in the Great Smoky Mountains National Park	37
The Ecology of Invasive species.....	38
The Ecology of Habitat Fragmentation.....	41
Community Ecology Statistics: Special Techniques	47

Table of Contents (continued)

	Page
2. THE GROUND FORAGING ANT FAUNA AT HABITAT BOUNDARIES BETWEEN GRASSLANDS AND ADJACENT FORESTS IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK	49
Introduction.....	49
Materials and Methods.....	52
Results.....	59
Discussion.....	80
Summary	84
3. <i>Pachycondyla chinensis</i> (Emery): A POTENTIALLY INVASIVE SPECIES IN THE SOUTH EASTERN UNITED STATES THAT THREATENS THE GREAT SMOKY MOUNTAINS NATIONAL PARK	86
Introduction.....	86
Materials and Methods.....	89
Results.....	93
Discussion.....	112
Summary	119
4. THE EFFECT OF TECHNIQUE, SEASONALITY, AND HABITAT ON THE SAMPLING OF ANT COMMUNITIES IN THE FOREST AND GRASSLAND HABITATS OF THE GREAT SMOKY MOUNTIANS NATIONAL PARK	121
Introduction.....	121
Materials and Methods.....	123
Results.....	126
Discussion.....	141
Summary	144

Table of Contents (continued)

	Page
5. SUMMARY AND DISCUSSION	146
Ecotonal Effects in Ant Communities at Forest Edges in Temperate North America	146
Evaluation of <i>Pachycondyla chinensis</i> (Emery) as an Invasive Threat in the GSMNP	147
Verification of Sampling Techniques	148
Discussion	149
LITERATURE CITED	146

LIST OF TABLES

Table		Page
1-1.	Ants known to inhabit the Great Smoky Mountains National Park and the surrounding region in North Carolina and Tennessee.....	10
1-2.	Formicid Biodiversity in Some Vegetation Types of the Great Smoky Mountains National Park (From Cole 1940).....	33
1-3.	Dominant Ant Species in Some Vegetation Types of the Great Smoky Mountains National Park (From Cole 1940).....	34
2-1.	Percent of total species richness captured as determined by comparison of richness predicted with the Incidence-Based Coverage Estimator (ICE) to observed values. The Great Smoky Mountains National Park: Cades Cove, Cataloochee, and Oconoluftee. July-August, 2003-2004.....	62
2-2.	Species richness and distribution within habitats, controls, and distances from edge. The Great Smoky Mountains National Park: Cades Cove, Cataloochee, and Oconoluftee. July-August, 2003-2004.....	63
2-3.	Mean values (\pm standard error) of habitat characteristics differentiating forest and grassland habitats, and showing ecotonal effects in forest and grassland habitats. Values within the same row that share the same letter are not significantly different (ANOVA, $\alpha = 0.05$). The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.....	78

List of Tables (Continued)

Table	Page
2-4. Habitat characteristics and tree species significantly related to individual ant species presence or absence as revealed with multiple logistic regression analysis. Only characteristics significant at the 0.05 α level or 0.10 α level (*) are included. All ant species are both significant indicator species and how ecotonal effects within forest or grassland habitats. A “-“ sign in the effect column indicates a negative coefficient in the multiple logistic regression model. A “+” sign indicates a positive coefficient. The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.....	81
3-1. World distribution of <i>Pachycondyla chinensis</i> organized via biogeographical realms and countries (states given for the USA).....	99
3-2. Colony characterization: <i>Pachycondyla chinensis</i> collected in Clemson, Pickens County, South Carolina, USA (2005-2006). Excavated colonies arranged in descending order of number of workers. ¹ Nest dimension variables: L = length, W = width, D = depth.....	102
3-3. Forest ant species from pitfall and leaf litter samples in order of ranked relative importance values.....	104
3-4. Non-metric Multidimensional Scaling: Stress in Relation to Dimensionality (Number of Axes).....	109
4-1. Comparison of pitfall and Winkler litter extraction techniques in field and forest habitats, the Great smoky Mountains National Park, July-August, 2003-2004.....	134
4-2. Mean abundance, diversity, species richness and evenness (per/station) in field and forest habitats as captured with pitfall trapping and Winkler litter extraction in the Great Smoky Mountains National Park July-August, 2003-2004.....	138

List of Tables (Continued)

Table	Page
4-3. Seasonal species richness of communities in a tri-annual sampling regime; the Great Smoky Mountains National Park, 2003-2004.....	141

LIST OF FIGURES

Figure	Page
2-1. Major artificially-maintained grasslands in the Great Smoky Mountains National Park, 2003-2004.....	56
2-2. Layout of a transition transect crossing the sharp edge between forest and grassland habitats.....	57
2-3. Ant abundance, species richness, and diversity averaged within habitats, distance from the edge, and control plots. Standard error bars indicate average standard error for the category (abundance, richness, or diversity). Means within the same category that share the same letter are not significantly different as determined with ANOVA ($\alpha = 0.05$). The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.....	67
2-4. Comparison of general trends in average richness per station and total richness within grassland and forest habitats at different distances from the edge and in control plots. The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.....	68
2-5. Tree pruning with indicator species analysis. A. Averaged P-values of indicator value significance level, at all cluster levels. B. Number of significant indicator species ($p \leq 0.05$) for each level of clustering. Minimum average p-value and maximum significant number of indicator species were both reached at the three cluster level.....	70
2-6. Dendrogram from agglomerative hierarchical cluster analysis of locations in species space (Sørensen distance metric). Symbols indicate groups formed by pruning the dendrogram at the three cluster level (see “/” marks) with multiple iterations of indicator species analysis. CC = Cades Cove, Cat = Cataloochee, Oco = Oconoluftee; Forest = forest control, Grass = grassland control; + distances = forest samples in transitional series, - distances = grassland samples in transitional series. The Great Smoky Mountains National Park. 2003-2004.....	71

List of Figures (Continued).

Figure	Page
2-7. Partial (3-cluster level) indicator species hierarchy showing all terminal and higher level groups from the pruned dendrogram (figure 3). Only statistically significant ($\alpha = 0.05$) indicator species of ground foraging ants are shown. The numbers for each species represents the percent of perfect indication (IV) in each subgroup. The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.....	72
2-8. Individual ant species response to distances from edge and control plots in forest and grassland habitats. Only species with significant responses as determined with ANOVA on abundance ($\alpha = 0.05$) are shown. Differential abundances within habitats and between controls, 45 m, and 15 m from the edge are indicated by diagonal lines with arrows. In example, <i>Pyramica rostrata</i> showed a decrease in abundance when the average at 45 m in the forest was compared with the average abundance in the forest control. No species showed a decreased abundance in the grassland control compared with grassland 45 m from the edge (first category). The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.....	74
2-9. Rank-abundance plots within grassland A. and forest B. habitats at controls, 45 m from the edge, and 15 m from the edge. The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.	76
3-1. Lateral view of posterior abdomen of <i>Pachycondyla chinensis</i> , collected in Clemson, South Carolina, USA, emphasizing the stinger. Scale bar = 0.2 mm.....	91
3-2. World distribution of <i>Pachycondyla chinensis</i>	99

List of Figures (Continued).

Figure	Page
3-3. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant’s Grove (<i>Pachycondyla chinensis</i> invaded site). Each point is a two dimensional representation of ant species composition at each sampling station. Stations that are close together in ordination space are more similar than those that are far apart.	109
3-4. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant’s Grove (<i>Pachycondyla chinensis</i> invaded site). Each point is a two dimensional representation of ant species composition at each sampling station. Stations that are close together in ordination space are more similar than those that are far apart. Abundance of <i>Pachycondyla chinensis</i> at each site is represented by the area of each symbol.	110
3-5. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant’s Grove (<i>Pachycondyla chinensis</i> invaded site). Each point is a two dimensional representation of ant species composition at sampling stations. Stations that are close together in ordination space are more similar than those that are far apart. Abundance of <i>Aphaenogaster rudis</i> complex at each site is represented by the area of each symbol.	111
3-6. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant’s Grove (<i>Pachycondyla chinensis</i> invaded site). Each point is a two dimensional representation of ant species composition at sampling stations. Stations that are close together in ordination space are more similar than those that are far apart. Relative abundance of <i>Myrmecina americana</i> at each site is represented by the area of each symbol.	112

List of Figures (Continued).

Figure	Page
3-7. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant’s Grove (<i>Pachycondyla chinensis</i> invaded site). Each point is a two dimensional representation of ant species composition at each sampling station. Stations that are close together in ordination space are more similar than those that are far apart. Relative abundance of <i>Paratrechina faisonensis</i> at each site is represented by the area of each symbol.....	113
3-8. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant’s Grove (<i>Pachycondyla chinensis</i> invaded site). Each point is a two dimensional representation of ant species composition at each sampling station. Stations that are close together in ordination space are more similar than those that are far apart. Relative abundance of <i>Ponera pennsylvanica</i> at each site is represented by the area of each symbol.....	114
4-1. Species accumulation curve for forest (A) and field (B) habitats. The curves were produced by repeated ($n = 500$) subsampling of the data for each possible subsample size and illustrate the effectiveness (accumulated species richness) of different methods: pitfall, Winkler, and a combination of both methods.	131
4- 2. Sørensen ecological distance curve for forest (A) and field (B) habitats. The curves were produced by repeated ($n = 500$) subsampling of the data for each possible subsample size and illustrate the effectiveness (community stability) of different methods: pitfall, Winkler, and a combination of both methods.	132

INTRODUCTION

Globally, the loss of native habitat is the principal contributing factor in the reduction of species diversity (Wilson 1992). Following primary habitat loss, enduring native habitats often remain as noncontiguous, relatively small tracts or fragments. Fragmentation disrupts ecosystems, causes the further decline of habitat, accelerates species loss (Saunders et al. 1991), and increases the likelihood of adventive species (sensu Frank and McCoy 1990) invasions (Hobbs and Huenneke 1992). Biological invasions, second only to habitat loss in terms of effects on native biota (Wilson 1992), have become commonplace due to the synergistic effects of ever-increasing human commerce and habitat fragmentation. The influence of edge effects, the size of remnant fragments, and the nature of native and invasive species determine the ability of undisturbed habitat reserves to support native species.

The theory of island biogeography (MacArthur and Wilson 1967) was applied to the problem of fragmentation (Diamond 1975) and the debate over single large or several small (SLOSS) reserves continues to be debated after more than three decades (Fischer and Lindenmayer 2005, Higgins et al. 2006 among others). As the size of remnant habitat patches is decreased, the ratio of edge-to-interior habitat increases, making the effects of edges more important (Ranney et al. 1981). On a biogeographic scale, these effects have been widely discussed whereas the physical changes that occur locally at edge zones have been under studied (Saunders et al. 1991). Appreciating forest edge effects at a microhabitat scale is central to understanding how fragments differ from continuous habitat in terms of community structure and ecosystem processes.

The Great Smoky Mountains National Park (GSMNP) is a sizable preserve with 207,199 protected hectares. Although areas affected by edges can be found within the Park, the forests are generally free from other types of disturbance such as logging and urbanization. The artificially maintained grasslands within the Park's boundaries and the naturally vegetated forests that surround them present the opportunity to study the ecology of forest edges in the southern Appalachians without the added complexity of otherwise developed areas.

The Formicidae are well suited as a focal taxon for the study of edge effects in the GSMNP. Ants are easily sampled and doing so does not disrupt or otherwise damage ecosystems. Ant diversity in the Park is ample (approximately 100 expected species) but not enormous and the taxonomy of ants is quasi-stable (Bolton 1995). Studies concerned with species diversity and distribution in temperate regions benefit from the variability of species found in differing habitats without being burdened by the difficult identifications associated with immense species richness in tropical ants. In addition, many ant species occupy highly specific microhabitats where feeding niches are likely saturated (Holldöbler and Wilson 1990). Niche saturation allows for detailed resolution of fine-scale habitat heterogeneity, making ants an ideal indicator taxon in studies designed to uncover subtle changes in habitat and biodiversity. As a keystone taxon (LaSalle and Gauld 1993), change in ant community properties are likely to reflect ecosystem-level changes. Ants are ecologically important as dominant consumers in multiple trophic levels, are responsible for large amounts of energy turnover in ecosystems, alter the chemical and physical properties of the soil, disperse fungi and plants, represent a large

portion of the biomass, and subsequently are a significant source of food for other organisms.

The effect that habitat boundaries between anthropogenically maintained grasslands and native forests have on microhabitat and ant species in the southern Appalachians is unknown. Studying edge effects and non-native species that threaten biodiversity might give land managers insight into the future stresses that this and other natural reserves will endure as native habitat outside and adjacent to protected lands is fragmented by development and resource use. Region-specific information of this type is invaluable, as theoretical generalizations do not always reflect local trends and their application does not necessarily lead to the most effective conservation strategy (Fischer and Lindenmayer 2005).

The overarching goal of this research is to better understand the properties of the ant community across the transition from undisturbed forest to disturbed grassland. A secondary and related goal is to ecologically assess the invasive potential of *Pachycondyla chinensis* (Emery), an adventive ant species native to Southeast Asia, that was discovered in the Park during the preliminary stages of this study. Specifically the goals and subsequent hypotheses of this research are the following:

Goal 1. Determine the distribution of all epigeic ant species across the habitat boundary between artificially maintained grasslands and forests to determine if the ant assemblage is influenced by edges.

Hypothesis: Ant-species assemblages in forests and grasslands are significantly different, with detectable boundaries and ecotonal effects.

Hypothesis: Individual ant species have significant indicator value within assemblages across the habitat boundary between forests and grasslands.

Hypothesis: Ant ecotonal effects can be predicted with biotic and abiotic habitat characteristics.

Rationale: Understanding edge influences on ant diversity will provide land managers in the southern Appalachians with information directly applicable to the SLOSS (single large or several small) debate by providing data useful in determining the size of reserve tracts that are able to support forest and grassland species. Defining representative ant species that are indicators of overall ant community properties might simplify sampling in management assessment studies and expedite land-use decision making. Identifying habitat characteristics associated with edge effects in ant species distributions is the first step in understanding the ultimate causes of ecotones and might define edge characteristics within a potentially manageable set of parameters.

Goal 2. Evaluate, within a formicid community context, the potential of *P. chinensis* as an invader of GSMNP.

Hypothesis: *Pachycondyla chinensis* is an invasive species with the ability to penetrate naturally vegetated forests in the southeastern United States where it becomes a dominant species.

Rationale: This work will increase knowledge of a little-known adventive species that was discovered at a forest edge in the Park. The species is not well

established in the Park at this time and understanding the potential and impacts of this species as an invader will be of interest to land managers.

Goal 3. Evaluate the effectiveness of Winkler litter extraction and pitfall trapping as complementary ant-sampling techniques in grassland and forest habitats in a tri-annual sampling schedule in GSMNP.

Hypothesis: Winkler litter extraction and pitfall trapping will differentially capture individual species comprising the ground-foraging ant community, and are as a result, complementary techniques.

Hypothesis: Summer sampling will capture the majority of the ground-dwelling ant species with respect to other seasons.

Rationale: Year-round sampling with multiple techniques increases labor efforts in ecological studies. In the literature, Winkler litter sifting and pitfall trapping have been considered complementary techniques and summer-only sampling has been generally accepted. Behavioral and seasonal differences might make certain species more likely to be captured with one collection technique over another at different times of the year. My work will elucidate community and individual species trends with respect to sampling technique and seasonality of sampling.

CHAPTER I

LITERATURE REVIEW

Mountain Ants of Southeastern North America

Natural History

The Appalachian Mountains were born of sedimentary rock, compressed by powerful tectonic movements in the Paleozoic Era, about 300 million years ago. These mountains predate the first formicids, which do not appear until the early Cretaceous, approximately 100 million years later. The fossil record reveals a few species of the ancestral subfamily Sphecomyrminae that were widespread during the middle to late Cretaceous across the northern hemisphere in what was then the supercontinent Laurasia (Wheeler 1917, Holldöbler and Wilson 1990). Sometime before the end of the Cretaceous Period, about 65 million years ago, adaptive radiation led to the evolution of most of our modern subfamilies, which are well represented in the fossil record of the Eocene Epoch (Burnham 1978, Grimaldi and Agosti 2000). Eastern North America appears to have been an important secondary center of evolutionary radiation because, with the exception of a number of Neotropical and Holarctic species, it is a unique region with many precinctive formicid species (Wheeler 1917, Cole 1940). Species of *Aphaenogaster*, *Formica*, *Leptothorax*, and *Myrmica* are examples that appear to have originated in the southeastern United States (Cole 1940). Many of these species are mountain inhabiting. The Appalachian Mountains and the relatively heterogeneous habitat they afford must have played an important role in the formicid adaptive radiation of the Cretaceous.

The Great Smoky Mountains National Park (GSMNP) located in the southern Appalachian Mountains of Eastern North America is home to many species endemic to this region as well as others that are more widespread. Mountainous regions with their high degree of relief and varied habitats have been recognized as areas with increased biodiversity in the Formicidae (Bruhl et al. 1999). This is especially true in the GSMNP where the elevation ranges from 475 to 2024 meters. The altitudinal gradient combined with the medial location of the GSMNP creates an interesting combination of formicids from both northern and southern elements of the Eastern North American fauna.

Species that are typically more northern or boreal in distribution can be found at higher elevations in the southern Appalachians (Dennis 1938, Cole 1940, Cole 1953, Carter 1962b, Van Pelt 1963). Populations of these species located as far south as GSMNP usually exist as diminutive southern extensions of vast and continuous northern populations. Additionally, the non-boreal ant fauna is to a large extent reduced or eliminated between the elevations of 610 m and 1524 m in the southern Blue Ridge Province (Van Pelt 1963). In the GSMNP, elevations above 1524 m are considered part of the Canadian zone based on the fauna and flora on these mountain tops (Cole 1940, Whittaker 1956). For example, the formicid genera *Myrmecina*, *Myrmica*, *Stenammina*, and some species of *Formica* and *Lasius* are psychrophilic and boreal in distribution, with many species and expansive ranges in the northern United States and Canada (Cole 1940, Van Pelt 1963). In the South, they have only moved into habitats that are similar to the cold and moist environment typical of the North. The higher altitudes of GSMNP

experience frequent heavy fog, abundant rainfall, and relatively low average temperatures and are ideal habitat for these species.

Conversely, the temperature range of the lower altitudes in GSMNP is more typical of conditions in the surrounding southern United States and is reflected by the fauna and flora found there (Dennis 1938, Cole 1940, Carter 1962a, Carter 1962b). Genera such as *Dorymyrmex*, *Forelius*, *Nievamymex*, *Strumigenys*, *Trachymymex* and some species of *Leptothorax* are relatively thermophilic and southern in distribution. Species from these genera can be found on the lower slopes and in the valleys of the Park.

Formicid Diversity of the Great Smoky Mountains National Park

A number of local checklists, surveys, and ecological studies contribute to our knowledge of the formicid species that have been found in GSMNP, as well as species that could potentially occur in the Park and are now known from the surrounding areas in North Carolina, Tennessee, and the transition and boreal zones of eastern North America. The following list of taxa has been compiled from these sources (Table 1-1) and the subsequent discussion details their individual contributions. In total, this list comprises six subfamilies, 38 genera, 192 species and 17 subspecies. Although many of these taxa will never be found in the mountainous region of the park, this list was compiled to provide a thorough understanding of the formicid diversity of the general area. New records for the park will no doubt come from this list which served as an important aid in identification during the course of this study.

The list (Table 1-1) is arranged in alphabetical order by subfamily to facilitate use. No phylogenetic relationships are implied. The taxonomy has been updated as per Bolton (1995). Locality information has been reduced to North Carolina, Tennessee, or GSMNP. More detailed collection information is in the original publications which have been included in the table.

Table 1-1. Ants known to inhabit the Great Smoky Mountains National Park and the surrounding region in North Carolina and Tennessee

Genus species/subspecies	Locality¹	Citation²
Sub-family DOLICHODERINAE		
<i>Dolichoderus mariae</i> Forel	NC, TN, GSMNP	1,3,5,6,7
<i>Dolichoderus plagiatus</i> (Mayr)	NC, TN, GSMNP	5,7,8
<i>Dolichoderus pustulatus</i> Mayr	NC	1,3,6,7,8
<i>Dolichoderus taschenbergi</i> (Mayr)	NC, TN, GSMNP	1,3,4,5,6,7,8
<i>Dorymyrmex flavus</i> McCook	NC	1,3
<i>Dorymyrmex pyramicus</i> (Roger)	NC, TN, GSMNP	3,4,5,6,7
<i>Forelius pruinus</i> (Roger)	NC, TN, GSMNP	3,4,5,6,7
<i>Linepithema humile</i> (Mayr)	NC	3,7
<i>Tapinoma sessile</i> (Say)	NC, TN, GSMNP	1,2,3,4,5,6,7,8
Sub-family ECITONINAE		
<i>Nievamyrmex carolinensis</i> (Emery)	NC, TN, GSMNP	1,4,5,6,7
<i>Nievamyrmex nigrescens</i> (Cresson)	NC, TN, GSMNP	1,4,5,7
<i>Nievamyrmex opacithorax</i> (Emery)	NC	1,6,7
Sub-family FORMICINAE		
<i>Acanthomyops claviger</i> (Roger)	NC, TN, GSMNP	1,2,3,4,5,6,7,8
<i>Acanthomyops interjectus</i> (Mayr)	NC, TN, GSMNP	2,3,4,5,6,7
<i>Acanthomyops latipes</i> (Walsh)	NC	2,3,7
<i>Acanthomyops murphyi</i> (Forel)	NC	1,2,3,6,7
<i>Acanthomyops subglaber</i> (Emery)	NC, TN, GSMNP	2,3,5,7,8
<i>Brachymyrmex depillis</i> Emery	NC, TN, GSMNP	1,3,4,5,6,7

Table 1-1. (continued)Ants known to inhabit the Great Smoky Mountains National Park and the surrounding region in North Carolina and Tennessee

Genus species/subspecies	Locality¹	Citation²
<i>Camponotus americanus</i> Mayr	NC,TN,GSMNP	1,2,3,4,5,6,7
<i>Camponotus caryae caryae</i> (Fitch)	TN	2,4
<i>Camponotus castaneus</i> (Latrielle)	NC,TN,GSMNP	2,4,5,6,7,8
<i>Camponotus chromaiodes</i> (Fabricius)	NC,TN,GSMNP	2,3,4,5,6,7
<i>Camponotus clarithorax</i> Creighton		2
<i>Camponotus decipiens</i> Emery	NC,TN	2,3,4,6,7
<i>Camponotus discolor</i> (Buckley)		2
<i>Camponotus floridanus</i> (Buckley)	NC	3,7
<i>Camponotus herculeanus</i> (Linnaeus)		2
<i>Camponotus impressus</i> (Roger)		2
<i>Camponotus mississippiensis</i> M.R. Smith	NC,TN	3,4,6,7
<i>Camponotus nearticus</i> Emery	NC,TN,GSMNP	2,3,5,6,7,8
<i>Camponotus noveboracensis</i> (Fitch)		2
<i>Camponotus pennsylvanicus</i> (De Geer)	NC,TN,GSMNP	1,2,3,4,5,6,7,8
<i>Camponotus pylartes fraxinicola</i> M.R. Smith	NC	3,6,7
<i>Camponotus pylartes pylartes</i> W. M. Wheeler	NC	7
<i>Camponotus snellingi</i> Snelling	NC,TN	3,4
<i>Camponotus socius</i> Roger	NC	3,7
<i>Camponotus subbarbatus</i> Emery	NC	2,3,6,7
<i>Lasius alienus</i> (Foerster)	NC,TN,GSMNP	1,2,3,4,5,6,7,8
<i>Lasius flavus</i> (Fabricius)	NC,TN,GSMNP	1,2,3,5,6,7,8
<i>Lasius minutus</i> Emery		2
<i>Lasius nearticus</i> W. M. Wheeler	NC,TN,GSMNP	2,3,5,7,8
<i>Lasius neoniger</i> Emery	NC,TN,GSMNP	1,2,3,4,5,6,7,8
<i>Lasius pallitarsis</i> (Provancher)	NC	2,3,7,8
<i>Lasius speculiventris</i> Emery	TN, GSMNP	2,5
<i>Lasius subumbratus</i> Viereck		2
<i>Lasius umbratus</i> (Nylander)	NC,TN,GSMNP	1,2,3,4,5,6,7,8
<i>Paratrechina parvula</i> (Mayr)	NC,TN,GSMNP	1,3,4,5,6,7,8
<i>Paratrechina longicornis</i> (Latreille)	NC	3,7
<i>Prenolepis imparis</i> (Say)	NC,TN,GSMNP	1,2,3,4,5,6,7,8
<i>Formica adamsi</i> Wheeler		2
<i>Formica argentea</i> Wheeler		2
<i>Formica dakotensis</i> Emery		2
<i>Formica difficilis</i> Emery	NC,TN,GSMNP	1,2,3,5,6,7,8

Table 1-1. (continued)Ants known to inhabit the Great Smoky Mountains National Park and the surrounding region in North Carolina and Tennessee

Genus species/subspecies	Locality¹	Citation²
<i>Formica exsectoides</i> Forel	NC,TN,GSMNP	1,2,3,5,7
<i>Formica ferocula</i> Wheeler		2
<i>Formica fusca</i> Linnaeus	NC,TN,GSMNP	3,5,6,7,8
<i>Formica impexa</i> Wheeler		2
<i>Formica integra</i> Nylander	NC	1,2,3,7,8
<i>Formica lasioides</i> Emery		2
<i>Formica montana</i> Wheeler		2
<i>Formica morsei</i> Wheeler		2
<i>Formica neogagates</i> Emery	NC	1,2,3,7,8
<i>Formica nepticula</i> Wheeler		2
<i>Formica neurofibarbis</i> Wheeler		2
<i>Formica nitidiventris</i> Emery	NC,TN,GSMNP	1,2,3,4,5,7,8
<i>Formica obscuripes</i> Forel		2
<i>Formica obscuriventris obscuriventris</i> Mayr	NC	2,8
<i>Formica pallidefulva</i> Latreille	NC,TN,GSMNP	2,3,4,5,6,7
<i>Formica pergandei</i> Emery		2
<i>Formica puberlua</i> Emery		2
<i>Formica querquetulana</i> Kennedy and Dennis	NC	8
<i>Formica rubicunda</i> Emery	NC,TN,GSMNP	1,2,3,4,5,7
<i>Formica schaufussi dolosa</i> W.M. Wheeler	NC,TN,GSMNP	2,3,4,5
<i>Formica schaufussi schaufussi</i> Mayr	NC,TN,GSMNP	1,2,3,4,5,6,7,8
<i>Formica scitula</i> Wheeler		2
<i>Formica subaenescens</i> Emery	NC,TN	2,3,4
<i>Formica subintegra</i> Emery	NC,TN,GSMNP	2,3,4,5,6,7,8
<i>Formica subsericea</i> Say	NC,TN	1,2,3,4
<i>Formica ulkei</i> Emery		2
<i>Formica vinculans</i> Wheeler		2
<i>Polyergus breviceps</i> Emery		2
<i>Polyergus lucidus longicornis</i> M.R.Smith	NC	1,2,3,6,7
Sub-family MYRMECINAE		
<i>Aphaenogaster ashmeadi</i> Emery	NC	3,7
<i>Aphaenogaster flemingi</i> M.R. Smith	NC	3,7
<i>Aphaenogaster floridana</i> M. R. Smith	NC	3,7

Table 1-1. (continued) Ants known to inhabit the Great Smoky Mountains National Park and the surrounding region in North Carolina and Tennessee

Genus species/subspecies	Locality¹	Citation²
<i>Aphaenogaster fulva</i> Roger	NC, TN, GSMNP	1,3,4,5,6,7,8
<i>Aphaenogaster lamellidens</i> Mayr	NC, TN, GSMNP	1,2,3,4,5,6,7
<i>Aphaenogaster mariae</i> Forel	NC	3,6,7
<i>Aphaenogaster picea picea</i> Emery	NC, TN, GSMNP	1,2,3,4,5,7,8
<i>Aphaenogaster picea rudis</i> Emery	NC, TN, GSMNP	1,2,3,4,5,6,7,8
<i>Aphaenogaster tennesseensis</i> (Mayr)	NC, TN, GSMNP	1,2,3,4,5,6,7,8
<i>Aphaenogaster texana carolinensis</i> W. M. Wheeler	NC, TN, GSMNP	2,3,4,5,6,7
<i>Aphaenogaster texana texana</i> (Emery)	NC, TN, GSMNP	5,7
<i>Aphaenogaster treatae</i> Forel	NC, TN, GSMNP	1,2,3,4,5,6,7,8
<i>Crematogaster ashmeadi</i> Mayr	NC, TN, GSMNP	3,5,6,7,8
<i>Crematogaster atkinsoni</i> W.M. Wheeler	NC	3,7
<i>Crematogaster cerasi</i> (Fitch)	NC, TN	3,4,6,7,8
<i>Crematogaster laeviscula</i> Mayr	NC, TN	1,3,4,6,7
<i>Crematogaster lineolata</i> (Say)	NC, TN, GSMNP	1,3,4,5,6,7,8
<i>Crematogaster minutissima minutissima</i> Mayr	NC	3,6,7
<i>Crematogaster minutissima missouriensis</i> Pergande	TN, GSMNP	4,5
<i>Crematogaster pilosa</i> Emery	NC	3,6,7
<i>Crematogaster punctulata</i> Emery	NC, TN	3,4,6,7
<i>Crematogaster vermiculata</i> Emery	NC	3,6,7
<i>Formicoxenus hirticornis</i> (Emery)		2
<i>Formicoxenus provancheri</i> (Emery)		2
<i>Leptothorax ambiguus</i> Emery		2
<i>Leptothorax curvispinosus</i> Mayr	NC, TN, GSMNP	2,3,4,5,6,7
<i>Leptothorax longispinosus</i> Roger	NC, TN, GSMNP	2,3,4,5,6,7
<i>Leptothorax muscorum</i> Nylander		2
<i>Leptothorax pergandei</i> Emery	NC, TN, GSMNP	1,3,4,5,6,7,8
<i>Leptothorax schaumii</i> Roger	NC, TN, GSMNP	2,3,5,6,7
<i>Leptothorax smithi</i> M.R. Smith	NC, TN, GSMNP	3,5,7
<i>Leptothorax texanus</i> W.M. Wheeler	NC	3,6,7
<i>Leptothorax texanus davisii</i> W.M. Wheeler	NC	2,3,7
<i>Leptothorax tuscaloosae</i> Wilson	NC	3,6,7
<i>Monomorium minimum</i> (Buckley)	NC, TN, GSMNP	1,2,3,4,5,7,8

Table 1-1. (continued) Ants known to inhabit the Great Smoky Mountains National Park and the surrounding region in North Carolina and Tennessee

Genus species/subspecies	Locality¹	Citation²
<i>Monomorium pharaonis</i> (Linnaeus)	NC, TN	3,4,6,7
<i>Myrmecina americana</i> Emery	NC, TN, MNP	1,2,3,4,5,6,7
<i>Myrmica americana</i> Weber	NC	3,6,7,8
<i>Myrmica fracticornis</i> Emery	NC, TN, GSMNP	2,3,4,5,7
<i>Myrmica incompleta</i> Provancher	NC, TN	1,2,3,4,7
<i>Myrmica latifrons</i> Starcke	NC	2,3,6,7,8
<i>Myrmica pinetorum</i> W.M. Wheeler	NC, TN	2,3,4,6,7,8
<i>Myrmica punctiventris</i> Roger	NC, TN, GSMNP	2,3,5,6,7,8
<i>Myrmica rubra</i> Linnaeus		2
<i>Myrmica sabuleti</i> Meinert	TN	4
<i>Myrmica scabrinodis</i> Nylander	NC	2,3
<i>Pheidole anastasii</i> Emery	NC	3,7
<i>Pheidole bahia</i> (Forel)	NC	3
<i>Pheidole bicarinata vinelandica</i> Forel	NC, TN, GSMNP	1,3,4,5,6,7,8
<i>Pheidole crassicornis</i> Emery	NC, TN, GSMNP	1,3,4,5,6,7
<i>Pheidole davisii</i> W.M. Wheeler	NC	3,7
<i>Pheidole dentata</i> Mayr	NC, TN, GSMNP	1,3,4,5,6,7
<i>Pheidole denticula</i> M.R. Smith	NC, TN, GSMNP	3,5,7
<i>Pheidole floridana</i> Emery	NC	3,7
<i>Pheidole guineensis</i> (Forel)	NC	3,7
<i>Pheidole metallescens</i> Emery	NC	3,7
<i>Pheidole morrisii</i> Forel	NC, TN, GSMNP	1,3,4,5,6,7
<i>Pheidole pilifera</i> Roger	NC	1,3,7
<i>Pheidole tysoni</i> Forel	NC, TN, GSMNP	1,3,4,5,6,7
<i>Pogonomyrmex badius</i> (Latrielle)	NC	1,3,7
<i>Protomognathus americanus</i> (Emery)	NC, TN, GSMNP	1,3,4,5,6,7
<i>Smithistruma bimarginata</i> (L.G. and R.G. Wesson)	NC	3,7
<i>Smithistruma carolinensis</i> Brown	NC	3,7
<i>Smithistruma clypeata</i> (Roger)	NC, TN, GSMNP	1,3,4,5,6,7
<i>Smithistruma creightoni</i> (M.R. Smith)	NC, TN, GSMNP	3,4,5,6,7
<i>Smithistruma dietrichi</i> (M.R. Smith)	NC	3,7
<i>Smithistruma filirrhina</i> Brown	NC	3,7
<i>Smithistruma laevinasis</i> (M.R. Smith)	NC	3,6,7
<i>Smithistruma missouriensis</i> (M.R. Smith)	NC	3,6,7

Table 1-1. (continued)Ants known to inhabit the Great Smoky Mountains National Park and the surrounding region in North Carolina and Tennessee

Genus species/subspecies	Locality¹	Citation²
<i>Smithistruma ohioensis</i> (Kennedy and Schramm)	NC,TN,GSMNP	3,5,6,7
<i>Smithistruma ornata</i> (Mayr)	NC,TN,GSMNP	3,5,6,7
<i>Smithistruma pergandei</i> (Emery)	NC	3,6,7
<i>Smithistruma pilinasis</i> (Forel)	NC	3,6,7
<i>Smithistruma pulchella</i> (Emery)	NC,TN, MNP	3,4,5,6,7
<i>Smithistruma reflexa</i> (L.G. and R.G. Wesson)	NC,TN,GSMNP	3,5,7
<i>Smithistruma rostrata</i> (Emery)	NC,TN,GSMNP	3,4,5,6,7
<i>Smithistruma talpa</i> (Weber)	NC,TN, MNP	3,5,6,7
<i>Solenopsis carolinensis</i> Forel	NC	1,3,7
<i>Solenopsis globularia littoralis</i> Creighton	NC	3,7
<i>Solenopsis molesta molesta</i> (Say)	NC,TN,GSMNP	2,3,4,5,6,7,8
<i>Solenopsis pergandei</i> Forel	NC	1,3,7
<i>Solenopsis picta</i> Emery	NC	3,7
<i>Solenopsis richteri</i> Forel	NC	3,7
<i>Solenopsis texana</i> Emery	NC	7
<i>Solenopsis truncorum</i> Forel	NC	1,3,7
<i>Solenopsis xyloni</i> McCook	NC	3,7
<i>Stenamma brevicorne</i> (Mayr)	NC	1,2,3
<i>Stenamma carolinense</i> M.R. Smith	NC	3,7
<i>Stenamma diecki</i> Emery	NC,TN,GSMNP	2,3,4,5,7,8
<i>Stenamma impar</i> Forel	NC	2,3,7,8
<i>Stenamma meridionale</i> M.R. Smith	NC	3,6,7
<i>Stenamma schmittii</i> W.M.Wheeler	NC	2,3,6,7,8
<i>Strumigeyns louisianae</i> Roger	NC,TN	3,4,6,7
<i>Strumigenys dietrichi</i> (M.R. Smith)	TN	4
<i>Tetramorium caespitum</i> (Linnaeus)	NC	3,6,7
<i>Trachymyrmex septentrionalis</i> (McCook)	NC,TN,GSMNP	1,3,4,5,6,7
Sub-family PONERINAE		
<i>Amblyopone pallipes</i> (Haldeman)	NC,TN,GSMNP	1,4,5,6,7,8
<i>Amblyopone trigonignatha</i> W.L. Brown	NC	7
<i>Cryptopone gilva</i> (Roger)	NC,TN,GSMNP	3,4,5,6,7
<i>Discothyrea testacea</i> Roger	NC	3,6,7
<i>Hypoponera opacior</i> (Forel)	NC, TN	4,5,6,7
<i>Pachycondyla chinensis</i> (Emery)	NC	7

Table 1-1. (continued)Ants known to inhabit the Great Smoky Mountains National Park and the surrounding region in North Carolina and Tennessee

Genus species/subspecies	Locality¹	Citation²
<i>Ponera exotica</i> M.R. Smith	NC	3,7
<i>Ponera pennsylvanica</i> Buckley	NC,TN,GSMNP	1,4,5,6,7,8
<i>Proceratium croceum</i> (Roger)	NC,TN,GSMNP	3,5,6,7
<i>Proceratium melinum</i> (Roger)	NC	1
<i>Proceratium pergandei</i> (Emery)	NC,TN,GSMNP	3,4,5,6,7
<i>Proceratium silaceum</i> Roger	NC,TN,GSMNP	3,4,5,6,7
Sub-family PSEUDOMYRMECINAE		
<i>Pseudomyrmex brunneus</i> (F.Smith)	NC	7
<i>Pseudomyrmex pallidus</i> (F.Smith)	NC	3,7

¹Abbreviations: GSMNP- Great Smoky Mountains National Park, NC- North Carolina, TN- Tennessee; ²Authors: 1- Wheeler 1904, 2- Wheeler 1917, 3- Wray 1976, 4- Dennis 1938, 5- Cole 1940, 6 Carter 1962a, 7- Carter 1962b, 8- Van Pelt 1963

The ants of this region were first studied by Auguste Forel who visited North Carolina in 1899. He made general observations and published on the habits of North American ants (Forel 1901).

The first annotated list of species from North Carolina was assembled by William Morton Wheeler (1904). This list was partially based on the findings of Forel (1901). However, the majority of the records were new from collections taken in Black Mountain by William Beutenmuller and from near the Piedmont town of Belmont by P.J. Schmitt. After the omission of synonyms and unrecognizable forms, this original list comprised 26 genera, 56 species and two subspecies (Table 1-1).

Later, Wheeler (1917) looked specifically at the mountain-inhabiting Formicidae of western North America. He examined existing collections and made several expeditions to the western states. At the time, there was still little known about the distribution of mountain-inhabiting ants of the East. However, the available information

was assembled in a table under the heading Eastern Transition and Boreal Zones.

Although many of these species have not been found in the Park to date, ants of these zones were thought to be likely inhabitants of the eastern mountains. When the taxonomy of this list is updated, it comprises 17 genera, 89 species, and five subspecies (Table 1-1).

Brimley (1938) published a list of the insects of North Carolina. The list was a summary of the catalog of the Division of Entomology of the North Carolina Department of Agriculture. The list included records from publications and a physical collection of specimens contributed primarily by Brimley. After taking taxonomic changes into account, there were 31 genera, 84 species, and six subspecies of ants known from North Carolina in 1938. This list was revised three times (Brimley 1942, Wray 1950, 1976) as more species were included. By 1976 the original list had been lengthened to include 37 genera, 172 species, and 11 subspecies (Wray 1976). Only this final version of the checklist is included in Table 1-1.

Clyde A. Dennis collected ants in Tennessee for five years. He produced a checklist for the state, described the distribution of the ants he found, summarized the known range of each species, and included brief notes on ecology (Dennis 1938). Although he focused mainly on the central to western portion of the state, some records from the eastern or Highland Province were taken. Of special interest are collections made by C. H. Kennedy in GSMNP and the species reported from 610-1524 meters and from above 1524 meters. When updated, this list comprises 28 genera, 72 species, and four subspecies (Table 1-1).

In 1939, A. C. Cole conducted the first and only published survey of the ants of the GSMNP and he published a guide to the species he discovered (Cole 1940). Due to time constraints, he was able to collect only from the Tennessee side of the Park. The guide includes a checklist of species, provides keys to their identification, describes nesting habits, and discusses the distribution of ants in different vegetation types and elevations. A supplementary checklist (Cole 1953) was published at a later date to reflect the major taxonomic changes of Creighton (1950) and Brown (1948, 1949) and to include new records discovered since his original survey. When current synonyms are considered and this list is further revised it comprises 28 genera, 76 species, and three subspecies (Table 1-1).

William G. Carter (1962a, b) surveyed the ants of North Carolina. In the first of these publications (Carter 1962a), he dealt exclusively with the ants of the North Carolina Piedmont. Species were collected from pitfall traps and Berlese samples. This was the first time collection methods of this type had been used on a large scale in this part of the country and the result was an extensive checklist that when updated includes 32 genera, 92 species, and five subspecies (Table 1-1). Relative abundance of species was estimated for 13 vegetation types and based on 5,102 collections and observations made over a 20 month period. Additionally, (Carter 1962a) discussed the nesting habits and seasonal surface activity of many of the species he found.

In a second publication, Carter (1962b) used the same groundbreaking collecting techniques to study the distribution of species across the entire state. In addition to the piedmont plateau, he included the mountain region and the coastal plain which he further

divided into the fall-line sandhills and the coastal area. An informative table indicates the presence of each species known from North Carolina in the three physiographic regions. Additionally, an annotated list comprised of 37 genera, 145 species, and nine subspecies (Table 1-1) was provided that includes a detailed distribution of each species in the state and notes on their ecology. By comparing multiple physiographic regions, this publication permits a more detailed understanding of the distribution of species in the southeastern United States in general. Specifically, 91 contemporary species are known to inhabit the mountains. Of these, only 14 are limited to this region, 11 are found in both the mountains and the piedmont plateau, and six are found in both the mountains and the coastal plain. The vast majority of these species (60) are widespread and inhabit all three of the physiographic regions in North Carolina.

Van Pelt (1963) looked specifically at the distribution of ants at high altitudes in the southern Blue Ridge Mountains of the eastern United States. Over a seven-year period, a large portion of the segment of the Blue Ridge Province south of Roanoke, Virginia, and above 1067, meters was sampled by hand collecting. The nesting habits of each species were categorized and the effects of forest type and percentage canopy were discussed. A checklist was provided that specified the relative abundance of species in seven altitudinal categories. With increasing altitude, a general pattern of reduction in both the number of ant species and in total colony abundance was described.

Remarkably, very few species- *Aphaenogaster rudis* complex (Enzman), *Crematogaster ashmeadi* Mayr, *Formica subsericea* Say, *Lasius neoniger* Emery, and *Tapinoma sessile* (Say) - were collected above 2012 meters. In total, after the consideration of synonymy,

23 genera, 63 species, and five subspecies were collected above 1067 meters in the southern Blue Ridge Province (Table 1-1).

According to Dennis (1938) and Cole (1940), 5 subfamilies, 28 genera, and 75 species have been found in GSMNP. Currently, 154 species are known from North Carolina and 89 are known from Tennessee. Tennessee, with only two checklists of the ants of this region, is largely under collected in comparison to North Carolina. Although the coastal area of North Carolina is habitat to some species that will more than likely not be found in Tennessee, this huge discrepancy in species richness is probably a result of sampling effort. The GSMNP with its relatively small area has been well sampled on the Tennessee side (Cole 1940). Carter (1962b) reported 91 species from the mountains of North Carolina, and Van Pelt's (1963) survey of high altitude ants from North Carolina added no new records. All indications suggest that the number of ant species in the GSMNP will not increase tremendously with additional sampling.

Ants and Ecosystems

The social organization of ants allows great efficiency in creating nests, gathering resources, and adapting to local conditions. This efficiency has led to the evolution of ants as insect dominants in many environments. In biomass, the ants are rivaled in the insect world only by another social group, the termites (Holldöbler and Wilson 1990). In a Brazilian rainforest, ants and termites alone make up three-fourths of the total insect biomass and outweigh all land vertebrates by approximately four times (Fittkau and Klinge 1973). Although the tropical rainforest might be an extreme example, this percentage is not thought to be unreasonable for many terrestrial biomes. Ants, with their

countless numbers and relentless efficiency, play a vital role in ecosystems and make significant impacts as they maintain nests, gather resources, and reproduce.

Nesting

Ant nests are generally made from materials that are readily available in a given habitat. The ants' capacity to occupy many different niches is enhanced by the plasticity of nest construction as it is adapted to differing conditions and availability of building materials (Rogers 1972, Wheeler and Wheeler 1983, Klotz 1986). The architecture of these nests is nearly as varied as the species that construct them, but they all serve the same fundamental purpose. The nest functions as a regulator of microhabitat conditions, a place where food is stored or cultivated, and protects the queen and her brood. The reproductive female's ability to remain in the nest, where she is protected, is a product of social life and has decreased by great extent the extrinsic mortality of queens (Petal 1978, Keller and Genoud 1997). Fecundity in the ants increases with age to an extent because a mature nest often takes years to construct, populate, and begin producing reproductives. The decrease in the extrinsic mortality rate combined with an age-dependent increase in fecundity has led to the evolution of an over-100-fold increase in lifespan of female reproductive ants when compared to solitary insects of the same size (Keller and Genoud 1997).

Some nests are permanent and might persist for up to 40 years, as in those of the desert species *Myrmecosystus mexicanus* Wesamel (Chew 1987), whereas others such as the Ecitoninae army ants construct temporary bivouac nests that are typically occupied for less than one day (Schneirla 1971). The construction and inhabitation of ant nests

alters the surrounding environs and collectively have broad-reaching effects on terrestrial ecosystems. Perhaps the most important effect, with regard to other species, is the alteration of soil. Both the physical and chemical properties of soil are modified by ant nests. These changes can be long lasting and have profound effects on physical attributes of the substrate, the distribution of nutrients, and plant growth in a local habitat (Oinonen 1956, Beattie and Culver 1977, Petal 1978, Briese 1982, Levan and Stone 1983, Holldöbler and Wilson 1990, Breen and O'Brien 1994, Wang et. al. 1995).

Physical Alteration of the Soil

Physical soil properties modified by ants pertain to the density and distribution of soil particles. In the role of soil movers, ants act primarily as aerators. The ant community of a saltbrush habitat moves 350-420 kg of soil/ha/yr (Briese 1982). As galleries and tunnels are excavated and inhabited by ants, smaller particles are moved to the surface, compacted materials are broken apart, and organic materials are taken below the surface. The common species *Formica fusca* Linnaeus excavates channels that reach at least 1.5 m below the surface in an old field in New York. This mound-building species homogenizes stratified soil profiles and alters surface soil texture (Levan and Stone 1983). The net result of this activity is a decrease in density of the soil containing and adjacent to the nest. *Pogonomyrmex occidentalis* nesting in sandy loam soil decreased the density from 1.54 to 1.47g per m² (Rogers 1972). The network of galleries and tunnels and the loosely piled mound allow water to more easily permeate greater soil depths. Less water is lost to runoff and the soil that makes up the mound is well drained. In addition to decreasing density and increasing porosity, the transport of organic material

below the substrate surface also increases the water-holding capacity of the soil dramatically (Petal 1978, Levan and Stone 1983). Changes in physical soil properties are most likely to affect plant growth by increasing the availability of water and allowing plant roots to penetrate more deeply into dense soils or even rock (Oinonen 1956).

Chemical Alteration of the Soil

Chemical modifications are associated with the organic remains of plants and animals that have been brought into the nest where they subsequently decompose and become mixed with the mineral elements of soil. Additionally, the remains of dead ants are often buried in the mound excavate or deposited on the surface near the entrance. This accumulation of organic debris is correlated with an increase in the bacteria and fungi responsible for the continued breakdown of these materials. In most cases, ants likely are directly responsible for the increase in bacteria and fungi through the active or passive mechanical transfer of these biological agents from one nest to another. This is especially distinct in the well-known leafcutter and fungus-growing ants that participate in a true mutualistic relationship with specific species of hyphae-producing fungi. With ants providing biological agents of decay, organic material, and the appropriate conditions, the typical ant nest becomes a crucible of intense organic decomposition. The reconstitution of these elements affects the pH and nutrient concentration of the soil. Although the mechanism is yet unknown, ants might have the ability to regulate the pH of their nest environment (Petal 1978, Levan and Stone 1983). The pH of nest soil decreases in alkaline soils, increases in acidic soils, and does not change in neutral soils. Changes in pH might persist for 10-20 years (Levan and Stone 1983). Most importantly, the nesting

site becomes an area with increased levels of potassium, carbon, and nitrogen (Briese 1982, Levan and Stone 1983, Holldöbler and Wilson 1990, Breen and O'Brien 1994). The potassium and phosphorous compounds that come from the organic decomposition that occurs in ant nests is easily absorbed by plants. The elevated concentrations of nutrient compounds can persist for more than two years after ants have left the mound (Petal 1978). The resulting heterogeneous distribution of resources leads to patches of plant species that colonize active and abandoned nesting sites (Beattie and Culver 1977, Briese 1982, Levan and Stone 1983, Breen and O'Brien 1994).

Ants as Consumers

The collection of food is an undertaking that ants pursue through energy-efficient strategies. As ant populations have responded to the variability of costs and benefits in space and time, both choice of food type and behavioral foraging strategies have evolved considerable diversity (Bernstein 1975, Traniello 1989). Many species have become highly specialized, sometimes developing mutualisms with other arthropods and plants, while others have remained catholic and opportunistic in their feeding habits.

At the community level, ants are omnivores. As herbivores, predators, and scavengers, they operate in, and obtain energy from multiple trophic levels. Their massive biomass coupled with their social adaptations in foraging and food storage allows them to exploit resources to an extent exceeding most other animals. This was demonstrated in an old field habitat in South Carolina (Golley and Gentry 1964). In populations of *Pogonomyrmex badius* (Latrielle), energy flow was estimated at 58-75 kJ per m²; this surpassed that of both the sparrow population at 17 KJ per m² and the mouse

population at 31 KJ per m² at that site. However, energy flowing through ant populations and their nests is not assimilated efficiently (Petal 1978). Organic materials brought back to the nest are quickly mineralized and lost to ant use as they enrich the surrounding soil. This loss or inefficiency reprocesses nutrients at an increased rate, quickly making them available to other organisms in the ecosystem. The large volume and high turnover rate of energy flowing through their populations make ants vital nutrient recyclers in terrestrial ecosystems.

As predators and mutualists, ants have profound effects on other consumers as well as primary producers. In the Blue Mountains of Oregon, a single supercolony of *Formica obscuripes* Forel needs an estimated 470 kg (dry weight of food) to maintain its current worker population. This amount is 11 times the dry weight of western spruce budworm that might occupy this forest during an outbreak of this defoliator (McIver et al. 1997). Wood ants, *Formica aquilonia* Yarrow, reduced defoliation through predation in white birch by 34% in ant-foraged trees versus ant-excluded controls (Karhu 1998). Additionally, forest stands with large populations of thatching ants experience less defoliation than those without (Laine and Niemela 1980). Such locations might serve as refuges during severe outbreaks of defoliating insects.

In the pine forests of southern Finland, *Formica* spp. related to the *aquilonia* complex, form large semi-permanent mounds and foraging trails, visiting the same food sources year after year. They tend aphids that feed on the pines, as well as defend the trees from other predators. A debate on the overall effect of these ants on pines is ongoing. However, trees visited most often by these ants show a decrease in annual

growth and lose an estimated 708g of sugar as homopteran honeydew (dry mass) per year to the ants alone (Rosengren and Sundstrom 1991). The tritrophic interactions involving ants as consumers, shape the community structure of these ecosystems to a measurable extent.

Ants dominate tropical rainforest canopies, comprising up to 94% of arthropods in fogging samples and 86% of the biomass of the samples (Davidson et al. 2003). Nitrogen isotope ratios of plants, known herbivores, arthropod predators, and ants reveal many ant species obtain little nitrogen from scavenging and predation. These species feed principally as “herbivores” of plant and insect exudates, and that microsymbionts of ants and their homopteran trophobionts play a key role in nutrition. Leigh and Windsor (1996) suggest that tropical-forest plant resources lost to insect herbivory are much greater than previously estimated, 0.8 tons/ha/year, and that ants are a major consumer in these canopies.

Seed dispersal is a byproduct of ant herbivory. Beattie and Culver (1981) demonstrated that myrmecochory is a major factor in forest herbaceous communities. Myrmecochorus species produce diaspores consisting of a seed and an elaisome. The elaisome is an ant-attracting food body attached to the seed coat. This nutrient rich meal is exchanged for transportation, as diaspores are often carried back to the nest where the undamaged seeds are typically left in abandoned galleries or buried in the excavate outside the nest (Culver and Beattie 1978). Seed relocation is advantageous because the ant nest provides protection from seed predators, a nutrient-rich environment, and an area free from competition with non-myrmecochores (Beattie and Culver 1981).

Subsequently, ant-dispersed species are rather abundant and comprise a large proportion of herbaceous diversity and abundance (Handel 1976). Up to an estimated 70% of the flora of mesic forests in the temperate regions of the world might be myrmecochores (Pudlo et al. 1980). In ten forests in West Virginia, 24 – 35% of the herbaceous flora were ant dispersed species (Beattie and Culver 1981). These results are comparable to the 29% in a New York deciduous forest where over half of the total number of stems sampled were myrmecochores (Handel et al. 1981). In four deciduous forests in South Carolina, 28 – 44% of the species were myrmecochores (Gaddy 1986). In the evolution of some ecological systems myrmecochory has shaped, and continues to influence, herbaceous community structure.

Ants as a Source of Food

The energy contained in ant tissues is available to other organisms as prey. Although birds are generally considered the primary predator of ants, the diets of many other vertebrates including amphibians and reptiles contain a large proportion of ants (Petal 1978, Levan and Stone 1983, Torgersen and Bull 1995, McIver et al. 1997). Even some groups of humans have traditionally fed on the sugar-rich repletes of *Camponotus* and *Myrmecosystus* (Holldöbler and Wilson 1990). Invertebrate predators and parasites such as spiders, phorid flies, assassin bugs, beetles, and parasitic wasps contribute to the mortality, and thus the turnover of ant-tissue energy (Petal 1978, Cade et al. 1978, Wojcik 1990). In the old fields of the Savannah River Site in South Carolina, the population of *Pogonomyrmex badius* represents 1.51 kJ of energy available to predators per m² per year (Golley and Gentry 1964).

The Influence of Habitat Characteristics on Formicid Communities

The nature of ant communities was influenced by stochastic events in evolution and biogeographic history. Also, formicid species assemblages are influenced by the less random factors of, dispersal, competition, and differential survival in varying environmental conditions. Spatial patterns emerge when ant species assemblages are compared with habitat characteristics (Talbot 1934, Cole 1940, Van Pelt 1956, Wheeler and Wheeler 1973, Schumacher and Whitford 1976, Wisdom and Whitford 1981, Wheeler and Wheeler 1986, Abensperg-Traun 1992, Johnson 1992, Lobry De Bruyn 1993, Olson 1994, Weseloh 1995, Niemela et al. 1996, Majer et al. 1997, Samson et al. 1997, Touyama et al. 1997, Human et al. 1998, Bruhl et al. 1999, Kaspari et al. 2000, Wang et al. 2001)

Countless biotic and abiotic factors potentially influence the morphology, abundance, and diversity of ant communities. Interactions between these factors are complex and in many instances they are correlated with one another. The inability to isolate most environmental factors in field-based experimental manipulations makes the elucidation of their specific effects on ants difficult. As a result, few studies have explicitly investigated the interactions between habitat characteristics and specific community properties (Aspenberg-Traun 1992, Niemela et al. 1996, Majer et al. 1997, Human et al. 1998, Kaspari et al 2000, Wang et al. 2001).

Geographic Scale

At the geographic scale, abundance in ants has been linked to variables associated with energy theory. Within this theory, the abundance of a taxon is directly related to its

ability to obtain and store energy. The biomass of a taxon or taxocene is determined by the amount of energy available in a given habitat and the rate at which that energy is lost through metabolic heat, excretion, and mortality. All of these variables are affected by temperature in ectotherms.

In a survey of 49 New World habitats, ant abundance was positively correlated with net primary productivity (Kaspari et al. 2000). Net primary productivity is often considered a baseline measure of productivity and the limiter of a taxocene's potential abundance (Wright et al. 1993). Ants are no exception to this trend. Additionally, net primary productivity has been used to predict diversity in various taxocenes (Rosenzweig and Abramsky 1993). In terrestrial habitats, the net primary productivity is limited by the amount of rainfall and solar radiation available to producers.

Abundance in ants is also positively correlated with mean temperature (Kaspari et al. 2000). Ants in general have been considered thermophilic (Brown 1973), and temperature ultimately affects their ability to forage. At a given mean temperature, ant abundance also increases in those habitats with longer colder winters. Kaspari et al. (2000) hypothesize that harsher winters allow ectotherms to more effectively sequester resources during times of low productivity.

Local Scale

Elevation - Elevation, in ecological terms, affects ants directly as a function of decreased atmospheric pressure (Kennington 1957) and indirectly as a function of a complex of other variables such as temperature, rainfall, humidity and terrain (Cole 1940, Van Pelt 1963). Decreased levels of available oxygen at higher altitudes have

physiological effects on ants. In *Camponotus pennsylvanicus* (DeGeer), an apparent physiological acceleration occurs in ants nesting at higher altitudes. Kennington (1957) found that populations of *C. pennsylvanicus* that were native to 3,231 meters consume more oxygen in the laboratory than populations native to 2,057 meters. Additionally, with respect to oxygen consumption, the high-altitude ants respond more acutely to temperature changes than do those from lower altitudes.

Generally, insect species richness decreases with increasing altitude (Lawton et al. 1987, McCoy 1990, Olson 1994, Bruhl et al. 1999). The ants of the southern Appalachian Mountains follow this trend (Cole 1940, Van Pelt 1963, Holldöbler and Wilson 1990). Cole (1940) reported 64 forms from 305-610m, 58 forms from 610-914m, 44 forms from 914-1219m, 28 forms from 1219-1524m, 10 forms from 1524-1829m, and only 2 forms from over 1829m. Although not as evident at the lower altitudes, VanPelt (1963) reported a similar trend: 37 species/subspecies from 1067-1219m, 37 species/subspecies from 1250-1372m, 41 species/subspecies from 1402-1524m, 28 species/subspecies from 1554-1676m, 9 species/subspecies from 1707-1829m, 7 species/subspecies from 1859-1981m, and 5 species/subspecies from 2012m and higher. VanPelt (1963), also described a marked reduction in abundance across all species with increasing altitude. Holldöbler and Wilson (1990) described areas above 1981 meters in the southern Appalachians as almost completely devoid of ants and noted a corresponding increase in other predatory arthropods such as spiders.

In an area such as GSMNP, the total habitat area declines with altitude. This reduction of physical space alone should contribute to the paucity of species that

develops. However, the decline in species richness and abundance is large even when quantified per area (personal observations, Cole 1940, VanPelt 1963). Other contributing factors might include resource diversity and net primary productivity, which decrease with altitude while unfavorable environmental conditions increase (Lawton et al. 1987, McCoy 1990).

Plant Communities - Historically, study of the properties of ant species assemblages has been largely limited to their associations with plant communities. Differences in ant species assemblages are expected because plant communities influence the microhabitat in terms of temperature, retained moisture, nesting sites, primary productivity, and resource diversity. While individual plant-ant interactions have been known to occur, the major influence of plants on ant communities is through habitat modification. Many authors have broken large areas into smaller regions defined largely by the dominant vegetation of these subunits and found unique combinations of ant species (Talbot 1934, Cole 1940, Van Pelt 1956, Wheeler and Wheeler 1973, Wheeler and Wheeler 1986). Cole (1940) divided the GSMNP into 13 vegetation types (Table 1-2). No two vegetation types were identical with respect to the ant species found. The most qualitative uniformity was in the ant populations of the grassland species.

Crematogaster lineolata, *Lasius alienus*, *Pheidole vinelandica*, and *Tapinoma sessile* were found in all grasslands sampled. Additionally, grasslands contained a large number of forms (n = 37) that was second only to ant assemblage of the mixed-cove hardwoods (n = 39). However, the typical grassland contained more species than other vegetation types, with 19 restricted to them, while only 9 were limited to the mixed-cove

hardwoods. No species was collected from all vegetation types. Some, however, were widespread, such as *C. lineolata*, *Prenolepis imparis*, and *T. sessile*. Forty species were rare or not widely distributed. These were restricted to one vegetation type only.

Table 1-2. Formicid Biodiversity in Some Vegetation Types of the Great Smoky Mountains National Park (From Cole 1940)

Plant Community	Number of Forms
Red Spruce Forest	3
Mixed Spruce Forest	6
Southern Balsam Fir Forest	2
Subalpine Beech Gap Forest	6
Hemlock Ridge Forest	11
Mixed Cove Hardwoods Forest	39
Buckeye-Basswood Forest	5
Oak-Pine Forest	25
Pine-Heath Forest	24
Old-Field Pine	18
Second-Growth Pine	22
Grassland	37

Cole (1940) renamed or defined the vegetative types in terms of the dominant ant species in them. The taxonomy of these forms has been updated (Table 1-3). In this representation of community structure, important ants, even those restricted to a particular vegetation type, might not be recognized if they were not the most abundant or frequently collected.

Table 1-3. Dominant Ant Species in Some Vegetation Types of the Great Smoky Mountains National Park (From Cole 1940)

Red spruce forest	<i>Aphaenogaster rudis</i> complex
Mixed spruce-fir forest	<i>Stenamma diecki</i> , <i>Aphaenogaster rudis</i> complex
Southern balsam fir forest	<i>Aphaenogaster rudis</i> complex
Subalpine beech gap forest	<i>Lasius neoniger</i> , <i>Aphaenogaster rudis</i> complex
Hemlock ridge forest	<i>Aphaenogaster rudis</i> complex, <i>Camponotus chromaoides</i>
Mixed cove hardwood forest	<i>Aphaenogaster rudis</i> complex, <i>Camponotus americanus</i>
Buckeye-basswood forest	<i>Aphaenogaster rudis</i> complex, <i>Myrmecina americana</i>
Oak-pine forest	<i>Formica exectoides</i> , <i>Crematogaster lineolata</i>
Pine-heath forest	<i>Lasius flavus</i> , <i>Crematogaster lineolata</i>
Old-field pine forest	<i>Pheidole dentata</i> , <i>Prenolepis imparis</i>
Second-growth pine	<i>Amblyopone pallipes</i> , <i>Aphaenogaster treatae</i>
Heath bald	<i>Brachymyrmex depilis</i> , <i>Lasius alienus</i>
Grassland	<i>Pheidole vinelandica</i> , <i>Lasius alienus</i>

Although some species of ants might have affinities for certain plants and vice versa, as in the myrmecochores, abiotic conditions dictate the distribution of both in part.

Insolation, climate, soil, and terrain influence the distribution of plant species. Similarly, stenotopic ants might be limited by similar requirements and apparent plant-ant associations might actually reflect similar affinities for abiotic conditions.

Nesting Sites

The availability and suitability of nesting sites, although sometimes difficult to quantify, play an important role in the distribution and abundance of ant species. The survival of newly-mated queens depends on their capacity to find suitable nesting sites. Success is decided by both the availability of such sites as well as the females' ability to migrate to other locations. The quality of the nesting site is determined by the edaphic, climatic, and biotic factors that control the temperature, moisture, structural stability, and proximity to food sources. Although many species' nest structures are highly plastic, patterns with respect to biotic and abiotic factors are evident (Dreyer and Park 1932, Hess 1958, Sanders 1970, Schumacher and Whitford 1976, Johnson 1992, Lobry De Bruyn 1993, Chen et al. 2002). These patterns are relics of differential survival or active selection of nesting sites by females.

Soil texture and moisture affect the stability of ant galleries. Galleries constructed in coarse-grained soils are more likely to collapse when dried than those made in finer soils such as clay (Hess 1958). In some species, notably the seed harvesters and the fungus growers, elaborate subterranean galleries are important for food storage or cultivation, and the ability to create and maintain these galleries is essential for their survival (Gregg 1947). Additionally, most ant species maintain larvae, pupae, and reproductives in an excavated chamber. The nest-building behavior in various species of

ants might be closely associated with soil texture and water holding capacity. In two ecologically similar species of seed harvesters, *Pogonomyrmex rugosus* Emery and *Messor pergandei* (Mayr), the latter occurs in finer textured soils with higher water retention (Johnson 1992).

The occurrence of stumps, logs, surface stones, and other objects or growths are an important factor in the distribution of ant nests (Cole 1940, Creighton 1950, Sanders 1970, Smith 1979, Torgersen and Bull 1995, Chen et al. 2002). Nesting sites in the GSMNP are seldom associated with soil only. Cole (1940) found only a few (n=8) species that formed nests in soil without the additional protection offered by objects such as stones or logs. In the Park, species nested in logs in varying states of decay (n=18), beneath logs (n=10), in the soil beneath logs (n=15), under the bark of standing dead trees (n=4), beneath moss on logs and the soil (n=3), beneath dry peat crust (n=2), beneath leaves (n=1), with mounds, craters, or domes (n=14), and inside twigs and stems (n=3). The vast majority of the ants collected in the GSMNP nested in the soil beneath stones (n=60).

Terrain - In mountain habitats, the gradient and direction of exposure influence ant communities. Although ant nest structure can be modified to adapt to differences in slope in some species (Klotz 1986), exceedingly steep slopes tend to be less colonized by ants (Wheeler 1917, Dennis 1938, Cole 1940). Although some slopes are probably stable, sheet erosion during heavy rains is cited as a prohibitive factor concerning ant nest construction and maintenance. On steep slopes, soils are typically drier and potentially

less stable as rainwater absorption declines with increasing runoff. Additionally, accelerated runoff is more likely to disturb the soil and stones associated with nests.

The direction of exposure on slopes differs ecologically in the intensity and timing of insolation. Cole (1940) noted that in the GSMNP ants were relatively few on north-facing slopes and abundant on those facing south and east. The soils of the latter slopes are warmed early in the day and retain their heat until late in the afternoon, even after they have been shaded (Wheeler 1917, Cole 1940). These conditions should be more favorable for foraging and the development of larvae.

In a primary terra-firme forest near Manaus, in central Amazonia, species richness and evenness is greater in valleys than on plateaus (Vasconcelos et al. 2003). Conversely, the occurrence of dominant species is relatively rare in valleys. Overall ant abundance doubles and nest densities are nearly three times higher on plateaus compared to valleys. Differences in soil texture and vegetation structure associated with topography, in turn, influence litter, an important food resource and nesting site, in ground foraging ants. Litter quantity is reduced in valleys compared to plateaus. Ordination analysis of species composition reveals valleys and plateaus as important indicators and demonstrates that topography on a local scale explains a significant proportion of the strong variability observed in abundance and diversity measures of ground-foraging ants and possibly promotes heterogeneity in community structure.

Anthropogenic Disturbance of Forests in the Great Smoky Mountains National Park

In the southern Appalachians, full-canopy forests composed of varying species of trees are typically the climax community. Today, approximately 130 species of trees are found in the GSMNP in five major climax communities including hemlock, spruce-fir, northern hardwood, pine-oak, hemlock, and cove hardwoods. Prior to the establishment of the GSMNP, portions of the forest were heavily logged and accidentally burned as late as the 1920s. In 1934, the park was established and the land fell under the management of the U.S. National Park Service whose philosophy theoretically excludes anthropogenic disturbances while allowing those of natural causes. Under this management, new anthropogenic disturbance to the forests has been limited to the introduction of exotic species (Harmon et al. 1983). One prime example includes the chestnut blight. In the GSMNP, the last mature chestnuts *Castanea dentate* (Marshall) to die were at higher elevations and some still had live branches in 1940 (Whittaker 1956). In communities where chestnut was dominant, species including *Acer rubrum* L., *Quercus prinus* L., and *Quercus rubra* L., have increased in importance to fill the canopy. The influence of this floral change on ant communities is not known. Additionally, two species of *Adelges* have been introduced to GSMNP and threaten to disrupt the forest structure. The balsam wooly aphid, *Adelges piceae* (Ratzeburg), and the hemlock wooly adelgid, *Adelges tsugae* Annand, attack fir and hemlock trees, respectively. Additionally, the exotic European wildboar, *Sus scrofa* (L.), disturbs native flora through its rooting behavior (Bratton et al. 1982).

Currently, limited areas in GSMNP are maintained through disruptive anthropogenic practices. Roadside verges throughout the park and several grasslands are maintained through mowing and recently, burning in some of the open field habitats such as Cataloochee. In addition, some of the mountaintop balds are maintained through the manual removal of saplings. These open habitats appear to be an important factor in local ant community structure, as well as Park-wide species richness, as Cole (1940) found more species (n=19) restricted to these artificially maintained grasslands than to any other habitat type in the GSMNP.

As is the case with many natural reserves, the extent of anthropogenic disturbance outside the boundaries of GSMNP continues to increase. While the urban areas of Gatlinburg and Cherokee continue to develop adjacent land, the forest outside the Park becomes further fragmented. Eventually, GSMNP might resemble an island of undisturbed forest surrounded by a mosaic of fragmented forest, urban areas, and agricultural land. Edge effects, especially pressure from disturbance-oriented exotics, are sure to impact the native fauna of the Park in the future.

The Ecology of Invasive Species

Invasion of ecosystems by adventive species (*sensu* Frank and McCoy 1990) can occur when organisms are transported to geographic locations outside their natural range, where they propagate and establish populations. Although biotic invasions in the strict sense are not exclusively anthropogenic, human transportation and commerce have the potential to carry species great distances in predictable and recurring patterns. The movement of organisms to new regions has increased with the expansion of human

transport and international trade (Elton 1958, di Castri 1989), with many countries documenting 10^2 - 10^4 adventive species established within their borders (Lodge 1993).

Invasive species – adventive species whose introduction can cause environmental harm through competition with native species – are among the most insidious consequences of human-caused environmental change on a global scale (Vitousek et al. 1997) and are considered second only to habitat destruction in this respect (Wilson 1992). Invader species often experience ecological release (Wilson 1961) and benefit from a surplus of dietary or spatial resources, more favorable environmental conditions, lack of predators, scarcity of competitors, or a combination of these factors (Shigesada and Kawasaki 1997). Invasive species can displace native species or reduce their abundance. These changes, though sometimes subtle, upset biological interactions and alter the function and organization of native ecosystems (Vitousek et al. 1997, Holway et al. 2002). Specifically, the breakdown of community assembly rules (Weiher and Keddy 1999) allows biological invaders to reduce biodiversity and transform highly evolved and ordered communities into random assemblages, which drastically alters the organization of relationships among persisting species (Gotelli and Arnet 2000, Sanders et al. 2003).

Ants as invaders

Many organisms, representing diverse taxonomic groups and geographic origins, have become established in foreign ecosystems (Mack et al. 2000). Among this broad array of taxa, the ants are a successful and destructive group, owing mainly to a few notable species. While ants represent a diverse family, with nearly 12,000 described species (Agosti and Johnson 2006), only 147 have become established outside their

native range and only 9 are considered invasive (McGlynn 1999). The six most widespread, and abundant invasive ants include *Anoplolepis gracilipes* (F. Smith), *Linepithema humile* (Mayr), *Pheidole megacephala* (Fabricius), *Solenopsis invicta* Buren, *Solenopsis geminata* (Fabricius), and *Wasmannia auropunctata* (Roger) (Holway et al. 2002). The potential for the emergence of new widespread invasive ant species is high. Suarez et al. (2005) identified 232 species of ants in 58 genera representing 12 subfamilies that were intercepted at U. S. ports-of-entry between 1927 and 1985. In addition, existing adventive species such as *Tetramorium rhenanum* Shultz, *Pheidole obscurithorax* Naves, and *Myrmica rubra* (L.) (Storz and Tschinkel 2004, Groden et al. 2005), among others, are well established in North America and appear to have expanding ranges.

Despite advances in invasion ecology, there are major gaps in our knowledge of even the most important invasive ants. Although *S. invicta* is possibly one of the best-studied social insects (Ross and Keller 1995), little is known about the biology and native range of other important invasive ants such as *A. gracilipes*. The disparity in research effort between these two invasive ants demonstrates the emphasis placed on a few model invaders while the ecologies of lesser-known invasive species have been overlooked (Holway et al. 2002). The diversity of ants being transported to foreign lands and their ability to act in many ecological roles, make the development of preventive strategies, based only on the biology of a few species, problematic. As conservation ecologists face one of the most daunting threats to global biodiversity – biotic homogenization – documentation of the distribution, habitat, ecological importance, and community

interactions of all organisms that might function as harmful invasive species is imperative.

The Ecology of Habitat Fragmentation

The growth of human populations, and consequent development of natural areas for different land uses, typically results in the fragmentation of homogeneous habitat, creating a mosaic of habitat patches of various condition. Stereotypically, fragmentation occurs when a forest habitat is divided into patches. However, more subtle fragmentation also occurs when openings are created that disrupt continuous canopy. Such openings can be caused by roads, and powerline rights-of-way. Other habitat types are also subject to fragmentation. For example, wetlands are fragmented by draining and development, whereas prairie habitats have been historically fragmented by agricultural use.

As fragmentation progresses, average fragment size and total fragment area decrease as the degree of insularity of fragments increases (Moore 1962, Webb and Haskins 1980). Habitat fragmentation has two primary and inseparable components, habitat loss and insularization (Wilcox and Murphy 1985). Habitat connectivity is decreased for a variety of species and edge characteristics become more influential as the edge-to-interior ratio increases (Ranney et al. 1981).

The theory of island biogeography (MacArthur and Wilson 1967) has been applied to the study of habitat fragmentation, and Diamond (1975) originally suggested that a single large preserve would protect more biodiversity than several smaller preserves with the same land area when combined. This prediction was based on the principle that species richness increases with habitat area. The intuitive idea was

popularized by other ecologists, and was incorporated into textbooks on conservation biology leading to real-world application by land managers. This idea was refuted by a former student of Wilson who suggested that the prediction was based on the unsupported assumption that smaller fragments were nested in species composition (Simberloff and Abele 1976, Simberloff and Abele 1982). The idea of nestedness implies that each larger fragment contains all the species present in smaller fragments in a hierarchical pattern. Conceptually, if two small reserves harbor unshared species, two or more smaller patches could support more species richness than a single large preserve. The debate over single large or several small (SLOSS) reserves has dealt primarily with the extent that smaller reserves share species. The Biological Dynamics of Forest Fragments Project (BDFFP) was established in 1979, generating data to address this practical issue in tropical rainforests. A notable feature of the project was the collection of abundance data for many species before the experimental isolation of forest patches was executed. The experimental nature of studies conducted under this project is the key to permitting a rigorous assessment of fragmentation effects that would be impossible to obtain by simply observing previously fragmented landscapes. Investigators in the BDFFP have produced over 450 peer-reviewed publications and nearly 100 graduate theses on the subject (Laurance et al. 2004). Additionally, the SLOSS debate has led to the development of the nested subset theory (Patterson and Atmar 1986), methods for identifying idiosyncratic species and sites (Atmar and Patterson 1993) and significance of nestedness (Berglund and Jonsson 2003). The SLOSS debate is ongoing (Fischer and Lindenmayer 2005, Higgins et al. 2006). However, trends in fragmentation effects are

widely accepted. In terms of biodiversity, habitat fragmentation causes increases in the number of generalists, number of multihabitat species, number of edge species, number of exotic species, nest predation, and extinction rate. Decreases are frequently seen in the dispersal of interior specialists, numbers of large-home-range species, and richness of interior species (Forman 1995).

Edge Effects

An edge is defined as the meeting point of two habitats, delimited by plant community type, successional stage, or land use, and can be a sharp boundary or an ecotone (gradual transition). Edges are either inherent or induced (Thomas et al. 1979). Inherent edges are natural, usually long-lasting features related to topographic differences, soil type, presence of open water, or other geomorphic features. Induced edges can be the result of both natural and anthropogenic disturbances such as fire, flood, erosion, timber harvest, planting, grazing, or urbanization. The term “edge effect”, originally used to describe a pattern of increased species richness observed at habitat boundaries (Leopold 1933, Odum 1971, Kunin 1998), has otherwise been used to describe abiotic characteristics (e.g., Kapos 1989, Chen et al. 1995) and population and community impacts (e.g., Saunders et al. 1991, Aizen and Feinsinger 1994). Since the concept was introduced (Clements 1907), the influence of edges on biodiversity has intrigued ecologists, and their study is now considered a fundamental concept in ecology (Wiens 1976). Leopold (1933) originally proposed, as a game-management principle, that maximizing the amount of edge in a habitat would increase biodiversity. This practice was broadly implemented by land managers, with little other than circumstantial evidence

of the benefits (Harris 1988). However, increased emphasis on plant and nongame wildlife (e.g., Wilson 1987b) in the last three decades has raised aesthetic, moral, and scientific issues (Yahner 1988) and revealed many characteristics of edges that are undesirable (e.g., Wilcove 1987, Saunders et al. 1991, Altverson et al. 1994, Moen and Jonsson 2003, Lehman et al. 2006).

Four general categories have been described that classify the mechanisms of edge-mediated effects on species distributions (Fagan et al. 1999). First, habitat edges can differentially alter the dispersal ability of species within a landscape. Second, habitat edges can differentially alter the mortality rate of species within a landscape. Third, habitat edges can result in “cross boundary subsidies” (Janzen 1986) where a dispersed species’ influence on a particular habitat is subsidized by feeding or reproductive success in an adjacent habitat. Fourth, edge zones can act as a unique habitat, possessing characteristics shared with the two adjoining habitats as well as characteristics unique to the edge, and allowing species normally restricted to one habitat type to interact.

Ant Community Response to Habitat Fragmentation

Disturbance of forest habitats alters ant community composition. High impact logging practices in an Amazonian rainforest did not alter ground-foraging ant species richness or the relative contribution of each subfamily to the total number of species (Kalif et al. 2001). However, drastic changes did occur at the genus and species levels, including a 2-fold reduction of the dominance of the hyperdiverse genus *Pheidole*. In the southern United States, a controlled forest clear-cutting experiment showed that logging altered the ant community by significantly reducing native ant abundance and increasing populations of a few species including *S. invicta* and *Pheidole* spp. (Zettler et al. 2004). In pine forested fall-line sandhills (USA Georgia), highly disturbed areas, essentially devoid of trees, had greater total numbers of ants, reduced species richness, and reduced equitability compared to lightly or moderately disturbed sites. Highly disturbed sites were dominated by *Dorymyrmex insanus* (Buckley) (Graham et al 2004). Understory burning has a significant negative effect on ant species richness in the forests of the Siskiyou Mountains of northern California, while relatively species-poor fen ant assemblages are not affected (Ratchford et al. 2005).

As a focal taxon in habitat-change studies, the response of ant communities specifically to habitat edges has been documented to a limited extent. In an Atlantic rain forest of Bahia, Brazil, certain species of ants had preferences for fields or particular distances into the adjacent forest (Majer et al. 1997). Eighty-five species were found in the forest and, 48 in the field, and 36 were common to both habitats. The ant fauna of the Atlantic rainforest was dramatically influenced by clearing, but the forest community

could persist even up to the interior edge of the forest. This study (Majer et al. 1997) looked only at epigeic ants and because many tropical species nest and forage in the canopy (Wilson 1987a), forest-inhabiting species diversity was underestimated, as was the influence on this community. In goldenrod-dominated old-field habitat of Ohio, USA, habitat patches were experimentally created by mowing. Unmowed habitats differed in terms of size, degree of isolation, and amount of edge. Lower species richness was associated with greater habitat edge, contrary to the expected edge effect of increased species richness at edges, and was more influential than habitat patch size or degree of isolation (Golden and Crist 2000). In crop fields, meadows and fallow land in Central Hesse, Germany, species richness and nest density were assessed at edges and in interiors. Edges between different land-use types did not influence overall species richness, or nest density, or harbor a unique ant fauna. However, most species showed an ‘ecotonal effect’ in which abundance either increased or decreased with relative distance to edge zones, leading to quantitatively different community structure at edges versus interiors. The authors noted that aggressive species had high nest density and colony size along edges and hypothesized that the presence of these species might reduce edge permeability for surface-dwelling arthropods, reducing movement between habitats (Dauber and Wolters 2004).

Many adventive and invasive ant species are disturbance oriented and move quickly through anthropogenically altered habitats. One such example is the red imported fire ant, *S. invicta*, native to South America. This species dominates disturbed habitats, and populations are increased by forest clear cutting (Zettler et al. 2004). They use

roadsides and pastures as corridors, allowing them to penetrate deeper into forested habitat where they might displace native species (Stiles et al. 1997, Stiles and Jones 1998). In a study of the impacts of urban sprawl on ant communities in naturally vegetated habitat patches in the Lower Florida Keys, native species richness was not influenced by the amount of development or proximity to roads. The number of adventive species however, was significantly positively correlated with the amount of development in the proximity (Forys and Allen 2005). In scrub-habitat fragments of coastal southern California, Argentine ants are widespread, found in all of the 40 habitat patches surveyed, and have strong influences on native ant communities. *Linepithema humile*, are most abundant in fragments near developed edges and the number of native species declines from >7 to <2 species in the presence of the Argentine ant. Numbers of remaining native ant species were best predicted with the abundance of Argentine ants, the size of the habitat patch, and the years since the patch was isolated (Suarez et al. 1999).

Community Ecology Statistics: Special Techniques

Nonmetric Multidimensional Scaling

In multivariate statistics, ordination techniques are used to explore data and test hypotheses by finding structure in multidimensional space. The primary objective of ordination is to reduce the dimensionality of data and present patterns in samples and species as faithfully as possible in low-dimensional space (Gauch 1982). Ordination orders data by the values of multiple variables and can address data that are nonnormal or on arbitrary scales. Data are arranged by distance in ordination space, with similar variables situated more close together than those that are dissimilar. Traditionally,

methods such as principal components analysis (Goodall 1954) have been used for this type of analysis. Principal components analysis is best suited for data with approximately linear relationships among data. Iterative optimization methods such as nonmetric multidimensional scaling (NMDS) allow for the visualization of a much wider range of structures and more complex relationships (Clarke 1993). NMDS was proposed by Shepard (1962a, b) and refined to a workable state by Kruskal (1964a, b). Historically, limited computational power was associated with the inability to find the ideal solution due to interfering local minima and long processing times. Advancements in computer technology and ready availability of sufficient computational power has eliminated these shortcomings and NMDS has become one of the most defensible statistical techniques during the process of scientific peer review (McCune and Grace 2002). The method is well suited to data that are typical of ecological studies including species-richness matrices, community data, and measured habitat characteristics.

NMDS calculations are based on an $n \times n$ distance matrix that is calculated from the $n \times p$ -dimensional data matrix (raw data). An iterative search for the best positions of n entries on k dimensions is performed that minimizes the stress of the k -dimensional configuration. Stress is a measure of the departure from similarity between the p -dimensional matrix and the k -dimensional ordination space. Iterations are performed as small step movements of points in the ordination space and are repeated until a minimum stress is reached (McCune and Grace 2002).

CHAPTER II

THE GROUND-FORAGING ANT FAUNA AT HABITAT BOUNDARIES BETWEEN GRASSLANDS AND ADJACENT FORESTS IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

Introduction

The composition of ant communities might be influenced by one or more complex factors including stochastic equilibrium, interspecific competition, and habitat specialization. Individual species may not react the same to different influences and, as a result, two ant biodiversity samples are seldom the same because the variability of composition of species and their abundance is too high to make duplication likely. This high degree of compositional variability and the unknown ultimate causes of it are significant challenges to conservation ecology. However, appreciating patterns of biodiversity in intact and human-disturbed habitats is important in understanding the effects of habitat change on ecosystems and will be instrumental in optimizing efforts to conserve natural areas in the face of human-caused habitat fragmentation.

The study of edge effects has been considered a fundamental concept in ecology (Wiens 1976), and has persisted for more than 100 years since the original introduction of the concept (Clements 1907). Historically, the term was used to describe a pattern of increased species richness at habitat boundaries (Leopold 1933). In a contemporary context, the term is typically used to describe drastic changes in vegetation type such as that between forests and fields (Fortin and Drapeau 1995). The term “ecotone” is commonly used to describe the tension zone or gradual functional response of species

across an area between two different and relatively homogeneous ecological community types (van der Maarel 1990).

Originally, edge zones were of interest because they described the borders of species assemblages (Clements 1907) and later because of the conservation implications of the higher species richness that these zones support (Leopold 1933). The practice of maximizing habitat edge was broadly implemented by land managers with the goal of maximizing biodiversity in reserves (Harris 1988). More recently, however, ecologists have revealed the negative influences of edges and ecotones on undisturbed tracts and the species that require them (e.g., Wilcove 1987, Saunders et al. 1991, Altverson et al. 1994, Moen and Jonsson 2003, Lehman et al. 2006). These influences are especially important as the clearing of native vegetation in land-use practices is increasing the prevalence of edges and ecotones on a global scale. The temperate forests of North America have not escaped the process of habitat fragmentation, though not as popularized as tropical forests in this respect. The major source of new anthropogenic disturbance and subsequent habitat fragmentation in North America is suburban development. Of all development that has happened in the United States, more than 16% occurred between 1982 and 1992 (Lassila 1999) and since 1980, populations in suburban areas have grown ten times faster than central-city populations (Benefield et al. 1999).

As with many natural reserves, development outside the borders of the Great Smoky Mountains National Park (GSMNP) continues to increase. While Gatlinburgh, TN, Cherokee, NC, and other urbanized areas continue to develop, the forests outside of the Park will become further fragmented. Eventually, the Park might become an island of

relatively undisturbed forest in a highly fragmented mosaic of land-use patterns and the various ecological communities associated with them.

Within GSMNP, three major artificial grasslands are maintained through mowing. The boundaries between these habitats and the naturally vegetated forests that border them provide the opportunity to study the ecology of edge effects in temperate forests. While the size of habitat patches and edge effects have varying impacts on ant communities in some systems (e.g., Majer et al. 1997, Golden and Crist 2000, Dauber and Wolters 2004), it is important to avoid the application of generalized edge effects in invertebrates because the exact effects of anthropogenic habitat alteration can vary strongly among systems and among the species within them (Kotze and Samways 2001).

The goal of my research is to observe the distribution of all epigeic ant species across the habitat boundary between the artificially maintained grasslands and the forests that border them in the GSMNP, and to determine if species distributions result in the composition of distinct ant assemblages separated by detectable boundaries. The data generated through quantitative sampling allowed the testing of the hypotheses that ants show patterns in richness, diversity, abundance, and composition that coincide with the human-induced edges between forests and grasslands in the GSMNP. An additional goal is to determine if the ant response is a true ecotonal effect and, if so, identify the scale and correlated environmental characteristics.

Materials and Methods

Study Area and Sampling

Three major grassland areas occur within the boundaries of the GSMNP. These grasslands are all maintained by mowing and are within 300 m of each other in elevation, with Cades Cove at 548 m, Oconoluftee at 701 m, and Cataloochee at 823 m. In July-August of 2003, each of these areas was sampled for ground-foraging ants along 180 m semi-permanent transects with sampling stations every 30 m. Prior to 2004 sampling, preliminary analysis of 2003 data indicated that sampling stations 45 m into the forest did not differ significantly from stations 75 m, 105 m, or 135 m into the forest in individual species abundance or in overall (average) abundance, diversity, or richness. In 2004 sampling, the number of stations was reduced in the forest to decrease sampling effort and laboratory time in sorting and identification. Stations at 75 m, 105 m, and 135 m were dropped from the 2004 sampling regime. Data from these stations in 2003 are not included when the entire (2003-2004) data set is analyzed (see Figure 2-2 for the layout of a transitional transect). At each of the three grasslands, one forest and one grassland control transect were established. The grassland control transect consisted of a transect located at least 140 m from the forest edge and in the center of the grassland habitat type. The forest control transect was located at least 140 m from grassland habitat and continued in undisturbed forest habitat. Transitional transects crossed the habitat boundary at sharp edges between the forests and the grasslands. Four transitional transects were established at Cataloochee and Oconoluftee and six were established at Cades Cove, the largest of the grassland habitats (Figure 2-1). Transitional transects

began in the grassland habitat 45 m from the transition to forest and continued into the forest habitat for an additional 135 m at 30 m increments.

At sampling stations, ants were collected with two complementary techniques, Winkler litter extraction (Bestlemeyer et al. 2000) from a 1-m² quadrat, and pitfall trapping in 2-cm diameter test tubes installed at the substrate surface as described in chapter IV. Ecological characterization was conducted at each of the sampling stations. Soil moisture and pH were measured at each sampling station with a Kelway® soil tester (Wykoff, NJ). The tester was inserted at the top of the mineral layer to a depth of approximately 7.6 cm. Humus depth at each sampling station was averaged from four samples. Each sample was taken three steps from the station in all cardinal directions. Percent canopy cover was estimated with a convex (to maximize the area of canopy sampled), spherical densiometer at each station (Robert E. Lemmon forest densiometers, Bartlesville OK). Elevation was measured with a digital altimeter (Suunto, Sylvan Lake, MI) at each sampling station. Substrate slope was estimated in degrees greater than level with a protractor and carpenter's level. Availability of nesting sites was assessed along a 20-m transect perpendicular to the main transect. All logs, stumps, standing dead trees, surface stones, moss patches, and twigs intersecting this transect were counted. Additionally, the percentages of the substrate along these secondary transects that were covered by leaf litter, grasses, bare ground, and woody herbaceous growth were estimated. At each sampling station, a Jim-Gem Cruz-All® (Forestry Suppliers Inc. Jackson, MS) die cut gauge was used to locate all trees >10cm in diameter at breast height and falling within the 5 and 20 basal area factor (BAF) categories of the gauge.

The BAF and the number of trees counted were used to calculate overall relative tree density. Additionally, all trees falling within the larger 20 BAF category were identified to species.

Figure 2-1. Major artificially maintained grasslands in the Great Smoky Mountains National Park, 2003-2004.

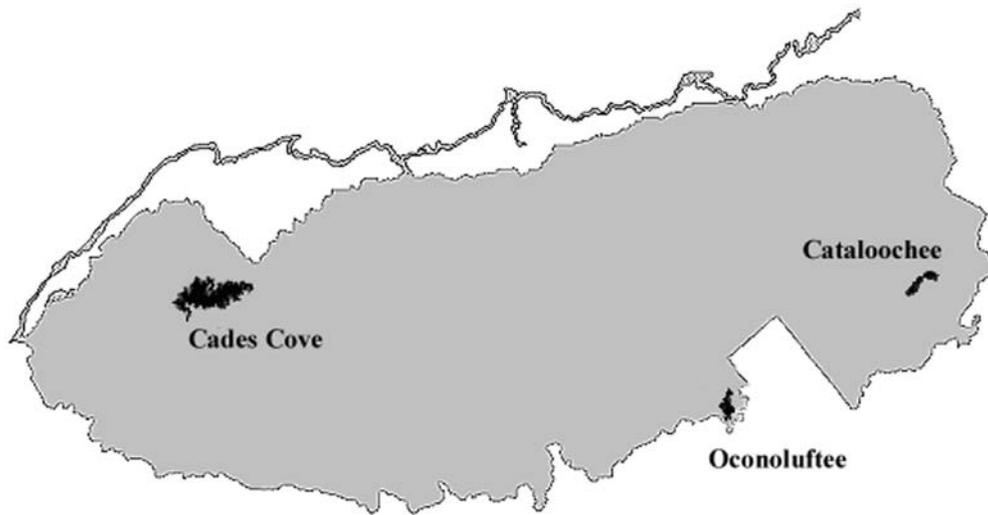
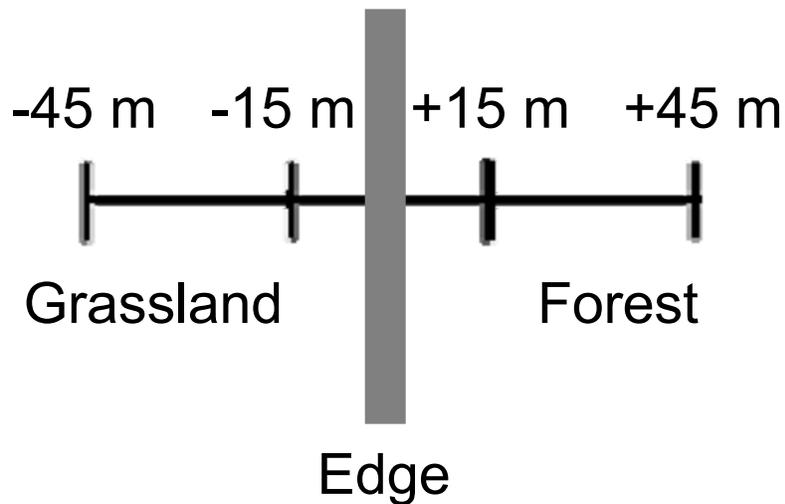


Figure 2-2. Layout of a transition transect crossing the sharp edge between forest and grassland habitats.



All ant species, with the exception of members of the *Aphaenogaster fulva-rudis-texana* complex (Umpfrey 1996), were identified to species following the taxonomy of Bolton (1995). The *Aphaenogaster fulva-rudis-texana* complex is a group of sibling species that can only be delimited reliably with cytotaxonomic techniques. Additionally, these techniques require preimaginal individuals and are not applicable to worker ants (Umpfrey 1996). Hereafter in the text, this complex is referred to as *A. rudis* complex for simplicity. The occurrence of queens or males was not included in the data because their presence does not necessarily indicate that a colony is established in the vicinity sampled (Fisher 1999). The abundance (number of workers) of each species was recorded for each sampling method at each station. Subsequent treatments of data are of pooled values combining pitfall and Winkler litter extraction capture at the sampling station level.

Voucher specimens for all species were deposited in the Clemson University Arthropod Museum.

Data Analysis

A species accumulation curve was constructed for each of the station categories (grassland control, grassland 45 m from edge, grassland 15 m from edge, forest 15 m from edge, forest 45 m from edge, and forest control) to assess the adequacy of sampling by comparison of the observed richness and the expected richness obtained from the Incidence-Based Coverage Estimator (ICE) over 1000 resampling runs with the 'Ws2m.exe' program (Turner et al. 2000), an algorithm based on species accumulation curves.

To determine the influences of edges on ground-foraging ant communities, a parametric analysis of variance (ANOVA) followed by Fisher's least significant difference test (LSD) was used to compare average community property values on a per station category basis. Station categories included grassland control, grassland 45 m, grassland 15 m, forest 15 m, forest 45 m, and forest control. Community property variables included diversity (Shannon's index), richness, and total abundance.

While comparison of diversity, richness, and abundance is important in assessing the extent of edge effects, these measures give little to no information on community composition, or species turnover between distances. For example, two communities might have similar richness but be composed of entirely different assemblages of species. Graphical and statistical techniques were used to investigate community structure. First, to delineate the ecological boundaries of ant communities within the data matrix,

hierarchical agglomerative cluster analysis was used to find groups of locations (defined by habitat, distance relative to edge, forest control, or field control) in multidimensional species space. Second, ANOVA was repeated for individual species abundance. Third, rank-abundance plots were used to visually compare the community structure within habitats at differing distances from the edge.

Hierarchical agglomerative cluster analysis was used to find similarities in species data from individual stations at each of three locations (Cades Cove, Oconoluftee, and Cataloochee). Data were compiled among controls, years, and within habitats at the same distances. Clustering was accomplished with the space-conserving flexible beta linkage method ($\beta = -0.25$) and the Sørensen (Bray-Curtis) distance metric. Indicator Species Analysis (PC-ORD version 4) provided a quantitative criterion for pruning the cluster dendrogram at an ecologically meaningful number of nodes and was used to identify the species that are significant indicators of each group. Indicator Species Analysis combines data on the extent of individual species abundance in a particular group with the faithfulness of occurrence within that group and is based on the method for the calculation of indicator values (IV) (Dufrêne and Legendre 1997). For example, a perfect indicator species of a given group is always present in the group and never occurs in other groups. Indicator values for individual species were tested for significant difference from random assemblages with 1,000-run Monte Carlo simulations. Group membership was written to separate files at each step (number of branches) in the cluster analysis. Indicator species p-values of all species were calculated for each group at each level of clustering. Then p-values were repeatedly averaged for each level. The clustering step

that had the smallest average p-value was considered the most informative level of branching in the dendrogram. In addition, the number of significant indicator species was counted and plotted against cluster level.

In the first step to assess habitat characteristics for ecotonal effects, individual characteristics were compared with a parametric ANOVA followed by Fisher's LSD used to compare average values on a per station category basis. Station categories included grassland control, grassland 45 m, grassland 15 m, forest 15 m, forest 45 m, and forest control.

Second, multiple linear regression was used to compare total ant abundance, diversity, and richness with habitat parameters to test the hypothesis that biotic and abiotic habitat characteristics can be used to predict ant community properties. In addition, principal components analysis (PCA) was used to collapse the original characteristics into a smaller number of statistically independent principal components (PCs) that might be better predictors than single characteristics alone. PCs are linear combinations of the original characteristics and each successively explains less of the variation and covariation in the original set of characteristics. All PCs with eigenvalues greater than 1.0 (Norusis 1985) were used in a multiple linear regression analysis. Interpretation of the PCs was based on rank correlations between the original characteristics and each PC (Ludwig and Reynolds 1988). In the analysis, soil moisture, humus depth, percent canopy cover, elevation, slope, percentages of ground cover types, nesting-site data, relative overall tree density (basal area factor), and abundance of individual tree species was entered into the analysis. A stepwise multiple regression was

used to detect any significant relationship between ant community properties, PCs, and higher order terms (original characteristics alone).

Third, stepwise multiple logistic regression was used to compare individual species presence/absence with habitat characteristics and tree species (20 BAF) to identify those that are correlated with specific ant species. This analysis was limited to those species identified as indicator ant species and showing ecotonal effects within forest or grassland habitats.

Results

Species richness approximation with the ICE estimator showed that the observed species richness captured from 88 to 94% of the actual richness estimated over 1000 runs (Table 2-1). The majority of forest ground-dwelling ants were collected during the study. Any species escaping detection are rare and infrequently encountered.

Table 2-1. Percent of total species richness captured as determined by comparison of richness predicted with the Incidence-Based Coverage Estimator (ICE) to observed values. The Great Smoky Mountains National Park: Cades Cove, Cataloochee, and Oconoluftee. July-August, 2003-2004.

	Grassland			Forest		
	Control	-45 m	-15 m	15 m	45 m	Control
Observed	30	31	37	38	33	27
ICE predicted	32	34	42	41	35	30
% Captured	94	91	88	93	94	90

A total of 11,503 individual ants, and 54 species, representing 5 subfamilies, were identified and counted. The following results and subsequent ecological metrics are based on abundance values for each species and are pooled totals from Winkler litter extraction and pitfall trapping. Twenty-nine of these species were common to both grassland and forest habitats, while only 16 and 9 species were restricted to forests and grasslands, respectively. Richness values within each habitat, distance from the edge, and control are totaled cumulatively and for each species (Table 2-2), with the lowest cumulative total richness (26) in the forest control and the highest richness (36) in the forest 15 m from the habitat boundary between the forest and grassland.

Table 2-2. Species richness and distribution within habitats, controls, and distances from edge. The Great Smoky Mountains National Park: Cades Cove, Cataloochee, and Oconoluftee. July-August, 2003-2004.

Ant Species (γ diversity = 54)	Grassland						Forest					
	Control (n=33)		-45 m (n=28)		-15 m (n=28)		15 m (n=28)		45 m (n=28)		Control (n=33)	
	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq
Dolichoderinae												
<i>Tapinoma sessile</i> (Say)	12	36.36	9	32.14	8	28.57	3	10.71	5	17.86	4	12.12
Ecitoninae												
<i>Neivamyrmex carolinensis</i> (Emery)	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00	0.00	0.00	0.00	0.00
Formicinae												
<i>Acanthomyops claviger</i> (Roger)	0.00	0.00	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00	0.00	0.00
<i>Brachymyrmex depilis</i> Emery	1	3.03	2	7.14	2	7.14	2	7.14	3	10.71	1	3.03
<i>Camponotus americanus</i> Mayr	0.00	0.00	0.00	0.00	0.00	0.00	2	7.14	0.00	0.00	0.00	0.00
<i>Camponotus chromaoides</i> (Fabricius)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	3.03
<i>Camponotus nearticus</i> Emery	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00	1	3.57	0.00	0.00
<i>Camponotus pennsylvanicus</i> (DeGeer)	0.00	0.00	0.00	0.00	2	7.14	2	7.14	4	14.29	0.00	0.00
<i>Formica schaufussi</i> Mayr	0.00	0.00	1	3.57	1	3.57	0.00	0.00	0.00	0.00	0.00	0.00
<i>Formica neogagates</i> Emery	17	51.52	4	14.29	4	14.29	1	3.57	0.00	0.00	0.00	0.00
<i>Formica subaenescens</i> Emery	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2	7.14	5	15.15
<i>Formica subcericea</i> Say	1	3.03	0.00	0.00	2	7.14	2	7.14	2	7.14	1	3.03
<i>Lasius ailenus</i> (Foerster)	3	9.09	14	50	12	42.86	11	39.29	11	39.29	5	15.15
<i>Lasius flavus</i> (Fabricius)	8	24.24	4	14.29	4	14.29	1	3.57	1	3.57	0.00	0.00
<i>Lasius neoniger</i> Emery	23	69.7	19	67.86	17	60.71	3	10.71	1	3.57	1	3.03
<i>Lasius umbratus</i> (Nylander)	2	6.06	1	3.57	3	10.71	1	3.57	1	3.57	1	3.03
<i>Paratrechina parvula</i> (Mayr)	11	33.33	8	28.57	6	21.43	3	10.71	0.00	0.00	0.00	0.00

Table 2-2 (continued). Species richness and distribution within habitats, controls, and distances from edge. The Great Smoky Mountains National Park: Cades Cove, Cataloochee, and Oconoluftee. July-August, 2003-2004.

Ant Species (γ diversity = 54)	Grassland						Forest					
	Control (n=33)		-45 m (n=28)		-15 m (n=28)		15 m (n=28)		45 m (n=28)		Control (n=33)	
	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq
<i>Paratrechina faisionensis</i> (Forel)	11	33.33	6	21.43	7	25	13	46.43	10	35.71	10	30.3
<i>Prenolepis imparis</i> (Say)	3	9.09	1	3.57	2	7.14	2	7.14	1	3.57	5	15.15
Myrmecinae												
<i>Aphaenogaster fulva</i> Roger	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00
<i>Aphaenogaster rudis</i> complex (Enzmann)	2	6.06	3	10.71	5	17.86	26	92.86	25	89.29	33	100
<i>Aphaenogaster tennesseensis</i> (Mayr)	0.00	0.00	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00	0.00	0.00
<i>Aphaenogaster treatae</i> Forel	19	57.58	15	53.57	15	53.57	1	3.57	0.00	0.00	0.00	0.00
<i>Crematogaster cerasi</i> (Fitch)	1	3.03	0.00	0.00	1	3.57	0.00	0.00	0.00	0.00	0.00	0.00
<i>Crematogaster pilosa</i> Emery	1	3.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Crematogaster punctulata</i> Emery	1	3.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Leptothorax curvispinosus</i> Mayr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2	7.14	2	6.06
<i>Leptothorax longispinosus</i> Roger	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00
<i>Monomorium minimum</i> (Buckley)	7	21.21	9	32.14	4	14.29	1	3.57	0.00	0.00	0.00	0.00
<i>Myrmecina americana</i> Emery	1	3.03	4	14.29	5	17.86	14	50	10	35.71	21	63.64
<i>Myrmica americana</i> Emery	6	18.18	1	3.57	2	7.14	1	3.57	0.00	0.00	0.00	0.00
<i>Myrmica latifrons</i> Starcke	15	45.45	17	60.71	16	57.14	3	10.71	1	3.57	0.00	0.00
<i>Myrmica pinetorum</i> W. M. Wheeler	7	21.21	5	17.86	6	21.43	1	3.57	1	3.57	0.00	0.00
<i>Myrmica punctiventris</i> Roger	0.00	0.00	5	17.86	2	7.14	9	32.14	8	28.57	14	42.42
<i>Myrmica</i> sp 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2	6.06
<i>Pheidole bicarinata</i> Mayr	3	9.09	2	7.14	1	3.57	0.00	0.00	0.00	0.00	0.00	0.00

Table 2-2 (continued). Species richness and distribution within habitats, controls, and distances from edge. The Great Smoky Mountains National Park: Cades Cove, Cataloochee, and Oconoluftee. July-August, 2003-2004.

Ant Species (γ diversity = 54)	Grassland						Forest					
	Control (n=33)		-45 m (n=28)		-15 m (n=28)		15 m (n=28)		45 m (n=28)		Control (n=33)	
	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq	Count	%Freq
<i>Pheidole crassicornis</i> Emery	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pheidole dentata</i> Mayr	4	12.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pheidole tysoni</i> Forel	24	72.73	16	57.14	12	42.86	1	3.57	0.00	0.00	0.00	0.00
<i>Pyramica clypeata</i> (Roger)	0.00	0.00	0.00	0.00	0.00	0.00	2	7.14	0.00	0.00	0.00	0.00
<i>Pyramica ohioensis</i> (Kennedy and Schramm)	0.00	0.00	0.00	0.00	0.00	0.00	5	17.86	2	7.14	2	6.06
<i>Pyramica pillinasis</i> (Forel)	0.00	0.00	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00	0.00	0.00
<i>Pyramica rostrata</i> (Emery)	0.00	0.00	1	3.57	1	3.57	10	35.71	6	21.43	2	6.06
<i>Pyramica talpa</i> (Weber)	0.00	0.00	1	3.57	3	10.71	5	17.86	2	7.14	2	6.06
<i>Stenammas brevicorne</i> (Mayr)	1	3.03	3	10.71	1	3.57	3	10.71	1	3.57	2	6.06
<i>Stenammas impar</i> Forel	1	3.03	1	3.57	0.00	0.00	4	14.29	9	32.14	21	63.64
<i>Stenammas schmittii</i> W.M. Wheeler	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	3.03
<i>Solenopsis carolinensis</i> Forel	10	30.3	7	25	9	32.14	1	3.57	1	3.57	0.00	0.00
<i>Solenopsis molesta</i> (Say)	19	57.58	13	46.43	15	53.57	3	10.71	4	14.29	1	3.03
Ponerinae												
<i>Amblyopone pallipes</i> (Haldeman)	0.00	0.00	0.00	0.00	0.00	0.00	4	14.29	4	14.29	12	36.36
<i>Hypoponera opacior</i> (Forel)	11	33.33	8	28.57	8	28.57	0.00	0.00	0.00	0.00	1	3.03
<i>Ponera pennsylvanica</i> Buckley	13	39.39	11	39.29	11	39.29	19	67.86	15	53.57	19	57.58
<i>Proceratium pergandei</i> (Emery)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1	3.57	0.00	0.00
<i>Proceratium silaceum</i> Roger	0.00	0.00	0.00	0.00	0.00	0.00	4	14.29	3	10.71	12	36.36
Species richness = α diversity	30		29		34		36		31		26	

Analysis of variance compared mean values for abundance, diversity, and richness for the groups, forest control, forest 45 m from edge, forest 15 m from edge, grassland 15 m from edge, grassland 45 m from edge, and grassland control. Different groupings of values were revealed in each of the three measures, and each measure displayed significant ($\alpha = 0.05$, d.f. =175) differences among the groups, specifically, showing decreasing trends towards deep forest habitat (Figure 2-3). The only ecotonal effect was in abundance values, which showed the only significant difference within a grassland or forest. The highest abundance value was in the grassland control and values decreased at grassland stations 45 and 15 m from the forest edge. The lowest average abundance was in the forest 45 m from the edge and was significantly lower than that of the grassland control and grassland 45 m from the edge. Average diversity (Shannon's diversity index) was highest in the grassland 45 m from the edge and was significantly lower in the forest at 45 m from the edge. Other diversity values showed no trends. Average species richness was also highest in the grassland control and was significantly higher than the lowest value at forest 45 m from the edge and the forest control. Trends in species richness varied between average species richness (Figure 2-3) and total species richness (Table 2-2). Figure 4. illustrates this difference by plotting the values with separate scales on the same plot. Average species richness shows a gradual decreasing trend from the grassland control to the forest control. Total species richness, however, shows a peak in richness in both habitats that occurs at 15 m from the habitat boundary between forest and grassland.

Figure 2-3. Ant abundance, species richness, and diversity averaged within habitats, distance from the edge, and control plots. Standard error bars indicate average standard error for the category (abundance, richness, or diversity). Means within the same category that share the same letter are not significantly different as determined with ANOVA ($\alpha = 0.05$). The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.

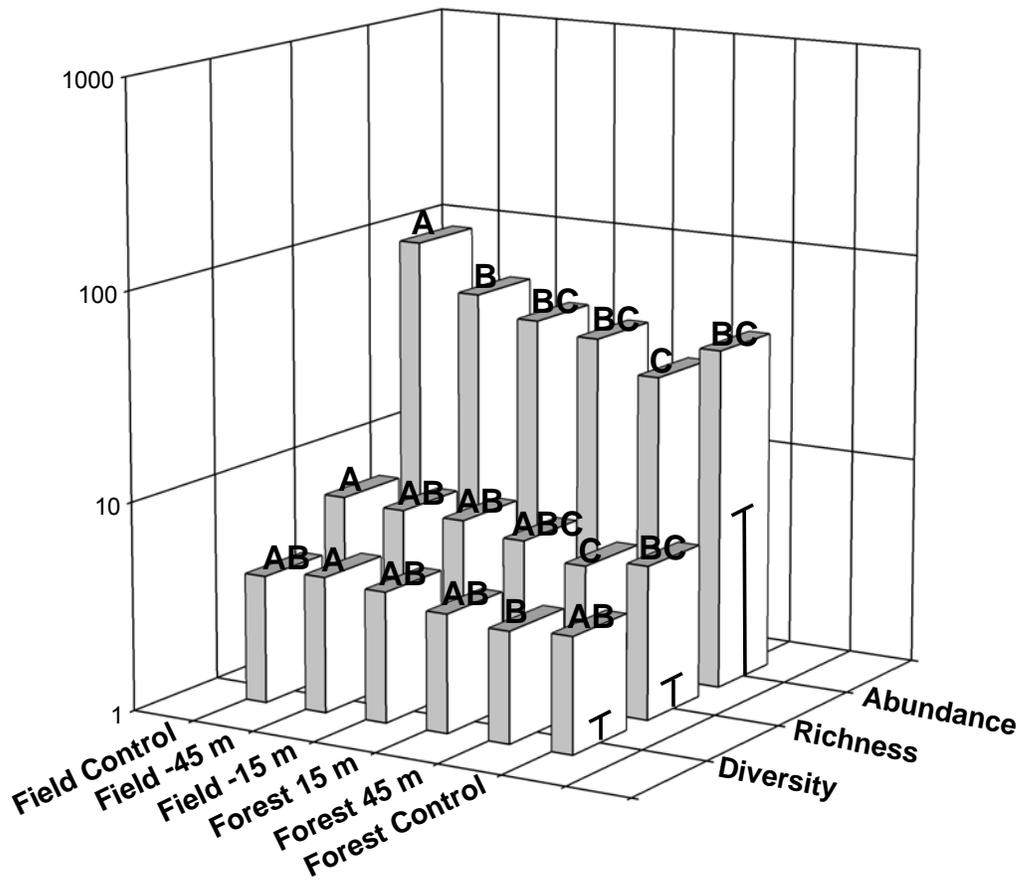
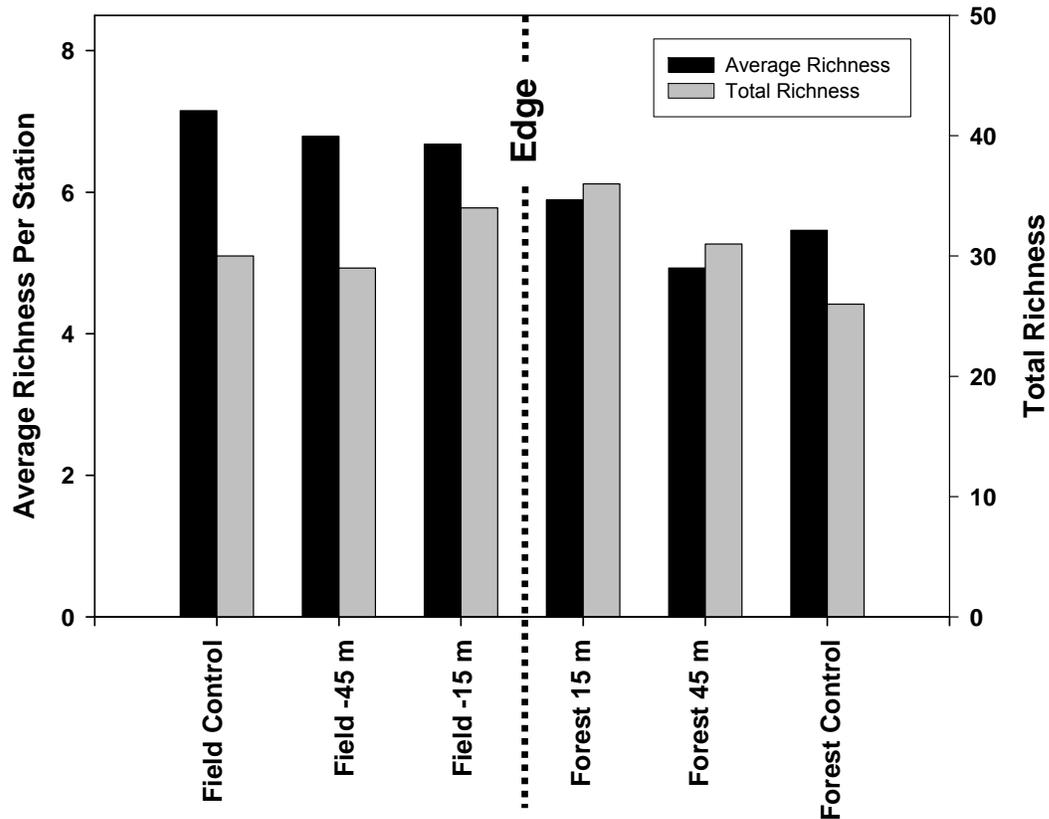


Figure 2-4. Comparison of general trends in average richness per station and total richness within grassland and forest habitats at different distances from the edge and in control plots. The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.



Hierarchical agglomerative cluster analysis based on the Sørensen (Bray-Curtis) distance metric resulted in a tree illustrating the similarity of sites (Cades Cove, Cataloochee, and Oconoluftee), habitats (forest, grassland), distance from the edge (-45 m, -15m, 15 m, and 45 m), and controls. The highest level division was between the forest and grassland habitats. In nearly all cases, terminal within-habitat clustering was greater within sites than within distances from the edge or controls. Indicator species

analysis was used to prune the tree and was run 15 times (at each level of clustering) and revealed that the lowest average p-value for all indicator species across clusters was at the three cluster level. Likewise, the maximum number of significant indicator species was also reached at the 3-4 cluster level (Figure 2-5). Based on these results, the tree was pruned at the three cluster level (Figure 2-6), revealing three significant groups: Cataloochee grassland, Cades Cove-Oconoluftee grassland, and all forest. All of the significant indicator species for these three groups and the higher order group of all grassland are illustrated with their respective percent of perfect indication (IV) (Figure 2-7). Twenty-seven of fifty-four total species in the plots were significant indicators at this level of clustering. Six significant indicators were found for the all-forest group. The higher order all-grassland group had the most with ten significant indicators. The two terminal subsets of this group had seven (Cataloochee) and four (Cades Cove-Oconoluftee) indicator species each.

Figure 2-5. Tree pruning with indicator species analysis. A. Averaged P-values of indicator value significance level, at all cluster levels. B. Number of significant indicator species ($p \leq 0.05$) for each level of clustering. Minimum average p-value and maximum significant number of indicator species were both reached at the three cluster level.

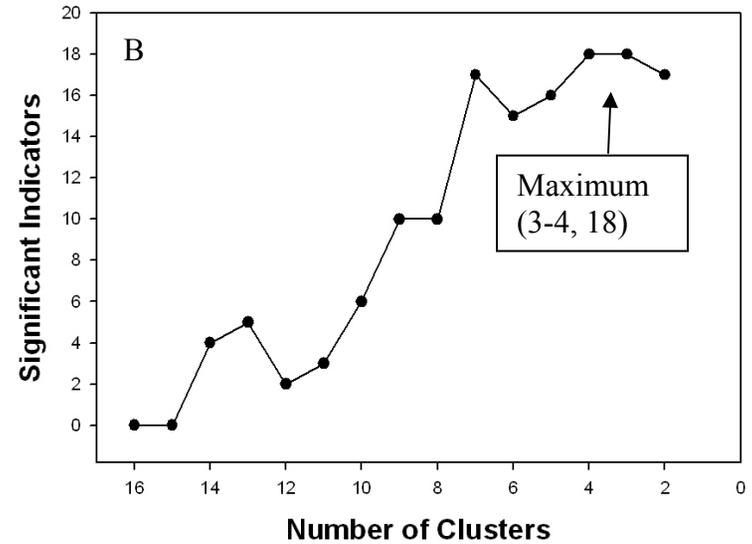
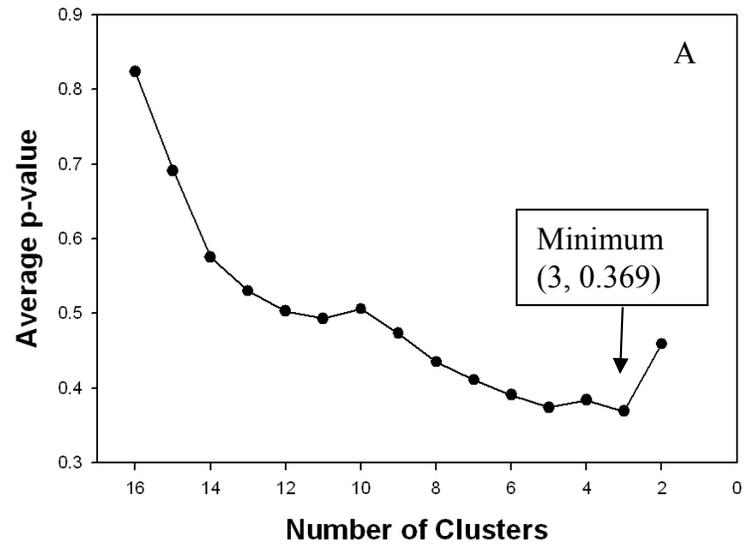


Figure 2-6. Dendrogram from agglomerative hierarchical cluster analysis of locations in species space (Sørensen distance metric). Symbols indicate groups formed by pruning the dendrogram at the three cluster level (see “/” marks) with multiple iterations of indicator species analysis. CC = Cades Cove, Cat = Cataloochee, Oco = Oconoluftee; Forest = forest control, Grass = grassland control; + distances = forest samples in transitional series, - distances = grassland samples in transitional series. The Great Smoky Mountains National Park. 2003-2004.

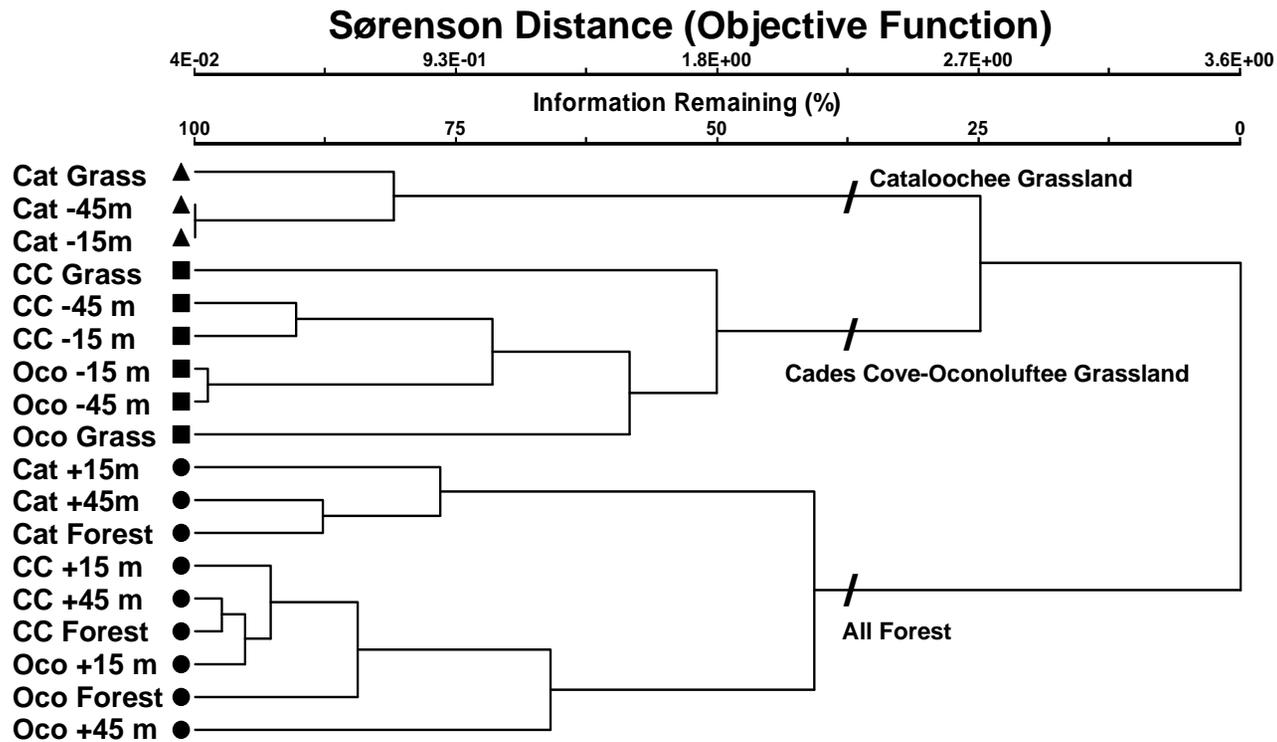
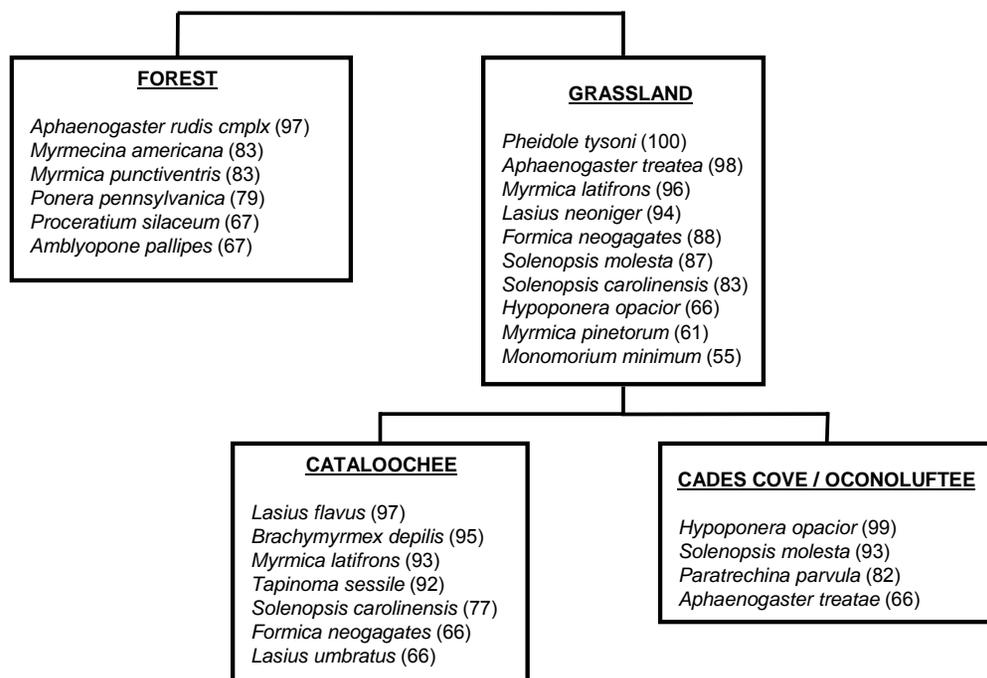
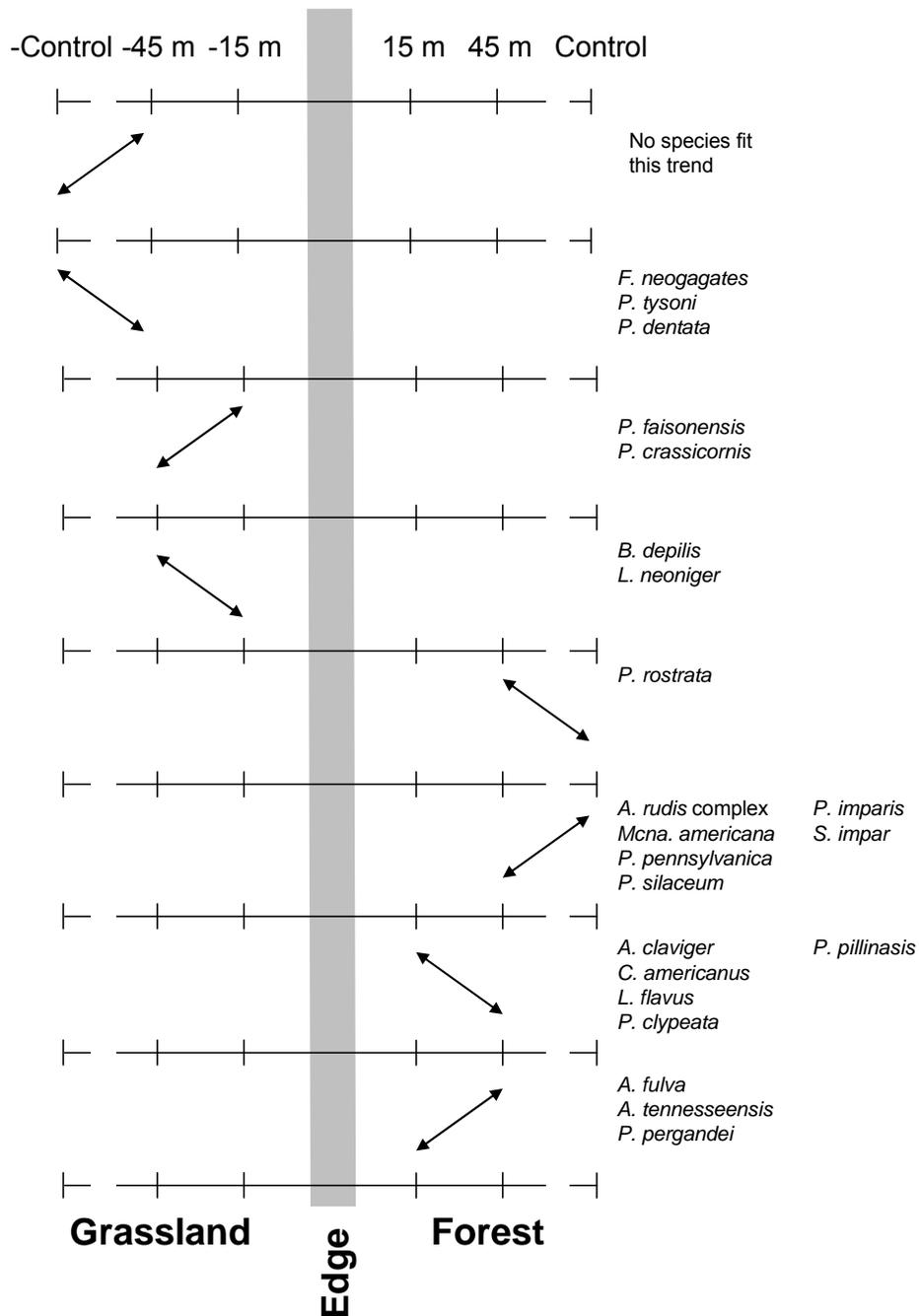


Figure 2-7. Partial (3-cluster level) indicator species hierarchy showing all terminal and higher level groups from the pruned dendrogram (Figure 3). Only statistically significant ($\alpha = 0.05$) indicator species of ground-foraging ants are shown. The number for each species represents the percent of perfect indication (IV) in each subgroup. The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.



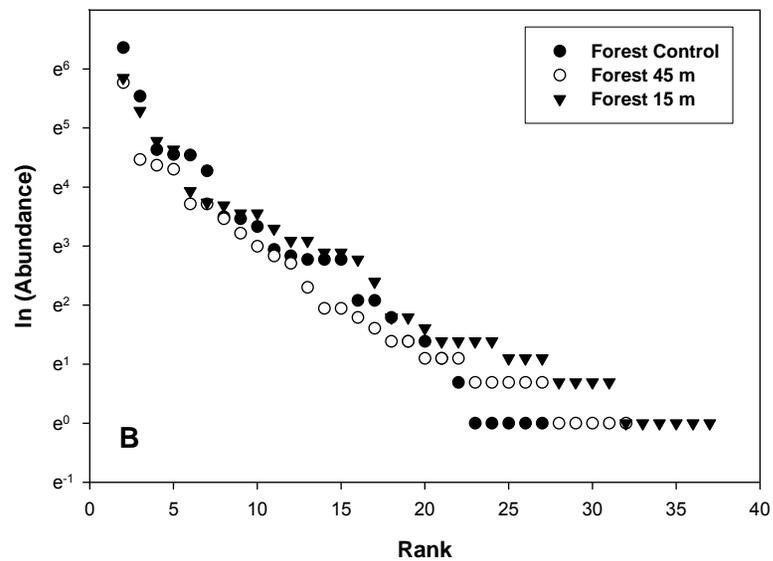
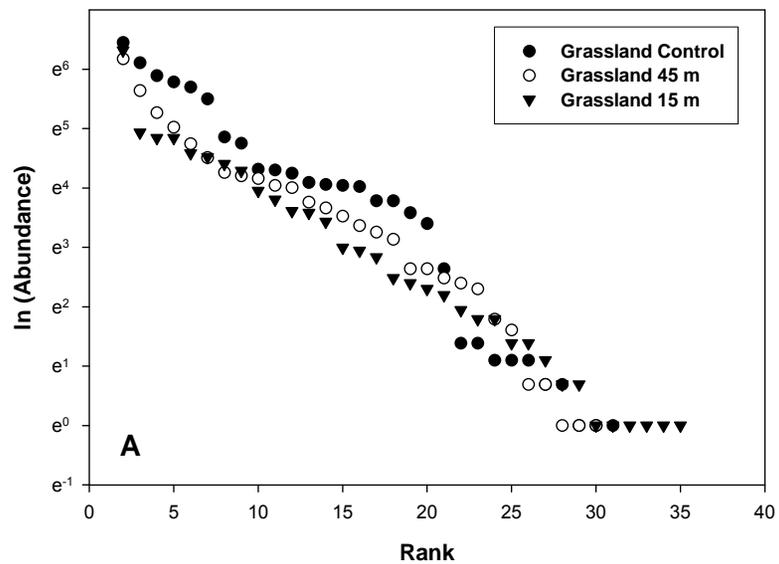
Analysis of variance on mean abundance of each species revealed several groups of species showing differential responses to controls and distances from the edge in grassland and forest habitats ($\alpha = 0.05$, d.f. = 177). These responses have been divided into four categories within each habitat (Figure 2-8). The categories are increase from 45 m to control, decrease from 45 m to control, increase from 15 m to 45 m, and decrease from 15 m to 45 m. Categories are not inherently mutually exclusive, i.e., a species can hypothetically occur in multiple categories. However, no species fell into more than one category. No species showed an increase in abundance from grassland control to grassland 45 m from the edge. Three species showed a decrease from grassland control to grassland 45 m from the edge. Two species showed an increase from grassland 45 m from the edge to grassland 15 m from the edge. Two species showed a decrease from grassland 45 m from the edge to grassland 15 m the edge. Five species decreased in abundance from forest at 15 m from the edge to forest 45 m from the edge. Three species increased from forest at 15 m from the edge to forest 45 m from the edge. A single species decreased in average abundance from the forest at 45 m from the edge to the forest control. Six species increased in average abundance from forest at 45 m from the edge to the forest control. This categorical response contained the most species.

Figure 2-8. Individual ant species response to distances from edge and control plots in forest and grassland habitats. Only species with significant responses as determined with ANOVA on abundance ($\alpha = 0.05$) are shown. Differential abundances within habitats and between controls, 45 m, and 15 m from the edge are indicated by diagonal lines with arrows. In example, *Pyramica rostrata* showed a decrease in abundance when the average at 45 m in the forest was compared with the average abundance in the forest control. No species showed a decreased abundance in the grassland control compared with grassland 45 m from the edge (first category). The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.



Community structure, as visualized by rank-abundance plots (Figure 2-9), varied little within the grassland habitat. However, plots revealed separation between controls, 15 m from the edge, and 45 m from the edge in the forest habitat. This separation is most clearly visualized at the 26th ranked species where the control has the lowest abundance, with 45 m from the edge at an intermediate abundance, and 15 m from the edge with the highest abundance.

Figure 2-9. Rank-abundance plots within grassland A. and forest B. habitats at controls, 45 m from the edge, and 15 m from the edge. The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.



Analysis of variance on mean values of each habitat characteristic revealed three classes: 1) characteristics that showed differential responses between grassland and forest habitats; 2) characteristics that showed differential response to controls and distances from the edge in forest habitats; and 3) characteristics that showed differential response to controls and distances from the edge in grassland habitats ($\alpha = 0.05$, d.f. = 175). Characteristics that separated between grassland and forest habitats and are associated with the presence of trees include the number of trees in both the BAF5 and BAF 20 category, humus layer depth, the number of logs, stumps, standing dead trees, and twigs on the forest floor (Table 2-3, Forest-Grassland). The second category showed an ecotonal effect in the forest habitat and included five characteristics: soil moisture, percentage grass cover, percentage litter cover, and percentage herbaceous cover. Soil moisture, percentage grass cover, and percentage herbaceous cover decreased with increasing depth into the forest habitat. Percentage litter cover increased with depth into the forest habitat. The final category includes a single characteristic, canopy cover, which increased in the grassland habitat at 15 m from the forest edge.

Table 2-3. Mean values (\pm standard error) of habitat characteristics differentiating forest and grassland habitats, and showing ecotonal effects in forest and grassland habitats. Values within the same row that share the same letter are not significantly different (ANOVA, $\alpha = 0.05$). The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.

	Grassland			Forest		
	Control (n=33)	-45 m (n=28)	-15 m (n=28)	15 m (n=28)	45 m (n=28)	Control (n=33)
Forest-Grassland Differences						
BAF 5 trees	0.00 \pm 0.67 a	0.18 \pm 0.71 a	1.50 \pm 0.71 a	19.96 \pm 0.71 b	20.39 \pm 0.71 b	20.94 \pm 0.67 b
BAF 20 trees	0.00 \pm 0.33 a	0.00 \pm 0.35 a	0.34 \pm 0.35 a	7.14 \pm 0.35 c	6.17 \pm 0.35 b	6.73 \pm 0.33 bc
Humus depth	1.24 \pm 0.31 a	1.14 \pm 0.32 a	1.48 \pm 0.32 a	3.01 \pm 0.32 b	3.00 \pm 0.32 b	2.82 \pm 0.31 b
Logs	0.00 \pm 0.20 a	0.00 \pm 0.21 a	0.00 \pm 0.21 a	1.89 \pm 0.21 b	2.00 \pm 0.21 b	1.55 \pm 0.20 b
Stumps	0.00 \pm 0.06 a	0.00 \pm 0.07 a	0.00 \pm 0.07 a	0.25 \pm 0.07 b	0.14 \pm 0.07 ab	0.24 \pm 0.06 b
Standing dead trees	0.00 \pm 0.06 a	0.00 \pm 0.07 a	0.00 \pm 0.07 a	0.18 \pm 0.07 ab	0.32 \pm 0.07 a	0.36 \pm 0.06 b
Twigs	0.00 \pm 0.79 a	0.00 \pm 0.85 a	0.04 \pm 0.85 a	14.07 \pm 0.85 b	12.54 \pm 0.85 b	12.42 \pm 0.80 b
Within Forest Ecotonal Effect						
Soil moisture	57.57 \pm 2.27 a	57.61 \pm 2.42 a	59.54 \pm 2.42 a	46.00 \pm 2.42 b	48.86 \pm 2.42 b	34.85 \pm 2.28 c
Percentage grass cover	98.18 \pm 2.37 a	99.64 \pm 2.52 a	97.86 \pm 2.52 a	15.00 \pm 2.52 b	7.79 \pm 2.52 bc	1.07 \pm 2.37 c
Percentage litter cover	0.00 \pm 4.43 a	0.00 \pm 4.71 a	0.00 \pm 4.71 a	67.14 \pm 4.71 b	76.07 \pm 4.71 bc	89.64 \pm 4.43 c
Percentage herbaceous cover	4.84 \pm 4.83 a	4.11 \pm 5.14 a	8.57 \pm 5.14 a	37.14 \pm 5.14 b	45.89 \pm 5.14 b	15.30 \pm 4.83 a
Within Grassland Ecotonal Effect						
Canopy cover	0.00 \pm 0.98 a	0.32 \pm 1.05 a	12.43 \pm 1.05 b	90.64 \pm 1.05 c	87.93 \pm 1.05 c	88.54 \pm 0.98 c

Multiple linear regression was used to determine habitat characteristics related to ant abundance, based on habitat characteristics. The process was repeated for total ant diversity and richness. The model for abundance contained percentage canopy cover and humus layer depth equation: (abundance = $66.71 - 0.48 \text{ canopy} + 4.49 \text{ humus}$). The terms were significant at $\alpha = 0.05$ and $R^2 = 0.19$. The model for Species richness contained percentage canopy cover and elevation equation: (richness = $8.74 - 0.02 \text{ canopy} - 0.01 \text{ elevation}$; $\alpha = 0.05$; $R^2 = 0.13$). The model for diversity contained percentage of ground covered by litter and elevation equation: (diversity = $5.59 - 0.01 \text{ litter} - 0.01 \text{ elevation}$; $\alpha = 0.05$; $R^2 = 0.13$). Principal components analysis was used to determine if a combination of habitat characteristics could better predict ant abundance, diversity, or richness. No combinations of characteristics (principal components) were better at predicting community values than were models based on single characteristics alone (i.e., multiple regression models).

Multiple logistical regression analysis was used to determine habitat characteristics and tree species that were associated with individual species presence/absence. Analysis was only applied to indicator ant species showing ecotonal effects in forest (*A. rudis* complex, *M. americana*, *P. pennsylvanica*, and *P. silaceum*) and grassland habitats (*B. depilis*, *F. neogagates*, *L. neoniger*, and *P. tysoni*). In general, the presence or absence of these ant species was affected by habitat characteristics (% moss cover, % bare ground, % canopy cover, % grass cover, elevation, humus depth, slope, number of stones, number of large trees, number of medium trees), and abundance of specific tree species (red maple, *Acer rubrum* L.; silver maple, *Acer saccharinum* L.;

sycamore, *Platanus occidentalis* L., beech, *Fagus grandifolia* Ehrh; black oak, *Quercus velutina* Lam.; black cherry, *Prunus serotina* Ehrh.; pitch pine, *Pinus rigida* Mill.; loblolly pine, *Pinus taeda* L.). Specific habitat characteristics and trees associated with specific ant species are shown in table 2-4.

Table 2-4. Habitat characteristics and tree species significantly related to individual ant species presence or absence as revealed with multiple logistic regression analysis. Only characteristics significant at the 0.05 α level or 0.10 α level (*) are included. All ant species are both significant indicator species and show ecotonal effects within forest or grassland habitats. A “-” sign in the effect column indicates a negative coefficient in the multiple logistic regression model. A “+” sign indicates a positive coefficient. The Great Smoky Mountains National Park: Cades Cove, Oconoluftee, and Cataloochee, 2003-2004.

	Habitat Characteristic	Effect
Forest Affected Species		
<i>A. rudis</i> complex	% moss cover	-
	% bare ground	-
	Red Maple abundance	-
	Sycamore abundance	-
<i>M. americana</i>	Loblolly Pine abundance	-
	Silver Maple abundance	-
	% Canopy	+
	Black Oak abundance*	+
<i>P. pennsylvanica</i>	Beech abundance*	+
	elevation	-
	% grass cover	-
<i>P. silaceum</i>	Black Cherry abundance	-
	% moss cover	+
	elevation	-
	Pitch Pine abundance	+
	Beech abundance	+
Grassland Affected Species		
<i>L. neoniger</i>	% grass cover	-
	humus depth	+
	% moss cover	+
	% bare ground	+
<i>F. neogagates</i>	slope	-
	% canopy	-
	% moss cover	+
<i>P. tysoni</i>	elevation	-
	number of stones	-
	large trees (BAF 20)	-
	% herbaceous cover*	-
	soil pH	+
	% moss cover*	+
<i>B. depilis</i>	soil moisture	-
	elevation	+
	medium trees (BAF 5)*	+

Discussion

Cluster analysis revealed a clearly defined boundary between forest and grassland and community composition that perfectly coincided with the induced edges between forests and artificially maintained grasslands. The significant indicator species that describe the communities at the three cluster level (Cataloochee grassland, Cades Cove-Oconoluftee grassland, and all forests) should be useful in future studies on these communities, allowing land managers and ecologists to abbreviate the intensive identification process typically associated with community-level studies by focusing on key indicator species from each habitat. Cluster analysis did not reveal ecotonal effects at lower-order group relationships. Within forest or grassland habitats, terminal grouping revealed that samples from controls, 15 m and 45 m were not consistently more similar than samples from the same region (Cades Cove, Oconoluftee, or Cataloochee). The Sørensen distance metric did not reveal a general edge effect within habitats.

Analysis of variance on the standard community measures including diversity, richness, and abundance revealed no trend (diversity) or a general and gradual decrease (abundance, richness) from grassland to forest when compared as sample means. The presence of ecotonal effects within grassland or field habitats was not revealed at this level, with the exception of a decrease in grassland abundance as the forest edge was approached. However, when comparing the total richness at each control and distance from the edge, a classical increase in species richness near the edge was observed. Habitat heterogeneity (Tews et al. 2004) and niche saturation (Holldöbler and Wilson 1990, Soares et al. 2001) near edges was most likely the underlying cause of the

difference between scales. Single samples are spatially limited to 1m² (Winkler sampling) or the foraging range of the species (pitfall sampling) and are a representation of species found in a particular microhabitat. They are not likely to encompass multiple microhabitats even at relatively heterogeneous edge zones. The evenness of averaged diversity and richness values (Figure 2-3) is probably a reflection of local microhabitat saturation and landscape level heterogeneity is not revealed until species lists are totaled for a particular distance from habitat boundaries.

When individual species abundance within forest and grassland habitats was examined with ANOVA, 22 species showed ecotonal responses to distances from edges and control plots (Figure 2-7). The majority of these species (15/22) showed responses within the forest. Subsets of the species showing significant responses were also significant indicator species (Figure 2-4) and are of particular interest. *Aphaenogaster rudis* complex, *Mcna. americana*, *P. pennsylvanica*, and *P. silaceum* are forest indicator species that also show an increase from 45 m from the edge in the forest habitat to the forest control. These species likely represent species that require deep forest habitat for maximum abundance. *Lasius flavus* is an example of a grassland indicator species that penetrates forests at edges with limited success and decreases in abundance from 15 m to 45 m within the forest. *Formica neogagates* and *P. tysoni* are grassland indicator species that show an increase from 45 m, from the edge in the grassland, to the grassland control and are possibly species that require open grassland habitat removed from forest edges. In addition, *B. depilis* and *L. neoniger* are grassland indicator species that showed an increase in abundance away from forest edges at 15 m to 45m.

Ranked-abundance plots in forest and grassland habitats showed a possible ecotonal effect in the forest where the community structure at the 22nd ranked species separated among the control, 45 m, and 15 m samples. This possible effect is not evident in higher ranked species and indicates that the effect is present in only those rarely collected species.

Several environmental characteristics were identified that correlate with habitats, distances from habitat boundaries, ant species richness, ant diversity, total ant abundance, and abundance of individual ant species. These data should be interpreted conservatively as no cause-effect relationship has been identified in this work. For example, *A. rudis* complex abundance was related to % moss cover, % bare ground, red maple abundance, and sycamore abundance. These variables are likely intercorrelated and separating true cause-effect relationships can only be done experimentally. These characteristics might not directly impact ant abundance and simply be likewise influenced by some other unmeasured characteristic. In addition, some relationships are likely the result of stochastic mechanisms that have no biological relevance. These data, however, might be useful in the development of hypothesis-testing studies that seek to understand the biotic and abiotic habitat characteristics that induce edge effects. This aspect of fragmentation ecology is greatly understudied (Saunders et al. 1991) and might hold value in conservation efforts.

The ecology of species assemblages is inherently multifaceted and can be impermanent. As a result of the complexity and contingency of this subject, community ecology is generally governed by few rules and the applicability of functional models are

often restricted geographically (Lawton 1999, Simberloff 2004). The study of edge effects on ant communities typifies this general condition in community ecology as a whole and the literature bears conflicting and varied patterns in species and community responses to edges. For example, in an agricultural landscape composed of meadows, crop fields, and fallow land in Central Hesse, Germany, ant species richness was not affected by the edges between habitats and edge habitats and did not support a specialized community (Dauber and Wolters 2004). However, most individual ant species did show ecotonal effects with respect to edges either decreasing or increasing with distance from habitat boundaries. The resulting interior and edge community structure was different. In Afri-montane forest fragments, ant assemblages were not affected by the sharp edges between forest fragments and surrounding grasslands although cluster analysis revealed distinct ant communities in grasslands, forest edges, and forest interiors, with the greatest species richness in grasslands (Kotze and Samways 2001). In forest habitat at grassland edges in an Atlantic rain forest, the interior forest ant community was able to exist in close proximity to the habitat boundary with grasslands (Majer et al. 1997). In contrast, this forest community differed in that the highest species richness was found in samples taken from the furthest distances into forest habitat, and lowest, in adjacent grasslands. In contrast to these studies, the response of ants to the experimental fragmentation of old field habitats in Ohio, USA, was more correlated with the amount of habitat edges than to interior habitat area (Golden and Crist 2000).

Despite the lack of a general unifying rule or model for edge effects on ant communities, studies that define these effects, though geographically limited in

applicability, are entirely essential for the success of conservation management. Many indices used to assess heterogeneity and fragmentation in landscape ecology are based on the size and intensity of edges (Forman and Godron 1981, O'Neill et al. 1988, Haines – Young and Chopping 1996, Hargis et al. 1998). The local application of these indices is important in resource planning and management in the face of global change and the phenomenon of land-use induced habitat fragmentation. The calculation of these values and ultimately their successful application is limited by the accuracy and relevance of assessment of edge effects and other community factors in specific habitats.

Summary

Forest ant communities in the southern Appalachians are severely influenced by the clearing of trees and maintenance of grassland habitats to such an extent that clearly different ant communities are found on either side of the boundary between these habitats. Significant indicator species for four distinct ant assemblages discovered during this study have been identified. On a landscape level, species richness is greatest near edge zones and total abundance increases in grassland habitats with distance from forest edges. In addition, more subtle ecotonal effects occur across forest-grassland habitat boundaries and involve abundance of individual species. Differential abundance is seen in significant indicator species in both grassland and forest habitats while differences in rarely collected species occurs in the forest habitat only. However, these changes are not great enough to create differences in the landscape-level ant-community assemblage that are significantly detectable with ecological distance metrics and hierarchical agglomerative cluster analysis or comparison of average per sample species richness or

diversity across distances from edges. The grassland and forest communities are intact up to 15 m from habitat boundaries in the GSMNP. Several biotic and abiotic habitat characteristics were identified that correspond with patterns in habitats and in ant distributions. Habitat characteristics are not causally related to biotic edge effects in this work and should be the basis for future hypothesis testing. In general, these results should be useful in other ecological and conservation endeavors in temperate forests and grasslands via the establishment of extensive species lists, identification of important indicator species, description of general and species-specific ecotonal effects, and identification of possible habitat characteristics associated with ant ecotonal effects.

CHAPTER III

***Pachycondyla chinensis* (Emery): A POTENTIALLY INVASIVE SPECIES IN THE SOUTHEASTERN UNITED STATES THAT THREATENS THE GREAT SMOKY MOUNTAINS NATIONAL PARK**

Introduction

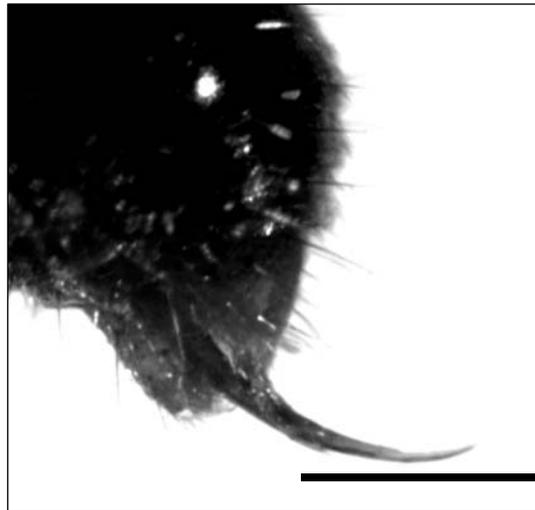
Pachycondyla chinensis (Emery) (Formicidae: Ponerinae) is a little-studied ant, precinctive (sensu Frank and McCoy 1990) to southeastern Asia. Its known range includes numerous locations in the Australasian, Oriental, and Nearctic regions. The first records of this immigrant ant in the New World were from Decatur, Dekalb County, Georgia, USA (1932), where they were well established over three adjacent city blocks. Populations also were discovered in North Carolina, Virginia, and the District of Columbia (Smith 1934). More recently, *P. chinensis* has been considered relatively uncommon in Central Atlantic USA, but well established in the above-mentioned areas (Creighton 1950, Smith 1979). No further studies have monitored its expansion or persistence in North America and it has been considered a rare ant. Although the circumstances that led to the arrival of this ant in North America are unknown, the introduction most likely resulted from human transport. *Pachycondyla chinensis* was intercepted by U. S. Department of Agriculture customs officials between 1927 and 1985 (Suarez et al. 2005). In Hamburg, Germany, the species was discovered in a shipment of plants (*Prunus* sp.) imported from Japan (Smith 1934). Plant shipments infested by *P. chinensis* possibly reached North America where the ant escaped detection and became established in the early 1900s.

Although the biology of *P. chinensis* is not well documented, the species has been found nesting in dark, damp areas, such as soil beneath stones, logs, stumps, and debris (Smith 1934, Creighton 1950, Smith 1979). In China, *P. chinensis* can be described as unusually dominant for a ponerine ant and is ubiquitous on rice-paddy dikes. It forages diurnally on the ground in open areas and on tree trunks in forested areas (Brown 1958). Creighton (1950) reported colonies ranging from approximately twenty to several hundred individuals, often with several dealated females per nest. Similar to most species of the genus that are generalist scavengers and predators (Wild 2002), *P. chinensis* feeds opportunistically on dead insects, fish scraps, and decaying fruit (Smith 1934) and preys on small, live arthropods (Smith 1979), including termites (Teranishi 1929). The species is amply defended with a robust sting (Figure 3-1) and protein-rich venom (Orivel and Dejean 2001). In Japan, *P. chinensis* is commonly referred to as “oo-hari-ari”, which translates to “giant needle ant”, a name that descriptively refers to the sting apparatus. The species is a stinger of humans (Smith 1934) and its stings induce anaphylaxis in South Korea, Japan and, recently North America (Ohtaki et al. 1988, Cho et al. 2002, Nelder et al. 2006).

After over 70 years as a rare adventive species, the range and density of *P. chinensis* appears to be increasing in the southeastern USA and it has become well established in southeastern forests and urban areas (personal observations). *Pachycondyla chinensis* was collected within the Great Smoky Mountains National Park (GSMNP) from a forest edge at the demonstration frontier farm near the Oconoluftee visitor center (Paysen unpublished data 2001). Although no further collections of the species have been

made within the park, a large population was identified in Gatlinburgh, TN at the northern boundary and in Cherokee, NC at the southern entrance (Paysen and Zungoli unpublished data 2005). Based on observations of other southeastern forests, it is reasonable to assume that this species has the potential to threaten the native arthropod communities of GSMNP. The goals of this research are to increase knowledge of *P. chinensis* distribution, natural history, and community ecology as a potentially invasive species, and compare the ant assemblage composition of GSMNP to that of another southeastern forest with a substantial *P. chinensis* population.

Figure 3-1. Lateral view of posterior abdomen of *Pachycondyla chinensis*, collected in Clemson, South Carolina, USA, emphasizing the stinger. Scale bar = 0.2 mm.



Materials and Methods

World distribution

A search of museum collections and regional faunal publications was conducted to update the known distribution of *P. chinensis*. Inquiries concerning *P. chinensis* holdings were made of southeastern and Central-Atlantic university insect museums. Included in the survey were the following land-grant institutions: Auburn, Clemson, Delaware, Florida, Georgia, Louisiana State, Maryland, Mississippi State, North Carolina State, Tennessee, Virginia Polytechnic and State University.

Five synonyms associated with the species were used as search criteria. *Pachycondyla chinensis* should not be confused with *Pachycondyla solitaria* (Smith F. 1860), a valid Indonesian species described from the male only.

Summary Systematics: *Pachycondyla chinensis* (Emery 1895)

Ponera solitaria Smith F. 1874; original description of worker, Hiogo, Japan

Ponera nigrita subsp. *chinensis* Emery 1895; description of worker, China; junior synonym

Euponera (Brachyponera) chinensis, Emery 1909; generic combination

Brachyponera chinensis, Brown 1958; generic combination, *Brachyponera solitaria* (Smith F. 1874) becomes junior homonym of *Brachyponera solitaria* (Smith F. 1860), first available replacement name [junior synonym]

Pachycondyla chinensis, Bolton 1995; generic combination

Nest characterization

The campus of Clemson University (Pickens Co., SC, USA, 34E40NN by 82E49NW) and surrounding area (i.e., urbanized, open-grassy, and forested areas) was surveyed visually for *P. chinensis* workers that could be followed to a nesting site. A nest site was identified as an aggregation of workers occupying excavated galleries. Nest sites < 25 cm apart and connected were considered part of the same polydomous nest. Nests were described and collected in September 2004, May 2005, and April 2006. Nests were excavated by loosening the ground surrounding the perimeter of the nest with a shovel and digging beneath it. Soil was removed to a depth where no ant-containing galleries were found. Colony dimensions and their depth in the soil were recorded. Excavated materials were placed in 18.8-L plastic buckets and returned to the laboratory where a multi-step process was used to separate ants from the soil. Excavate was sifted to separate ants from fine organic material and ants, larger debris, and soil particles were spread evenly in a 58 cm x 38 cm x 15 cm plastic pan coated with Fulon[®]. Test tubes (2.5 cm x 23 cm length) containing moist sponges were wrapped in aluminum foil and placed horizontally in the bottom of the pan. Ants aggregated in the test tubes as the soil dried. After 12-48 hr, the test tubes were removed and ants were collected by aspiration and placed in 6-dram vials with 85% ethanol. All ants remaining in the soil were hand collected. Ants were counted using a dissecting microscope (12x) and the number of workers and dealated females was recorded. Pearson's product-moment correlation coefficient was calculated to measure the strength of the correlation between worker and

queen numbers within nests. Calculations were performed in Sigma-Stat (SPSS, Inc., Chicago, Illinois).

Ecological characterization in a Formicid community context

To evaluate the ecology of *P. chinensis* the ant community was characterized in the Fant's Grove area (Pickens and Anderson Co., SC, USA, 34°38'N by 82°50'W) of the Clemson University Experimental Forest, a 7,074-ha tract of primarily second-growth forest with intermittent, maintained pasturelands. This site was chosen as an example of a southeastern forest with a well established population of *P. chinensis*.

Six, 180-m transects were established, with three transects positioned in forest habitat and three in open-field, grassland habitat. Sampling stations were established at 30-m intervals along transects, with seven stations per transect. At each sampling station, pitfall traps were used that consisted of test tubes (2 cm x 15 cm) half filled with propylene glycol and inserted into outer sleeves of PVC piping to facilitate removal. Pitfall traps were left in the field for 1 wk. Additionally, in the forest transects, the complementary technique of mini-Winkler litter extraction (Bestelmeyer et al. 2000) was used. Forest litter from a 1-m² quadrat was sifted through a 7-mm sieve and resulting condensed litter and arthropods were transported to the laboratory in nylon bags for mini-Winkler litter extraction. Litter was transferred into a mesh sac and suspended inside a closed, hanging, nylon outer sac with an alcohol collection receptacle at the bottom. Litter was allowed to dry at room temperature for 48 hr, and escaping ants and other arthropods were captured in 80% ethanol. Ants from 42 forest samples (21 pitfall, 21 litter) were pooled by sampling station for analyses. All ant species, with the exception of

members of the *Aphaenogaster fulva-rudis-texana* complex (Enzmann) (Umphrey 1996), were identified to species, following the taxonomy of Bolton (1995). Voucher specimens for all species were deposited in the Clemson University Arthropod Museum.

A species accumulation curve was constructed to assess the adequacy of sampling by comparison of the observed richness and the expected richness obtained from the Incidence-Based Coverage Estimator (ICE) over 1000 resampling runs with the 'Ws2m.exe' program (Turner et al. 2000). Descriptive statistics, including density, frequency, relative density, relative frequency, and relative importance were calculated for each species to describe the ant community (McCune and Grace 2002). A modified relative importance value was calculated by averaging relative frequency and relative density. Because the data were not normally distributed and the samples were related, overall comparison of species density was accomplished with a Friedman one-way repeated measures ANOVA based on ranks. Comparisons among pairs of species were made using Tukey's method of multiple comparisons at a family-wise error rate of 5%. All calculations were performed in Sigma-Stat (SPSS). Comparison of the presence/absence frequency distribution between all pairs of species was carried out using chi-square analyses or in some cases Fisher Exact tests when more than 20% of the expected values were less than five (SPSS). The distribution of relative importance values was assessed for extreme values, with a combination of a box and whisker plot, normal distribution percentiles, and exponential distribution percentiles. An importance value was considered extreme if it was beyond the upper fence of the box and whisker plot or beyond the 95th percentile of the normal or exponential distribution. Interspecific

associations were measured with an adapted version of Cole's C_7 coefficient (Ratliff 1982) and associations were tested to determine if they were significantly different from zero with chi-square analyses.

Comparison of the forests ant communities of GSMNP to that of a forest populated by *P. chinensis* in the southeastern USA

To compare the ant communities of three sites in the GSMNP with those of the Fant's Grove area, twenty one ant samples (from combined litter and pitfall catches identical to those performed in Fant's Grove) were obtained from forests at each of three areas within the park: Cades Cove, Cataloochee, and Oconoluftee. These samples were obtained in July-August of 2003 and 2004 and were randomly selected from a larger data set (Paysen unpublished data). Non-metric multidimensional scaling (NMDS) in PC-ORD version 4.34 (McCune and Mefford 1999) used the Sørensen ecological distance measure to determine how ant communities varied among the four sites in terms of species assemblages. NMDS does not assume linear relationships among variables, performs well with non-normal data, and allows overlays of individual species data to be illustrated on the whole-community model (McCune and Grace 2002).

Results

World distribution

In North America, *P. chinensis* has been documented from Georgia, North Carolina, South Carolina, and Virginia (Smith 1934, Carter 1962ab, Hunter 1974, Hunter and Farrier 1975, Smith 1979, Mackay and Vinson 1989, Peck et al. 1998, Zettler et al. 2004, Nelder et al. 2006) (Table 3-1). Along with the new record for GSMNP (Oconoluftee Visitors Center), specimens were taken from the following seven South

Carolina counties during this study: Anderson, Beaufort, Greenville, Lancaster, Oconee, Pickens, and York. The populations in these adjacent counties (excluding Beaufort), though limited to forested and urban habitats, might be contiguous and are possibly interbreeding. In Tennessee, *P. chinensis* has been collected in Knoxville, Alcoa/Maryville, Pigeon Forge, Oak Ridge, and Gatlinburg (Karen Vail pers. comm., Paysen and Zungoli unpublished data). Specimens were also identified from Guntersville, Alabama, and Cherokee, North Carolina, further extending the range of *P. chinensis* in the southeastern USA (Paysen unpublished data).

The world distribution of *P. chinensis* is limited to China, Japan, Myanmar, New Zealand, South Korea, Taiwan, United States, and Vietnam. However, holdings at the Harvard University, Museum of Comparative Zoology (MCZ) expand the range within Australasian, Oriental, and Palearctic locations (Stefan Cover pers. comm.) (Table 3-1, Figure 3-2).

Table 3-1. World distribution of *Pachycondyla chinensis* organized via biogeographical realms and countries (states given for the USA)

Geographic locations	References
Australasian	
New Zealand	Brown 1958, Green 1992
Papua New Guinea	MCZ ¹
Solomon Islands	MCZ
Nearctic	
United States	
Alabama	Paysen unpublished data
District of Columbia	Smith 1934
Georgia	Smith 1934, Smith 1979, Mackay and Vinson 1989, Ipser et al. 2004
North Carolina	Smith 1934, Carter 1962, Hunter 1974, Hunter and Farrier 1975, Nuhn 1977, Smith 1979, Mackay and Vinson 1989, Peck et al. 1998,
South Carolina	Zettler et al. 2004, Nelder et al. 2006, Paysen unpublished data
Tennessee	Paysen unpublished data, Vail pers. comm.,
Virginia	Smith 1934, Smith 1979, Mackay and Vinson 1989
Oriental	
China	Gist 1924, Zhenghui 1994
Guam (USA)	MCZ
India	MCZ
Indonesia	MCZ
Myanmar	Emery 1895, MCZ
Nepal	MCZ
Philippines	MCZ
Sri Lanka	MCZ
Taiwan	Wheeler 1921
Thailand	MCZ
Vietnam	Eguchi et al. 2005
Palearctic	
China	Emery 1895, Wheeler 1921, Gist 1924
Japan	Smith 1874, Teranishi 1929, Sawada 1953, 1959, Imai and Kubota 1972, Kondoh 1978, Kondoh and Kitazawa 1984, Terayama and Yamane 1984, Ogata 1987, Ohtaki et al. 1988, Xu 1994, Xu et al. 1994, Fukuzawa et al. 2002, Matsuura and Nishida 2002
South Korea	Choi and Park 1991, Bae et al. 1999, Yun et al. 1999, Kim et al. 2001, Cho et al. 2002

Notes: ¹ MCZ = Museum of Comparative Zoology, unpublished records.

Figure 3-2. World distribution of *Pachycondyla chinensis*



Nest characterization

Nesting sites were located in three habitat types: urbanized areas around buildings and landscaping (6/13), forest edges (4/13), and interior forests (3/13) (Table 2). No nests were found in open-grassy areas. Nest entrances were cryptic with little excavate or other debris around the opening. Galleries of all nests were associated with structural objects including logs (6/13), rocks (3/13), subterranean tree roots (1/13), and bricks, boards, or other human-made debris (5/13). All nests were shallow, reaching maximum depths of approximately 3 to 10 cm (Table 3-2) beneath the surface in loose soil or were located above the surface in decomposing logs. Occasionally, in urban habitats only, nests were polydomous (4/13) with dense aggregations of nest chambers < 25 cm apart and situated under materials associated with landscaping or debris piles. Nests were usually (9/13) monodomous. Nest sites were sometimes (5/13) associated with subterranean termites, *Reticulitermes* spp. (Isoptera: Rhinotermitidae), and occupied abandoned and active termite galleries in surface and subterranean decaying wood. During the disruptive process of nest excavation, *P. chinensis* workers stung termites and carried them in their mandibles. The number of workers varied (Table 3-2) from 39 to 5,719 (mean = $1,044 \pm 448.8$, $n = 13$). One single queen and three queenless nests were found. All remaining colonies had multiple dealated females per nest. The number of workers was positively correlated with the number of dealated females in the nests ($P < 0.022$, $r = 0.628$). Queen numbers varied from 0 to 37 (mean = 11.7 ± 3.70 , $n = 13$). The maximum percentage of dealated females was 18% in a colony of 118 ants. Male and female alates were observed at nest entrances in July 2005 and May-July 2006. No female reproductives were seen

flying from the nests. However, females ($n=158$) and males ($n=1984$) were captured in light traps (June-August 2006) in Pendleton, SC, and alates of both sexes were observed away from nest sites.

Table 3-2. Colony characterization: *Pachycondyla chinensis* collected in Clemson, Pickens County, South Carolina, USA (2005-2006). Excavated colonies arranged in descending order of number of workers. ¹ Nest dimension variables: L = length, W = width, D = depth

Colony	Number Workers	Number Queens	Percent Queens	Nest Dimensions ¹ L, W, D (cm)	Habitat	Structural Objects	Nest Structure
1	5,719	22	0.38	726, 30, 9	urban	rocks	polydomous
2	2,692	36	1.33	457, 61, 8	urban	rocks and boards	polydomous
3	1,818	37	2.03	2500, 41, 8	urban	rocks and other materials	polydomous
4	1,048	18	1.72	152, 76, 10	urban	oak tree roots	monodomous
5	766	7	0.91	31, 31, 8	urban	concrete blocks	monodomous
6	738	5	0.68	152, 152, 3	urban	concrete blocks and bricks	polydomous
7	210	6	2.86	25, 25, 10	forest edge	decomposing log	monodomous
8	132	2	1.52	N/A	forest	decomposing log	monodomous
9	121	0	0.00	15, 15, 8	forest edge	manmade cellulose debris	monodomous
10	118	0	0.00	91, 46, 5	forest	decomposing log	monodomous
11	100	18	18.00	N/A	forest	decomposing log	monodomous
12	71	0	0.00	28, 41, 8	forest edge	decomposing log	monodomous
13	39	1	0.26	30, 15, 8	forest edge	decomposing log	monodomous

Notes: ¹ Nest dimension variables: L = length, W = width, D = depth

Ecological characterization in a Formicid community context

This study at Fant's Grove yielded 792 individual ants, comprising 22 species, from the combined techniques of litter sifting and pitfall trapping at 42 sampling stations (Table 3-3, forest habitats). Four species were new South Carolina records: *Pyramica clypeata* (Roger), *Pyramica ornata* (Mayr), *Pyramica rostrata* (Emery), and *Strumigenys louisiane* Roger. Open-field transects did not yield *P. chinensis* foragers and were characterized by five ant species (in order of highest to lowest abundance): *Solenopsis invicta* Buren, *Solenopsis molesta* (Say), *Ponera pennsylvanica* Buckley, *Aphaenogaster treatae* Forel, and *Pheidole bicarinata* Mayr. Data from open-field transects were not included in further community analyses.

Pachycondyla chinensis and 16 additional species were collected in pitfall and litter samples from forest transects (Table 3-3). The vegetation in this forest habitat is characterized as mesic oak-hickory that reestablished on a cotton plantation more than 80 years ago. The canopy is dominated by loblolly pine (*Pinus taeda* L.), shortleaf pine (*Pinus echinata* Miller), black oak (*Quercus velutina* Lam.), southern red oak (*Q. falcata* Michx.), turkey oak (*Q. laevis* Walt.), water oak (*Q. nigra* L.), white oak (*Q. alba* L.), and willow oak (*Q. phellos* L.). Other trees making up the canopy were American holly (*Ilex opaca* Ait.), beech (*Fagus grandifolia* Ehrh.), eastern red cedar (*Juniperus virginiana* L.), flowering dogwood (*Cornus florida* L.), redbud (*Cercis canadensis* L.), red maple (*Acer rubrum* L.), sweetgum (*Liquidambar styraciflua* L.), tulip tree (*Liriodendron tulipifera* L.), and wild black cherry (*Prunus serotina* Ehrh.).

Table 3-3. Forest ant species from pitfall and leaf litter samples in order of ranked relative importance values.

Rank	Species	Descriptive Statistics				
		Total		Relative		
		Density ¹	Frequency ²	Density ³	Frequency ⁴	Importance ⁵
1	<i>Paratrechina faisonensis</i> (Forel)	206 ^a	17 ^a	0.274	0.187	0.231
2	<i>Pachycondyla chinensis</i> (Emery)	209 ^{bd}	6 ^b	0.278	0.062	0.170
3	<i>Aphaenogaster rudis</i> cmplx (Enzmann)	107 ^{ab}	17 ^a	0.142	0.187	0.165
4	<i>Ponera pennsylvanica</i> Buckley	85 ^{abd}	12 ^a	0.113	0.135	0.124
5	<i>Myrmecina americana</i> Emery	30 ^{abd}	13 ^a	0.040	0.145	0.092
6	<i>Crematogaster ashmeadi</i> Mayr	73 ^{cd}	6 ^b	0.097	0.062	0.079
7	<i>Amblyopone pallipes</i> (Haldeman)	11 ^{cd}	7 ^b	0.014	0.072	0.043
8	<i>Leptothorax curvispinosus</i> Mayr	8 ^{cd}	3 ^{bc}	0.010	0.041	0.026
9	<i>Solenopsis molesta</i> (Say)	4 ^{cd}	4 ^{bc}	0.005	0.041	0.023
10	<i>Hypoponera opacior</i> (Forel)	7 ^{cd}	2 ^{bc}	0.009	0.031	0.020
11	<i>Prenolepis imparis</i> (Say)	2 ^{cd}	2 ^{bc}	0.002	0.020	0.011
12	<i>Pyramica ornata</i> (Mayr)*	2 ^{cd}	2 ^{bc}	0.002	0.020	0.011
13	<i>Camponotus americanus</i> Mayr	1 ^{cd}	1 ^{cd}	0.001	0.010	0.005
14	<i>Proceratium silaceum</i> Roger	1 ^{cd}	1 ^{cd}	0.001	0.010	0.005
15	<i>Pyramica clypeata</i> (Roger)*	1 ^{cd}	1 ^{cd}	0.001	0.010	0.005
16	<i>Pyramica rostrata</i> (Emery)*	1 ^{cd}	1 ^{cd}	0.001	0.010	0.005
17	<i>Strumigenys louisiane</i> Roger*	1 ^{cd}	1 ^{cd}	0.001	0.010	0.005

Notes: ¹Density = Sum of all individuals captured at 21 stations, values with the same letter are not significantly different at $P < 0.05$;

²Frequency of occurrence at 21 stations; values with the same letter are not significantly different $\alpha = 0.05$; ³Relative Density, of 750 individuals collected; ⁴Relative Frequency, of 96 occurrences; ⁵Relative Importance Value = (Relative density + Relative

Frequency)/2; * New South Carolina State record

The ground cover and undergrowth (i.e., vegetation < 5 m tall) was a mixture of shrubs, trees, and vines dominated by beech (*F. grandifolia*), poison ivy (*Toxicodendron radicans* (L.)), saw greenbrier (*Smilax bona-nox* L.), shagbark hickory (*Carya ovata* (Mill.)), southern red oak (*Q. falcate*), sweetgum (*L. styraciflua*), and white oak (*Q. alba*). Other plants making up the understory were American holly (*I. opaca*), American snowbell (*Styrax americanus* Lam.), bigleaf snowbell (*Styrax grandifolius* Ait.), common vetch (*Vicia sativa* L.), eastern red cedar (*J. virginiana*), groundcedar (*Lycopodium complanatum* L.), muscadine (*Vitis rotundifolia* Michx.), redbud (*Cercis canadensis* L.), red maple (*A. rubrum*), silktree (*Albizia julibrissin* Durazz.), and turkey oak (*Q. laevis*). The canopy cover for these sites was approximately 83%, with ground plants receiving little direct sunlight. The soil consisted of clay covered by leaf litter composed primarily of pine needles and oak leaves with logs and stumps.

Although the ant-species accumulation curve calculated from forest ant data did not reach an upper-limit asymptote, a reduction in the increase of species richness values above the 10-sample level was reached. The observed species richness (17) captured 81% of the ICE predicted richness (mean = 20.98, variance = 1.07, for $n = 1000$ runs). I conclude that the majority of forest, ground-dwelling ants were collected during this study and that any species escaping detection are rare and infrequently encountered.

Friedman's analysis of ranked-density data revealed significant differences among the species, and the Tukey's test indicated four significantly different groupings of species (Table 3-3). The six most abundant species, *P. chinensis*, *Paratrechina faisonensis* (Forel), *A. fulva-rudis-texana* complex, *Crematogaster ashmeadi* Mayr,

Myrmecina americana Emery, and *Ponera pennsylvanica* Buckley, accounted for approximately 85% of all individuals collected. *Pachycondyla chinensis*, with 209 collected workers, was the most abundant ant in the study.

Pairwise analyses of frequency contingency tables revealed four significantly different groupings of species (Table 3-3). The four most frequently collected taxa, *P. faisonensis*, *A. fulva-rudis-texana* complex, *P. pennsylvanica*, and *M. americana*, accounted for 61% of all collections. *Paratrechina faisonensis* and *A. fulva-rudis-texana* complex were the most frequently collected taxa and were each found in 17 of 21 samples.

Relative importance values (RIV) had an exponential distribution, with three species in the upper end of the distribution: *P. faisonensis*, *P. chinensis*, and *A. fulva-rudis-texana* complex. The value for *P. faisonensis* (RIV = 0.231) was the highest and was significantly different, falling outside the upper fence on the box and whisker plot, above the 99th percentile on the exponential distribution, and had a normal distribution percentile of 99.2%. The relative importance value for *P. chinensis* (RIV = 0.171) was the second highest and fell inside the upper fence on the box and whisker plot, at the 95th percentile on the exponential distribution, and had a normal distribution of 94.8%. The third highest value for *A. fulva-rudis-texana* complex (RIV = 0.165) fell inside the upper fence on the box and whisker plot, within the 90th percentile on the exponential distribution and had a normal distribution of 92.8%. Interspecific species associations (Adapted C_7 coefficient values) were calculated for pairings between *P. chinensis* and five other ecologically similar ants with the highest importance values: *A. fulva-rudis-*

texana complex, *C. ashmeadi*, *M. americana*, *P. faisonensis*, and *P. pennsylvanica*.

Pachycondyla chinensis and *P. faisonensis*, the two most important ants in the community in terms of RIVs, had a significant negative association ($C_7 = -0.4$; $X^2 = 8.26$, $df = 1$, $P < 0.005$). No other species pairings revealed C_7 values significantly different from zero, indicating that no other strong associations were present in the data matrix.

Comparison of the forests ant communities of GSMNP to that of a forest populated by *P. chinensis* in the southeastern USA

Ordination of ant community assemblages at Cades Cove, Cataloochee, Oconoluftee (three GSMNP sites) and Fant's Grove (*P. chinensis* invaded site) with NMDS produced a six-dimensional solution with 72% of the variation explained by the first three axes. The six dimensional solution was selected because it maximized the reduction of stress between the actual and reduced dimensional matrices and was highly significant ($p = 0.0196$) in comparison to a 50-run Monte Carlo simulation where values in the real matrix were randomly shuffled within species (Table 4). The Fant's Grove site did not separate from the GSMNP sites (Figure 3) with the exception of three sites with high *P. chinensis* abundance (Figure 4). Abundance of the other dominant ants in Fant's grove, *A. fulva-rudis-texana* complex, *M. americana*, *P. faisonensis*, and *P. pennsylvanica*, was distributed across sites (Figures 3-8).

Table 3-4. Non-metric Multidimensional Scaling: Stress in Relation to Dimensionality (Number of Axes)

Axes	Stress in real data 40 run(s)			Stress in randomized data Monte Carlo test, 50 runs			p
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	
1	36.560	40.789	44.747	42.064	47.267	58.101	0.0196
2	25.098	27.212	39.239	26.213	30.991	43.129	0.0196
3	19.493	23.051	41.513	19.803	26.389	40.087	0.0196
4	16.956	19.948	27.610	17.401	25.800	56.817	0.0196
5	15.273	21.199	55.752	15.074	22.893	49.087	0.0392
6	13.366	18.728	51.652	13.965	22.154	51.718	0.0196

Notes: p = proportion of randomized runs with stress < or = observed stress;
i.e., $p = (1 + \text{no. permutations} \leq \text{observed}) / (1 + \text{no. permutations})$

Figure 3-3. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant's Grove (*Pachycondyla chinensis* invaded site). Each point is a two dimensional representation of ant species composition at each sampling station. Stations that are close together in ordination space are more similar than those that are far apart.

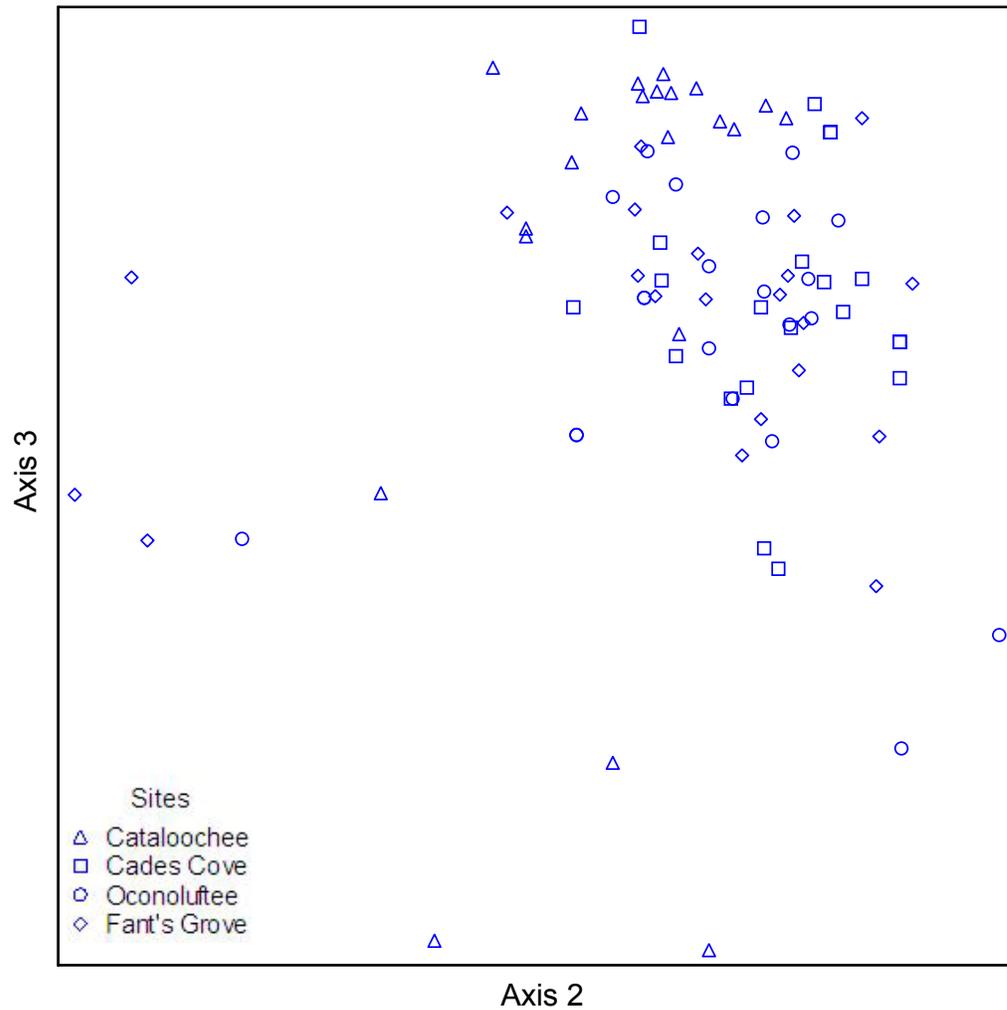


Figure 3-4. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant's Grove (*Pachycondyla chinensis* invaded site). Each point is a two dimensional representation of ant species composition at each sampling station. Stations that are close together in ordination space are more similar than those that are far apart. Abundance of *Pachycondyla chinensis* at each site is represented by the area of each symbol.

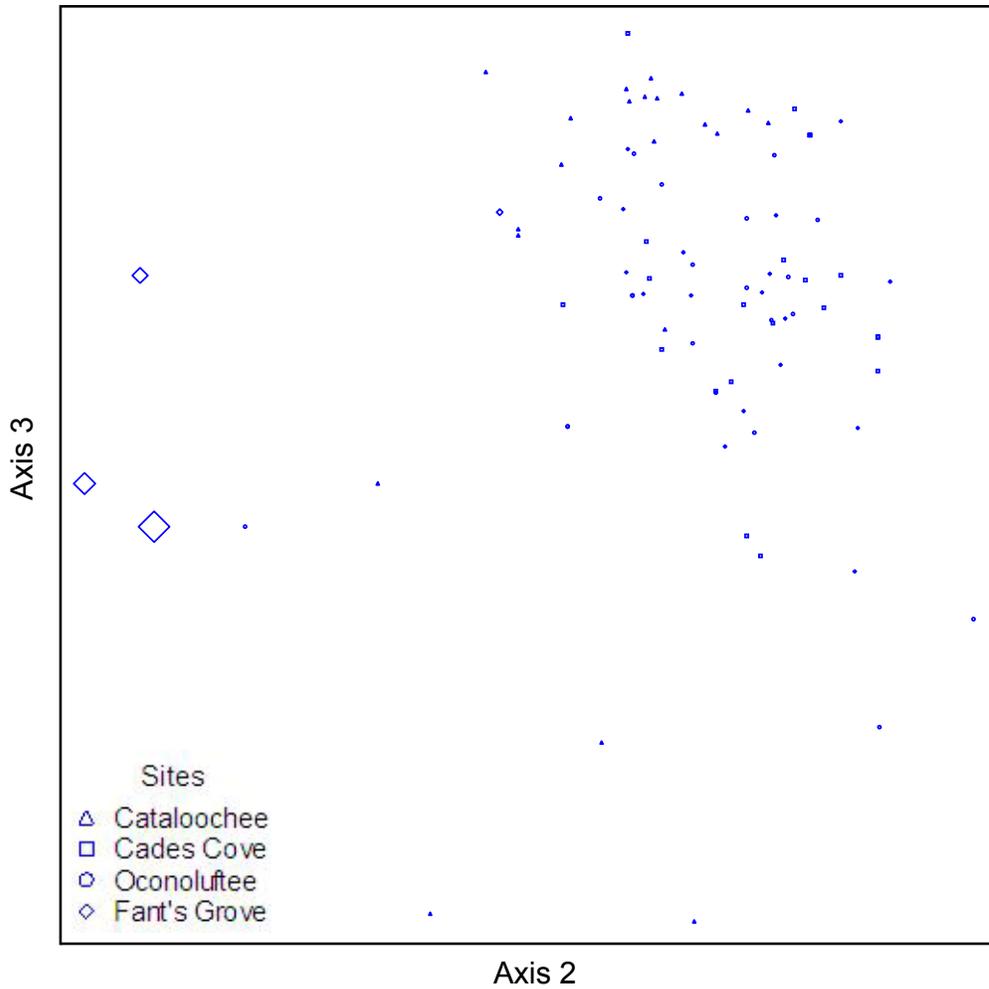


Figure 3-5. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant's Grove (*Pachycondyla chinensis* invaded site). Each point is a two dimensional representation of ant species composition at sampling stations. Stations that are close together in ordination space are more similar than those that are far apart. Abundance of *Aphaenogaster rudis* complex at each site is represented by the area of each symbol.

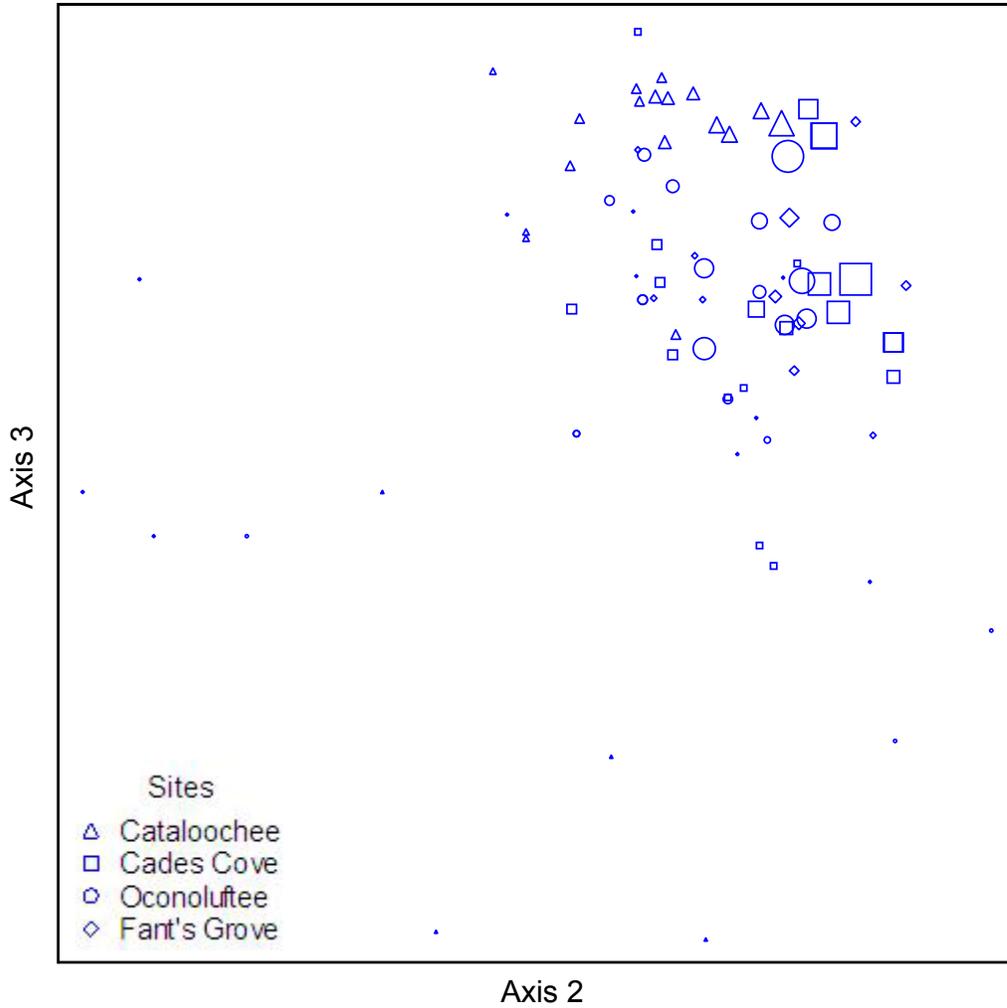


Figure 3-6. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant's Grove (*Pachycondyla chinensis* invaded site). Each point is a two dimensional representation of ant species composition at sampling stations. Stations that are close together in ordination space are more similar than those that are far apart. Relative abundance of *Myrmecina americana* at each site is represented by the area of each symbol.

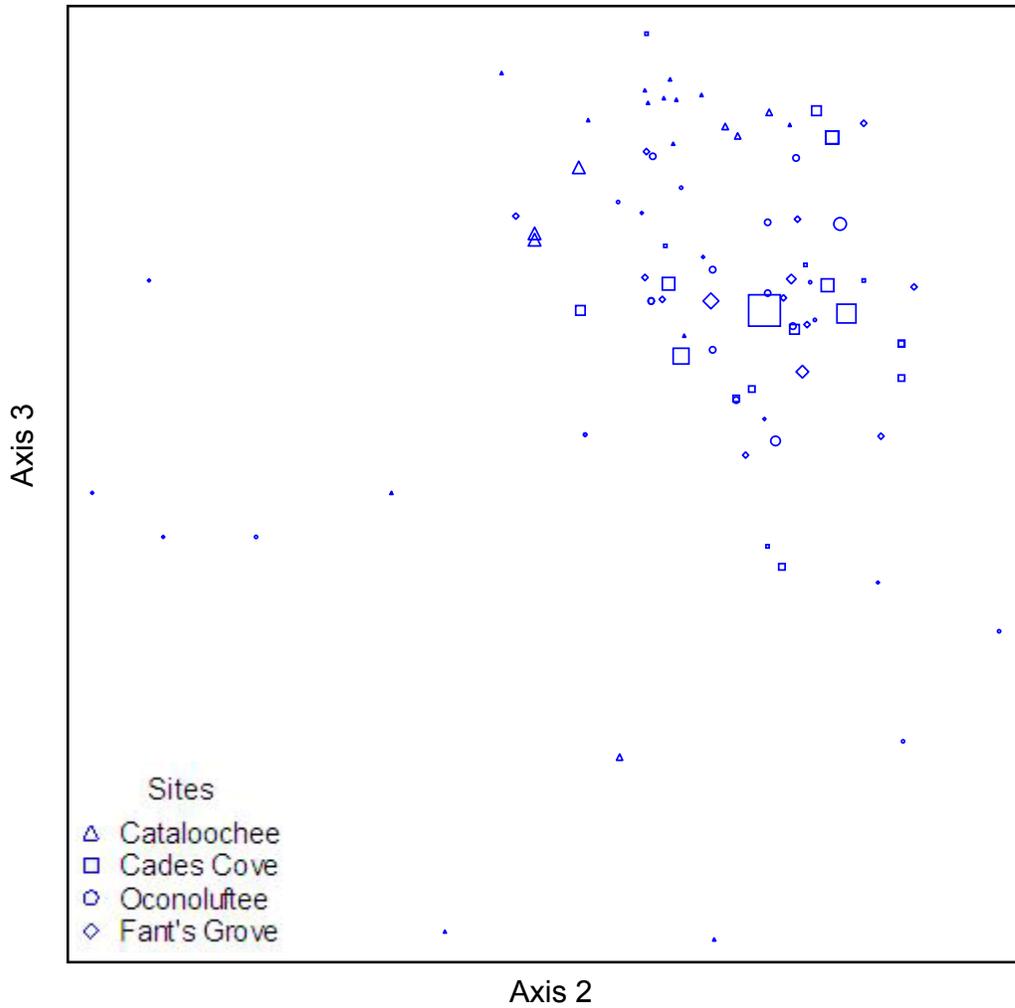


Figure 3-7. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant's Grove (*Pachycondyla chinensis* invaded site). Each point is a two dimensional representation of ant species composition at each sampling station. Stations that are close together in ordination space are more similar than those that are far apart. Relative abundance of *Paratrechina faisonensis* at each site is represented by the area of each symbol.

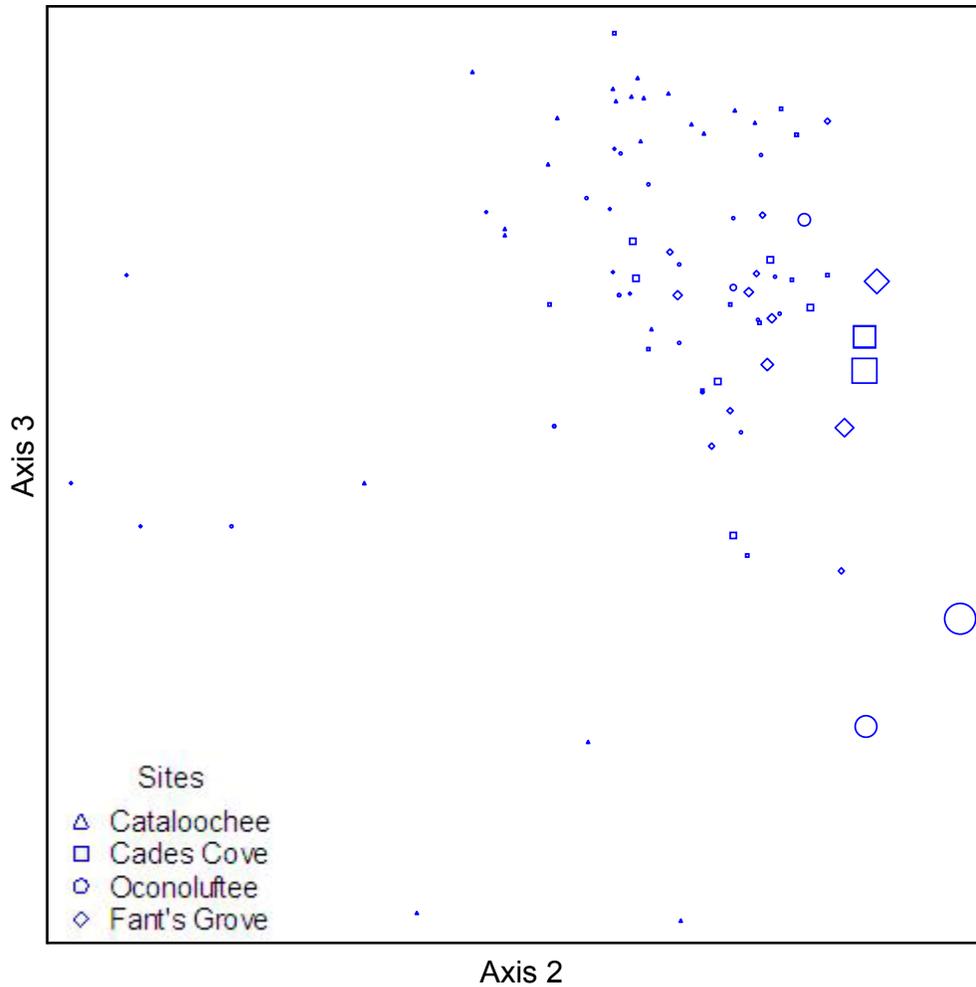
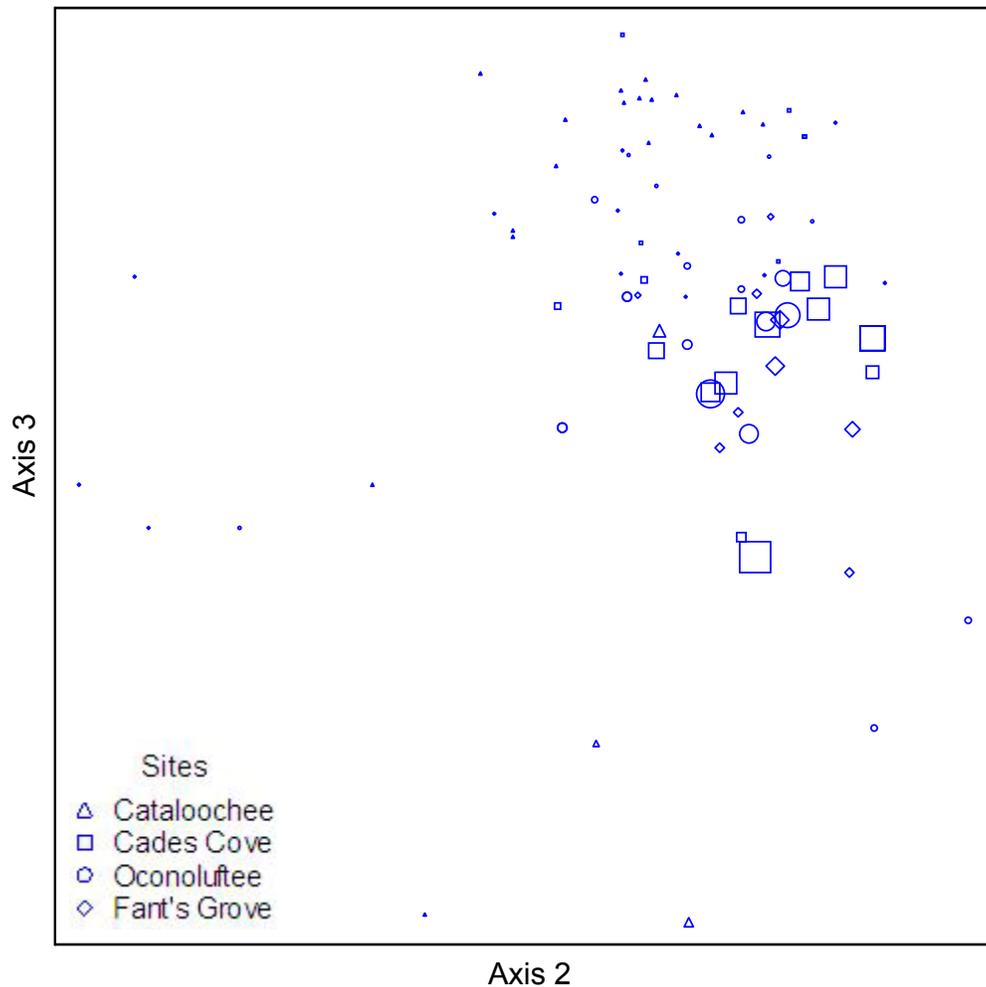


Figure 3-8. Non-metric multidimensional scaling of ant assemblage composition at four sites: Cades Cove, Cataloochee, Oconoluftee (GSMNP sites) and Fant's Grove (*Pachycondyla chinensis* invaded site). Each point is a two dimensional representation of ant species composition at each sampling station. Stations that are close together in ordination space are more similar than those that are far apart. Relative abundance of *Ponera pennsylvanica* at each site is represented by the area of each symbol.



Discussion

World distribution

The rates of population growth and range expansion of invasive species can vary markedly among species and habitats. An inherent lag phase follows the arrival of an adventive species in which populations persist at low levels of abundance and frequency. This initial lag phase is common to all species invasions, although in some cases the expansion or invasion phase occurs immediately following establishment, whereas in other cases prolonged lags occur in local population growth and/or range expansion (Shigesada and Kawasaki 1997). Prolonged lag phases can persist for decades, during which populations of invasive species often remain undetected by biologists (Crooks and Soulé 1999). The complex dynamics of delayed population growth are affected by ecological and evolutionary factors (Cox 2004, Kowarik 1995, Shigesada and Kawasaki 1997).

Pachycondyla chinensis was established in North America in at least three isolated locations by 1932 (i.e., Georgia, North Carolina, and Virginia), suggesting multiple primary or secondary introductions. This original pattern of widespread, isolated, and locally abundant populations does not rule out the possibility of secondary introductions but suggests that multiple, primary North American introductions occurred in the early 1900s. Because no quarantine measures have targeted this species, introductions might have continued over the last 100 yr. *Pachycondyla chinensis* has been intercepted in commerce at least twice (Smith 1934, Suarez et al. 2005), supporting this hypothesis. Continual, subsequent introductions might have overcome the negative

biological ramifications of bottleneck effects associated with inbreeding and allowed viable populations to emerge through the addition of new genetic diversity in North American populations.

Another explanation for the sudden emergence of *P. chinensis* as an important, widespread species might be adaptation to local conditions. These conditions include abiotic as well as biotic factors such as competitors and food sources. Small populations with limited genetic diversity are slow to evolve new mechanisms for dealing with new niches and can lead to prolonged lag phases if the species is maladapted to the new environment. As the populations of reproducing individuals increase, the likelihood of the emergence of novel beneficial traits also increases. Large populations of *P. chinensis* might be quickly evolving to new North American habitats. The large nest size and polydomous colony structure in South Carolina colonies might be an adaptation that has emerged since the observations by Creighton (1950) and Smith (1947) who reported much smaller colonies. Larger nests with more cooperating workers could allow the species to displace competing organisms and monopolize resources more frequently.

The local environment might have changed in a way that benefits *P. chinensis*. The southeastern United States has experienced an influx of *S. invicta*, altering the ant community (Gotelli and Arnett 2000) and possibly benefiting other invasive species, including *P. chinensis*. In addition, a long-term drought beginning in 2001 in this region might have influenced the recent population explosion of *P. chinensis* in the southeastern USA by negatively affecting native competing species that do not nest in association with moisture-retaining structural objects.

A delay in the long-range spread of *P. chinensis* also could be associated with a dependence on human transport of infested materials. This dependence is especially pronounced in tramp species that reproduce primarily through budding and do not have the ability to disperse through long-range nuptial flights. Although local populations of these species grow quickly, leading to dense concentrations of nests and a monopolization of resources, long-range expansion is slow and unpredictable. The dense local populations described in the initial observations of this species (Smith 1934) appear to fit this profile.

Myrmica rubra (Linnaeus), another immigrant ant, experienced a lag phase (Groden et al. 2005) similar to that of *P. chinensis*. Precinctive to the North Palearctic (Czechowski et al. 2000), *M. rubra* was first reported in the United States nearly one hundred years ago from Massachusetts (Wheeler 1908) and subsequently multiple locations in Maine. This aggressive, stinging species is unlikely to have avoided detection in new areas. In the late 1990s, its range and density increased dramatically in coastal areas of Maine. Groden et al. (2005) suggested that the cause of the recent spread of dense populations of *M. rubra* is the result of postintroduction adaptation and subsequent population growth or increased annual temperatures in the northeastern USA.

Nest characterization

This study revealed that nests of *P. chinensis* vary in size but can become large polydomous colonies with nearly 6,000 workers. Colonies of this magnitude are uncommon in ponerine ants (Peeters 1993); these excavations might represent the largest known colonies in this subfamily. These results contrast with the observations made 50 yr

ago in North America that colonies contained 20 to several hundred individuals (Creighton 1950) and were “small” (Smith 1947). Colonies were similar to those described by Creighton (1950) in having multiple dealated females per nest. The majority of colonies excavated in this study were polygynous, with queens representing as much as 18% of the total individuals, suggesting a remarkable reproductive potential. The functionality of these dealated females however is unknown, warranting further work to determine the genetic origins of females and their respective contributions to egg laying. *Pachycondyla* species have varied reproductive strategies (Peeters 1993). Winged reproductives (queens) represent the ancestral state whereas the loss of the reproductive caste and subsequent reproduction by workers (gamergates) is a derived condition. *Pachycondyla chinensis* might represent an additional category where both queens and workers contribute genetically to the colony.

In several areas, nests occurred at high density in proximity to what I considered separate colonies (> 25 cm apart). Although the interactive behavior of nests and colonies was not examined experimentally in this research, no aggressive behaviors were noted between colonies during my observations. Some (3/13) of the nesting sites had no dealated reproductives. Reproduction by workers cannot be ruled out in the genus *Pachycondyla*, but the lack of a morphologically distinct reproductive suggests that these nesting sites were peripheral to other nests and connected through polydomy as a queenright colony. These observations, plus apparent polygyny in most (9/13) colonies, indicate that *P. chinensis* has some characteristics of a unicolonial species, a condition that could explain how these ants reach such high population densities. Unicolonial

species are characterized by the reproduction of multiple individuals in a single colony, low relatedness of nestmates, and low levels of aggression between neighboring nests/colonies and individuals (Keller 1995). This social structure is important in invasive species because a lack of territoriality among nests allows the formation of supercolonies comprising many nests that can extend over large ranges. This fluid colony organization allows unicolonial species to dominate native species, which compete among colonies for territories and resources, and has contributed to their overwhelming success and rapid invasions. Many unicolonial species reproduce effectively through colony fission or budding. This strategy preadapts invasive or tramp species to competition for limited nesting sites or other resources (Hölldobler and Wilson 1990, Hiebeler 2004), but also limits their long-range dispersal abilities. Tramp species are often dependent on humans for transport into uninvaded areas. Although I have collected male and female alates at light traps these catches are always heavily male biased. My hypothesis that colony budding might serve as a primary or secondary mode of reproduction in *P. chinensis* is supported by the positive correlation between worker and queen numbers, polydomous nesting habits, and male-biased alate flights. In addition, ponerine ants typically do not possess well-developed wing musculature (Peeters 1993) and probably are not capable of long-range flight. New queens, therefore, might disperse through nuptial flights, remain in the parent nest, or join nearby nests where they mate and have the potential to become functional egg layers. A combination of these possibilities is most likely.

The possibility of a unicolonial social structure and budding in *P. chinensis* should be explored. Genetic characterizations of reproducing individuals and assessments

of gene flow and worker/brood exchange between nesting sites within the expanded range of *P. chinensis* in North America are warranted. Additionally, behavioral studies should examine internest interactions, territoriality, and possible partitioning of resources in areas of high *P. chinensis* density. This type of work will reveal the nature of these populations and determine if they are unicolonial, on local or regional scales, a characteristic not previously associated with a ponerine ant.

Ecology of *P. chinensis* invasions

In Fant's Grove forest plots, *P. chinensis* was the most abundant and the second most important ant in the community. Several studies have reported *P. chinensis* in the southern USA. For example, *P. chinensis* has been recorded from Georgia in five, Piedmont-ecoregion counties (Ipser et al. 2004), from North Carolina in unknown location(s) (Peck et al. 1998), and from South Carolina in a single county in the Piedmont ecoregion (Zettler et al. 2004). These studies did not consider *P. chinensis* a significant part of the formicid communities and it was an uncommon ant in the southeastern USA, at least before 2001. Zettler et al. (2004) surveyed ground-dwelling ants in the same experimental forest as in this study but their sites had a different floral composition and sampling was done in October 2001. They collected 34 species of ants, with *Prenolepis imparis* Say and *Aphenogaster* species most common. Significant changes in the formicid-community in this experimental forest might have occurred in the 4 years since the sampling by Zettler et al. (2004) in 2001. My data demonstrate that *P. chinensis* was negatively correlated with *P. faisonensis*, the most important species in Fant's Grove, an important species in GSMNP (Paysen unpublished data), and perhaps the most common

native ant of the southeastern forests of North America (Lynch et al. 1980, Trager 1984). *Paratrechina faisonensis* nests in microhabitats similar to those of *P. chinensis*, such as in rotting logs and under cover objects (Lynch et al. 1980, Nuhn et al. 1992). I speculate that *P. chinensis* and *P. faisonensis* compete directly with one another for nesting sites. Whether this distributional relationship is directly attributable to negative interactions between these species should be the focus of future ecological work.

The complexity of ecological communities makes predicting biological invasions uncertain at best. The interactions of countless biotic and abiotic variables will ultimately determine the ability of an adventive species to invade a native ecosystem. However, the similarity of the ant communities in GSMNP and Fant's Grove, the observation of well established populations in the vicinity of the park (Gatlinburgh and Cherokee), and the collection of a colony within the park (Oconoluftee, visitor center) are strong circumstantial evidence that this species has the potential to invade the forests of GSMNP.

Within its precinctive range in China, Brown (1958) described *P. chinensis* as unusually dominant for a ponerine ant. My findings, coupled with this description, suggest that *P. chinensis* could threaten forest ecosystems in North America. Behavioral and ecological (abundance and frequency) dominance is important in structuring ant communities (e.g., Floren and Linsenmair 2000). *Pachycondyla chinensis* might have a significant effect on the community, considering its chemical defenses and numerical importance in this study. Ecological outcomes of invasion by *P. chinensis* are speculative, but likely will be negative with respect to the species richness not only of the

formicid community but also the arthropod community, as seen with other invasive ants, such as *S. invicta* (Vinson 1997, Wojcik et al. 2001) and *Linepithema humile* (Mayr) (Erickson 1971, Cole et al. 1992, Human and Gordon 1997).

Besides threatening ecological processes and biodiversity in the region, *P. chinensis* is a significant threat to public health and was recently linked to a case of anaphylaxis in a South Carolina sting victim (Nelder et al. 2006). Stings to humans cause local reactions (swelling, itching, and pain >2h) in 80% of victims, with approximately 1% demonstrating more serious large-local reactions (swelling > 5cm, pruritic papules, and symptoms lasting days to weeks).

Summary

Following a prolonged lag phase since its introduction in the early 1900s, *P. chinensis* has become well established in the southeastern United States. Nests of *P. chinensis* studied in South Carolina have abundant workers, are polygynous, and possess some of the characteristics of a unicolonial species, factors that contribute to a high reproductive potential and characterize ants capable of dominating the formicid community and organisms beyond. I have demonstrated that *P. chinensis* is functioning as a true invasive species with the ability to penetrate naturally forested areas where it becomes dominant, possibly out competing and displacing native species. Additionally, I have shown that the forests of GSMNP are similar in terms of ant assemblage composition and hypothesize that populations of *P. chinensis* in the surrounding area have the potential to invade the forests of the Park. The ecological outcomes of *P. chinensis* invasion are only speculative, but might be comparable to invasions by *L.*

humile and *S. invicta* in the United States and other countries. With ever-increasing global trade and travel, human-assisted transport, and the biological characteristics of the species in North America, the threat of significant range expansions by *P. chinensis* is a legitimate concern. The ecological and medical importance of this ant justifies further studies to understand its interactions with native biota and to develop control measures that are feasible and effective.

CHAPTER IV

THE EFFECT OF TECHNIQUE, SEASONALITY, AND HABITAT ON THE SAMPLING OF ANT COMMUNITIES IN THE FOREST AND GRASSLAND HABITATS OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK

Introduction

Bioindicator taxa are used in the comparative study of diversity in varying habitats and ideally, are sensitive to habitat conditions, reacting quickly to habitat change and allowing researchers to monitor environmental alteration with limited knowledge of the status of whole ecosystems. Although invertebrates have a history of successful use in the monitoring of aquatic habitats (e.g., James and Evison 1979), the widespread use of terrestrial arthropods has not been implemented until recently. This development is in large part due to increasing awareness of arthropods as a group that is numerically dominant in biomass and diversity (e.g., Wilson 1987b, Kim 1993), and has led to their use as bioindicators in many different ecosystems (Kremen 1992, Williams 1993, Longcore 2003). Ants have successfully been used as bioindicators in mine-site restoration where they accurately reflect changes in other invertebrate groups (Andersen 1997). Ants also have been useful bioindicators in monitoring the impact of fire, grazing, and logging (Neumann 1992, York 1994, Vanderwoude et al. 1997).

Ants are especially suited for monitoring programs in a bioindicator capacity because most species inhabit perennial nests that are relatively stable. The foraging range from these centrally located hubs of activity is limited compared to the range of other insects whose frequent inter-habitat movements are driven by nutrition, reproduction, or nesting requirements. Monitoring ants is reliable because they have a more constant presence than other insect groups (Alonso 2000). This type of presence is typically only seen in the sessile floral components of terrestrial ecosystems. Many ant species are also microhabitat specialists occupying highly specific feeding niches that usually are saturated. Niche saturation allows detailed resolution of fine-scale habitat heterogeneity and sensitivity to changes in habitat and biodiversity (Holldöbler and Wilson 1990).

Another important attribute of bioindicator taxa is the availability of sampling techniques that are both efficient and reliable in assessing biodiversity. Several well-defined techniques have been used to sample ant faunas (Bestlemeyer et al. 2000). Delabie et al. (2000) conducted a detailed study of the efficacy of different combinations of various techniques in the tropical rainforest of Bahia, Brazil. The most successful individual techniques included (ordered most to least efficient) Winkler litter extraction, Berlese funnel extraction, manual dead wood inspection, manual inspection of small soil samples, and seven-day pitfall sampling. Based on an analysis of the grouping of various techniques, they recommended the combination of Winkler litter extraction and seven-day pitfall traps as complementary techniques for sampling ground-foraging ants. These methods have become standard practice in inventory and monitoring programs (e.g.,

Fisher 1999) although their efficacy in temperate regions has not been investigated extensively (Martelli et al 2004, King and Porter 2005).

Winkler litter extraction has typically been used to assess ground-foraging species in forests (Bestlemeyer et al. 2000) and actively removes ants from the litter layer, capturing both nesting and foraging individuals. Conversely, pitfall trapping is a passive technique that relies on the foraging activity of ants that fall into subsurface collection devices and the varying sizes, habitats, foraging behavior, and activity levels of particular species can influence the likelihood of their capture with different techniques (Olson 1991, Melbourne 1999, Martelli et al 2004). Season and habitat likely will differentially alter the efficacy of these fundamentally different collection methods. The objective of my work is to evaluate the effectiveness of Winkler litter extraction and pitfall trapping as complementary techniques in grassland and forest habitats of the Great Smoky Mountains National Park (GSMNP) at three sampling times throughout the season.

Materials and Methods

As part of a larger study evaluating the edge effects on ant communities in the GSMNP, pitfall traps and mini-Winkler litter extraction were used to capture epigeic ants. A detailed account of landscape level sampling design is presented in Chapter II. Briefly, ants were sampled in the three major grasslands and the forests adjacent to these sites in GSMNP. Sites include Cades Cove, Cataloochee, and Oconoluftee. Sampling was conducted tri-annually for two calendar years (beginning July 2003) in December-January, March-April, and July-August. July-August sampling was the most intensive

with 220 sampling stations compared to the reduced, 24 sampling stations of December-January, and March-April sampling.

At each sampling station, pitfall traps consisted of test tubes (2 cm x 15 cm) half filled with propylene glycol and inserted into outer sleeves of PVC piping to facilitate removal. PVC sleeves were installed at ground level into holes in the soil that were formed using a slide hammer with a soil sampling attachment. Pitfall traps were left in the field for 1 wk. Mini-Winkler litter extraction (Bestelmeyer *et al.* 2000) also was used at each sampling station at a distance of 2 m from the pitfall site in an area free from foot traffic associated with sampling. Forest litter and other organic debris such as twigs, stems and nuts were broken up with a machete and collected from a 1-m² quadrat. These materials were sifted through a 7-mm sieve and resulting condensed litter and arthropods were transported to the field station in nylon bags for mini-Winkler litter extraction. Litter was transferred into a mesh sac and suspended inside a closed, hanging, nylon outer sac with an alcohol collection receptacle at the bottom. Litter was allowed to dry at ambient temperature for 48 hr and escaping ants and other arthropods were captured in 80% ethanol.

All ant species, with the exception of members of the *Aphaenogaster fulva-rudis-texana* complex (Enzmann) (Umphrey 1996), were identified to species, following the taxonomy of Bolton (1995). The *Aphaenogaster fulva-rudis-texana* complex is a group of sibling species that can only be delimited with cytotaxonomic techniques. Additionally, these techniques require preimaginal individuals and are not applicable to worker ants (Umphrey 1996). Hereafter in the text, this complex is referred to as *A. rudis* complex for

simplicity. The abundance (number of workers) of each species was recorded for each sampling method at each site. The occurrence of queens or males was not included because their presence does not necessarily indicate that a colony is established in the area sampled (Fisher 1999). Voucher specimens for all species were deposited in the Clemson University Arthropod Museum.

Several measures were used to characterize the performance of the two sampling techniques in the different seasons and habitats. Overall abundance, frequency of collection, species richness, and evenness were totaled as a descriptive statistic for each collection technique at each date and in each habitat. In addition, these variables were compared on an average per station basis with a Kruskal-Wallis one-way analysis of variance based on ranks (ANOVA). To isolate groups that differed, an all-pairwise multiple comparison procedure was used (Dunn's Method). This test was appropriate for non-normal data and independent samples. All calculations were performed in Sigma-Stat (SPSS). Bias towards pitfall or Winkler litter extraction was evaluated on a per species basis with Chi-square one-sample test for goodness of fit. The analysis was based on 2x2 contingency tables consisting of counts of species presence/absence with equal distributions as the expected values. Chi-square calculations were performed in a Microsoft Excel spreadsheet (Microsoft). Species-area curves for pitfall and Winkler extraction techniques were produced for forests and grasslands. These curves were produced by repeated ($n = 500$) subsampling of the data for each possible subsample size. These classical species area curves were supplemented with a calculation of the average Sørensen ecological distance between subsamples and the cumulative (total) species

composition of the entire sample. These values were plotted at each subsample size. This curve, unlike the species-area curve is a measure of species richness and species abundance. Using a combination of these curves is especially useful if the goal is to determine the sample size that is required to reach a consistent species composition as well as a stable species list. Species-area and Sørensen ecological distance curve calculations were performed in PC-ORD version 4.34 (McCune and Mefford 1999).

Results

Sampling Techniques

A total of 12,291 individual ants representing 59 species and 5 subfamilies were identified. In both forest and field habitats, a combination of pitfall trapping and Winkler litter extraction yielded greater species richness, at all subsample sizes, than either of the constitutive methods alone (Figure 1). Consistency of species composition, measured by average Sørensen ecological distance, was reached at nearly equal rates across sampling techniques and habitats (Figure 4-2).

Figure 4-1. Species accumulation curve for forest (A) and field (B) habitats. The curves were produced by repeated ($n = 500$) subsampling of the data for each possible subsample size and illustrate the effectiveness (accumulated species richness) of different methods: pitfall, Winkler, and a combination of both methods.

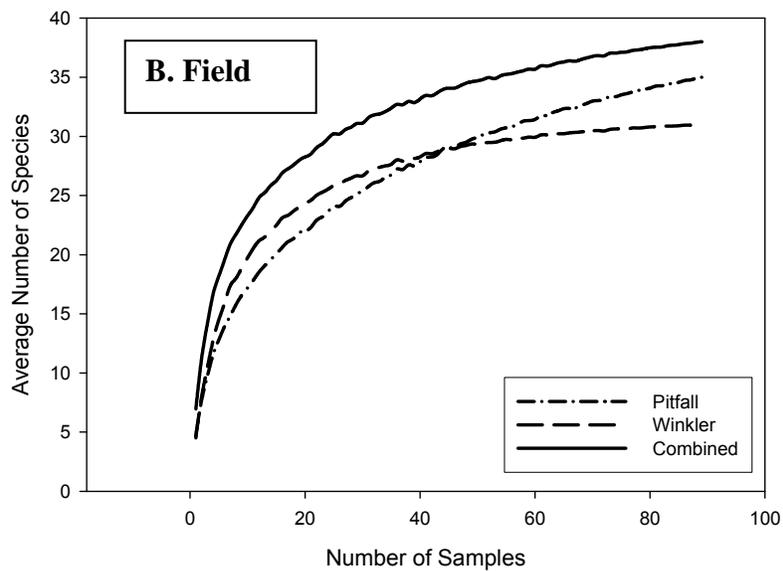
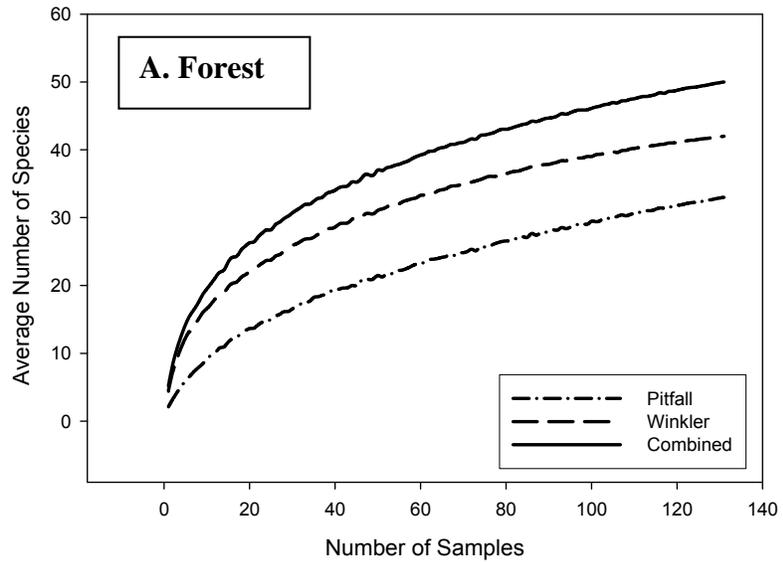
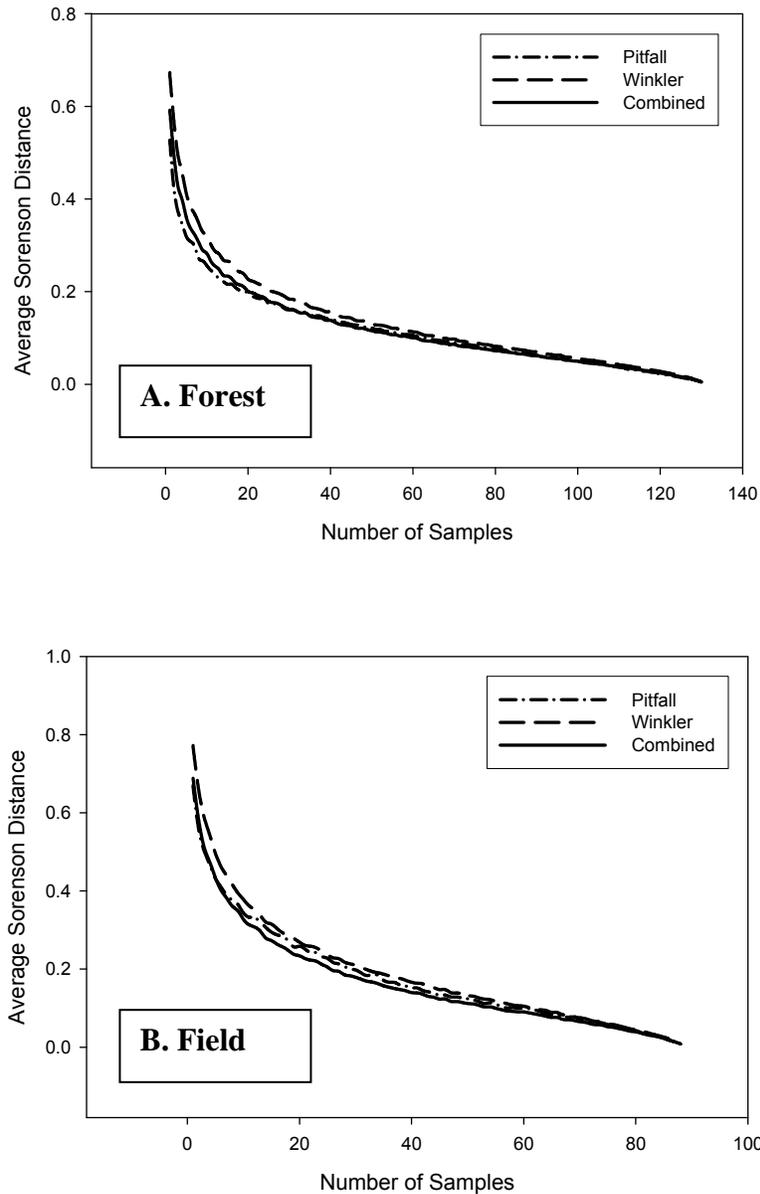


Figure 4- 2. Sørensen ecological distance curve for forest (A) and field (B) habitats. The curves were produced by repeated ($n = 500$) subsampling of the data for each possible subsample size and illustrate the effectiveness (community stability) of different methods: pitfall, Winkler, and a combination of both methods.



In the forest habitat, 33 species were captured with pitfall sampling, 42 with Winkler litter extraction, and 50 species with the combination of techniques (Table 4-1).

In forests, Winkler litter extraction consistently yielded more species than did pitfall trapping across all subsample sizes (1 – 131) (Figure 4-1. A). In addition, 12 species were biased towards Winkler litter extraction and one species was biased towards pitfall trapping in the forest (Table 1., $\alpha = 0.05$, d.f. = 1, X^2 critical value = 3.84). Analysis of variance revealed ($\alpha = 0.05$) that pitfall sampling differed from Winkler litter extraction and a combination of both techniques in terms of averaged sample-level abundance, richness, and diversity. There was no difference between Winkler litter extraction and the combined techniques in terms of these variables. Pitfall and Winkler litter extraction differed in terms of evenness, with the combined technique representing an intermediate value (Table 4-2).

Table 4-1. Comparison of pitfall and Winkler litter extraction techniques in field and forest habitats, the Great smoky Mountains National Park, July-August, 2003-2004.

Ant Species (γ -diversity = 58)	Field (n = 89)					Forest (n = 131)				
	Pitfall		Winkler		Bias	Pitfall		Winkler		Bias
	Count	%Freq	Count	%Freq		Count	%Freq	Count	%Freq	
Dolichoderinae										
<i>Tapinoma sessile</i> (Say)	19	21.35	24	26.97	none	3	2.29	11	8.40	Winkler
Ecitoninae										
<i>Neivamyrmex carolinensis</i> (Emery)	0	0.00	1	1.12	-----	0	0.00	0	0.00	-----
Formicinae										
<i>Acanthomyops claviger</i> (Roger)	0	0.00	0	0.00	-----	1	0.76	0	0.00	-----
<i>Brachymyrmex depilis</i> Emery	0	0.00	5	5.62	-----	1	0.76	9	6.87	Winkler
<i>Camponotus americanus</i> Mayr	0	0.00	0	0.00	-----	2	1.53	0	0.00	-----
<i>Camponotus chromaoides</i> (Fabricius)	0	0.00	0	0.00	-----	1	0.76	0	0.00	-----
<i>Camponotus nearticus</i> Emery	1	1.12	0	0.00	-----	1	0.76	0	0.00	-----
<i>Camponotus pennsylvanicus</i> (DeGeer)	2	2.25	0	0.00	-----	11	8.4	1	0.76	pitfall
<i>Camponotus subbarbatus</i> Emery	0	0.00	0	0.00	-----	0	0.00	1	0.76	-----
<i>Formica schaufussi</i> Mayr	1	1.12	1	1.12	-----	0	0.00	0	0.00	-----
<i>Formica neogagates</i> Emery	16	17.98	17	19.1	none	1	0.76	0	0.00	-----
<i>Formica subaenescens</i> Emery	0	0.00	0	0.00	-----	5	3.82	3	2.29	-----
<i>Formica subcericea</i> Say	3	3.37	0	0.00	-----	2	1.53	3	2.29	-----
<i>Lasius alienus</i> (Foerster)	21	23.6	19	21.35	none	17	12.98	35	26.72	Winkler
<i>Lasius flavus</i> (Fabricius)	1	1.12	16	17.98	Winkler	0	0.00	3	2.29	-----
<i>Lasius nearticus</i> W. M. Wheeler	0	0.00	0	0.00	-----	2	1.53	2	1.53	-----

Table 4-1 (continued). Comparison of pitfall and Winkler litter extraction techniques in field and forest habitats, the Great smoky Mountains National Park, July-August, 2003-2004.

Ant Species (γ -diversity = 58)	Field (n = 89)					Forest (n = 131)				
	Pitfall		Winkler		Bias	Pitfall		Winkler		Bias
	Count	%Freq	Count	%Freq		Count	%Freq	Count	%Freq	
<i>Lasius neoniger</i> Emery	52	58.43	25	28.09	pitfall	1	0.76	4	3.05	-----
<i>Lasius umbratus</i> (Nylander)	2	2.25	4	4.49	-----	1	0.76	2	1.53	-----
<i>Paratrechina parvula</i> (Mayr)	22	24.72	19	21.35	none	1	0.76	2	1.53	-----
<i>Paratrechina faisionensis</i> (Forel)	16	17.98	23	25.84	none	16	12.21	46	35.11	Winkler
<i>Paratrechina terricola</i> (Buckley)	0	0.00	0	0.00	-----	0	0.00	1	0.76	-----
<i>Prenolepis imparis</i> (Say)	3	3.37	3	3.37	-----	5	3.82	8	6.11	none
Myrmecinae										
<i>Aphaenogaster fulva</i> Roger	0	0.00	0	0.00	-----	0	0.00	1	0.76	-----
<i>Aphaenogaster rudis</i> complex (Enzmann)	3	3.37	7	7.87	none	120	91.6	112	85.50	none
<i>Aphaenogaster tennesseensis</i> (Mayr)	0	0.00	0	0.00	-----	1	0.76	0	0.00	-----
<i>Aphaenogaster treatae</i> Forel	47	52.81	12	13.48	pitfall	1	0.76	1	0.76	-----
<i>Crematogaster cerasi</i> (Fitch)	0	0.00	2	2.25	-----	0	0.00	0	0.00	-----
<i>Crematogaster pilosa</i> Emery	1	1.12	0	0.00	-----	0	0.00	0	0.00	-----
<i>Crematogaster punctulata</i> Emery	1	1.12	0	0.00	-----	0	0.00	0	0.00	-----
<i>Leptothorax curvispinosus</i> Mayr	0	0.00	0	0.00	-----	1	0.76	7	5.34	-----
<i>Leptothorax longispinosus</i> Roger	0	0.00	0	0.00	-----	0	0.00	2	1.53	-----
<i>Monomorium minimum</i> (Buckley)	13	14.61	11	12.36	none	0	0.00	1	0.76	-----
<i>Myrmecina americana</i> Emery	3	3.37	8	8.99	none	10	7.63	57	43.51	Winkler
<i>Myrmica americana</i> Emery	4	4.49	6	6.74	none	0	0.00	1	0.76	-----
<i>Myrmica latifrons</i> Starcke	45	50.56	28	31.46	pitfall	2	1.53	3	2.29	-----

Table 4-1 (continued). Comparison of pitfall and Winkler litter extraction techniques in field and forest habitats, the Great smoky Mountains National Park, July-August, 2003-2004.

Ant Species (γ -diversity = 58)	Field (n = 89)					Forest (n = 131)				
	Pitfall		Winkler		Bias	Pitfall		Winkler		Bias
	Count	%Freq	Count	%Freq		Count	%Freq	Count	%Freq	
<i>Myrmica pinetorum</i> W. M. Wheeler	16	17.98	7	7.87	none	2	1.53	0	0.00	-----
<i>Myrmica punctiventris</i> Roger	4	4.49	4	4.49	-----	33	25.19	34	25.95	none
<i>Myrmica</i> sp 1	0	0.00	0	0.00	-----	0	0.00	2	1.53	-----
<i>Pheidole bicarinata</i> Mayr	3	3.37	4	4.49	-----	0	0.00	0	0.00	-----
<i>Pheidole crassicornis</i> Emery	1	1.12	0	0.00	-----	0	0.00	0	0.00	-----
<i>Pheidole dentata</i> Mayr	1	1.12	3	3.37	-----	0	0.00	0	0.00	-----
<i>Pheidole tysoni</i> Forel	47	52.81	25	28.09	pitfall	0	0.00	2	1.53	-----
<i>Pyramica clypeata</i> (Roger)	0	0.00	0	0.00	-----	0	0.00	2	1.53	-----
<i>Pyramica laevinasis</i> (M.R. Smith)	0	0.00	0	0.00	-----	0	0.00	2	1.53	-----
<i>Pyramica ohioensis</i> (Kennedy and Schramm)	0	0.00	0	0.00	-----	3	2.29	12	9.16	Winkler
<i>Pyramica pillinasis</i> (Forel)	0	0.00	0	0.00	-----	0	0.00	1	0.76	-----
<i>Pyramica rostrata</i> (Emery)	1	1.12	2	2.25	-----	1	0.76	21	16.03	Winkler
<i>Pyramica talpa</i> (Weber)	1	1.12	4	4.49	-----	0	0.00	12	9.16	Winkler
<i>Stenamma brevicorne</i> (Mayr)	3	3.37	3	3.37	-----	1	0.76	5	3.82	-----
<i>Stenamma impar</i> Forel	2	2.25	0	0.00	-----	12	9.16	38	29.01	Winkler
<i>Stenamma schmittii</i> W.M. Wheeler	0	0.00	0	0.00	-----	1	0.76	0	0.00	-----
<i>Solenopsis carolinensis</i> Forel	10	11.24	21	23.6	Winkler	0	0.00	3	2.29	-----
<i>Solenopsis molesta</i> (Say)	32	35.96	36	40.45	none	5	3.82	3	2.29	-----
Ponerinae										
<i>Amblyopone pallipes</i> (Haldeman)	0	0.00	0	0.00	-----	2	1.53	29	22.14	Winkler

Table 4-1 (continued). Comparison of pitfall and Winkler litter extraction techniques in field and forest habitats, the Great Smoky Mountains National Park, July-August, 2003-2004.

Ant Species (γ -diversity = 58)	Field ($n = 89$)					Forest ($n = 131$)				
	Pitfall		Winkler		Bias	Pitfall		Winkler		Bias
	Count	%Freq	Count	%Freq		Count	%Freq	Count	%Freq	
<i>Hypoponera opacior</i> (Forel)	9	10.11	27	30.34	Winkler	0	0.00	1	0.76	-----
<i>Ponera pennsylvanica</i> Buckley	4	4.49	34	38.2	Winkler	9	6.87	68	51.91	Winkler
<i>Proceratium pergandei</i> (Emery)	0	0.00	0	0.00	-----	0	0.00	1	0.76	-----
<i>Proceratium silaceum</i> Roger	0	0.00	0	0.00	-----	0	0.00	26	19.85	Winkler
Species Richness = α diversity	35		31			33		42		
Total Bias (Pitfall-Winkler)					4-4					1-12

Notes: Count = frequency of occurrence for each species; n = number of samples taken per habitat with each collection method. Significance of different species proportions between collection methods (Bias) was determined with a Chi Square one-sample test for goodness of fit ($\alpha = 0.05$, d.f. 1, critical value 3.84). Calculations were completed for all species that were collected a least 10 times in a given habitat.

Table 4-2. Mean abundance, diversity, species richness and evenness (per/station) in field and forest habitats as captured with pitfall trapping and Winkler litter extraction in the Great Smoky Mountains National Park July-August, 2003-2004.

	Abundance ¹ (\pm SE)	Richness ² (\pm SE)	Diversity ³ (\pm SE)	Evenness ⁴ (\pm SE)
Forest				
Pitfall	7.50 \pm 0.54 a	2.10 \pm 0.11 a	0.49 \pm 0.04 a	0.50 \pm 0.04 a
Winkler	28.90 \pm 1.95 b	4.41 \pm 0.17 b	1.05 \pm 0.04 b	0.74 \pm 0.02 b
Combined	36.97 \pm 2.13 b	5.19 \pm 0.20 b	1.14 \pm 0.04 b	0.72 \pm 0.02 ab
Field				
Pitfall	31.20 \pm 4.74 b	4.61 \pm 0.18 b	1.08 \pm 0.05 b	0.73 \pm 0.02 b
Winkler	44.74 \pm 4.74 b	4.51 \pm 0.20 b	0.98 \pm 0.04 b	0.67 \pm 0.03 ab
Combined	75.67 \pm 6.98 c	6.96 \pm 0.20 c	1.37 \pm 0.04 c	0.72 \pm 0.02 ab

Notes: ¹total number of ants; ² count of non-zero values for each species; ³ Shannon's diversity index; ⁴Diversity / ln (Richness); values within columns followed by the same letter are not significantly different $\alpha = 0.05$

In the grassland habitat, 35 species were captured with pitfall sampling, 31 with Winkler litter extraction, and 38 species with the combination of techniques (Table 1). In grasslands, Winkler litter extraction yielded less species than pitfall trapping up to the 40 subsample level. Beyond 40 samples (40 – 89), pitfall trapping captured the most species as the curve for Winkler litter extraction neared an asymptote (Figure 4-1. B.). Species bias towards Winkler litter extraction and pitfall trapping was equal, with four species biased towards each technique (Table 4-1., $\alpha = 0.05$, d.f. = 1, X^2 critical value = 3.84). Analysis of variance revealed ($\alpha = 0.05$) that the combination of techniques differed from Winkler litter extraction and pitfall trapping in terms of averaged sample-level abundance, richness, and diversity. There was no difference between Winkler litter extraction and pitfall trapping in terms of these variables. Pitfall, Winkler litter extraction, and the combination of techniques did not differ in evenness within the grassland (Table 4-2).

Seasonality

Sampling during the July-August time period yielded the majority of species, both in terms of presence-absence and percentage frequency, equalizing skewed sampling effort (Table 4-3). December-January sampling captured 18 species, March-April sampling captured 24 species, and July-August captured 58 species. Additionally, most species captured in December-January and March-April had reduced percentage frequency ($n = 15$) when compared to July-August. Some species ($n = 7$), however, did show an increase in percentage frequency in December-January or March-April. These species are *Acanthomyops claviger*, *Lasius flavus*, *Prenolepis imparis*, *Myrmica* sp.1.,

Stenamma brevicorne, *Stenamma meridionale*, and *Stenamma schmittii* (Table 4-2). The comparatively species-poor assemblages captured in December-January and March-April were perfectly nested sets of the greater richness collected in July-August with the exception of one species. *Stenamma meridionale*, a new record for the GSMNP, exhibited peak percentage frequency in December-January when it was captured in 46% of the samples (n = 24), intermediate percentage frequency in March-April (8.3% n= 24), and no occurrences in July-August (n = 220).

Table 4-3. Seasonal species richness of communities in a tri-annual sampling regime; the Great Smoky Mountains National Park, 2003-2004.

Season Species (γ -diversity = 59)	Dec - Jan ($n = 24$)		Mar - Apr ($n = 24$)		Jul - Aug ($n = 24$)	
	Count	%Freq	Count	%Freq	Count	%Freq
Dolichoderinae						
<i>Tapinoma sessile</i>	0	0.0	3	12.5	55	25.0
Ecitoninae						
<i>Neivamyrmex carolinensis</i>	0	0.0	0	0.0	1	0.5
Formicinae						
<i>Acanthomyops claviger</i>	0	0.0	1	4.2	1	0.5
<i>Brachymyrmex depilis</i>	0	0.0	0	0.0	14	6.4
<i>Camponotus americanus</i>	0	0.0	0	0.0	2	0.9
<i>Camponotus chromaoides</i>	0	0.0	0	0.0	1	0.5
<i>Camponotus nearticus</i>	0	0.0	0	0.0	2	0.9
<i>Camponotus pennsylvanicus</i>	0	0.0	0	0.0	14	6.4
<i>Camponotus subbarbatus</i>	0	0.0	0	0.0	1	0.5
<i>Formica schaufussi</i>	0	0.0	0	0.0	2	0.9
<i>Formica neogagates</i>	0	0.0	0	0.0	1	0.5
<i>Formica subaenescens</i>	0	0.0	0	0.0	8	3.6
<i>Formica subcericea</i>	0	0.0	0	0.0	8	3.6
<i>Lasius ailenus</i>	3	12.5	6	25.0	72	32.7
<i>Lasius flavus</i>	1	4.2	4	16.7	19	8.6
<i>Lasius nearticus</i>	0	0.0	0	0.0	4	1.8
<i>Lasius neoniger</i>	2	8.3	4	16.7	64	29.1

Table 4-3. (continued) Seasonal species richness of communities in a tri-annual sampling regime; the Great Smoky Mountains National Park, 2003-2004.

Season Species (γ -diversity = 59)	Dec - Jan ($n = 24$)		Mar - Apr ($n = 24$)		Jul - Aug ($n = 24$)	
	Count	%Freq	Count	%Freq	Count	%Freq
<i>Lasius umbratus</i>	0	0.0	0	0.0	9	4.1
<i>Paratrechina parvula</i>	0	0.0	0	0.0	28	12.7
<i>Paratrechina faisionensis</i>	2	8.3	2	8.3	73	33.2
<i>Paratrechina terricola</i>	0	0.0	0	0.0	1	0.5
<i>Prenolepis imparis</i>	5	20.8	3	12.5	19	8.6
Myrmecinae						
<i>Aphaenogaster fulva</i>	0	0.0	0	0.0	1	0.5
<i>Aphaenogaster rudis</i> complex	5	20.8	8	33.3	135	61.4
<i>Aphaenogaster tennesseensis</i>	0	0.0	0	0.0	1	0.5
<i>Aphaenogaster treatae</i>	0	0.0	0	0.0	51	23.2
<i>Crematogaster cerasi</i>	0	0.0	0	0.0	2	0.9
<i>Crematogaster pilosa</i>	0	0.0	0	0.0	1	0.5
<i>Crematogaster punctulata</i>	0	0.0	0	0.0	26	11.8
<i>Leptothorax curvispinosus</i>	0	0.0	0	0.0	8	3.6
<i>Leptothorax longispinosus</i>	0	0.0	0	0.0	2	0.9
<i>Monomorium minimum</i>	0	0.0	0	0.0	21	9.6
<i>Myrmecina americana</i>	4	16.7	6	25.0	71	32.3
<i>Myrmica americana</i>	0	0.0	1	4.2	10	4.6
<i>Myrmica latifrons</i>	1	4.2	4	16.7	52	23.6
<i>Myrmica pinetorum</i>	0	0.0	1	4.2	20	9.1
<i>Myrmica punctiventris</i>	1	4.2	2	8.3	55	25.0

Table 4-3. (continued) Seasonal species richness of communities in a tri-annual sampling regime; the Great Smoky Mountains National Park, 2003-2004.

Season Species (γ -diversity = 59)	Dec - Jan ($n = 24$)		Mar - Apr ($n = 24$)		Jul - Aug ($n = 24$)	
	Count	%Freq	Count	%Freq	Count	%Freq
<i>Myrmica</i> sp 1	0	0.0	3	12.5	2	0.9
<i>Pheidole bicarinata</i>	0	0.0	0	0.0	6	2.7
<i>Pheidole crassicornis</i>	0	0.0	0	0.0	1	0.5
<i>Pheidole dentata</i>	0	0.0	0	0.0	4	1.8
<i>Pheidole tysoni</i>	3	12.5	1	4.2	54	24.6
<i>Pyramica clypeata</i>	0	0.0	0	0.0	2	0.9
<i>Pyramica laevinasis</i>	0	0.0	0	0.0	2	0.9
<i>Pyramica ohioensis</i>	1	4.2	0	0.0	14	6.4
<i>Pyramica pillinasis</i>	0	0.0	0	0.0	1	0.5
<i>Pyramica rostrata</i>	0	0.0	1	4.2	23	10.5
<i>Pyramica talpa</i>	0	0.0	0	0.0	16	7.3
<i>Stenamma brevicorne</i>	0	0.0	2	8.3	11	5.0
<i>Stenamma impar</i>	3	12.5	2	8.3	46	20.9
<i>Stenamma meridionale</i>	11	45.8	2	8.3	0	0.0
<i>Stenamma schmittii</i>	2	8.3	2	8.3	1	0.5
<i>Solenopsis carolinensis</i>	2	8.3	1	4.2	42	19.1
<i>Solenopsis molesta</i>	1	4.2	1	4.2	29	13.2
Ponerinae						
<i>Amblyopone pallipes</i>	1	4.2	3	12.5	30	13.6

Table 4-3. (continued) Seasonal species richness of communities in a tri-annual sampling regime; the Great Smoky Mountains National Park, 2003-2004.

Season Species (γ -diversity = 59)	Dec - Jan ($n = 24$)		Mar - Apr ($n = 24$)		Jul - Aug ($n = 24$)	
	Count	%Freq	Count	%Freq	Count	%Freq
<i>Hypoponera opacior</i>	0	0.0	0	0.0	28	12.7
<i>Ponera pennsylvanica</i>	4	16.7	10	41.7	105	47.7
<i>Proceratium pergandei</i>	0	0.0	0	0.0	1	0.5
<i>Proceratium silaceum</i>	0	0.0	0	0.0	26	11.8
Diversity	$\alpha = 18$	$\beta = 3.2$	$\alpha = 24$	$\beta = 2.5$	$\alpha = 58$	$\beta = 1.0$

Notes: Count = frequency of occurrence for each species; n = number of samples taken per sampling period; γ -diversity = total species richness across sampling periods; α = species richness per sampling period; $\beta = \gamma / \alpha$.

Discussion

Sampling

The theoretical association of multiple collection techniques and more complete species lists is a logical assumption that is well supported in the ant literature (Longino and Colwell 1997, Majer 1997, Longino et al 2002, King and Porter 2005). Structured inventories that use multiple quantitative and qualitative techniques are considered a standard practice in the strict inventories (Longino and Cowell 1997) typically carried out by systematists, museum collectors, and researchers conducting all-taxa biological inventories where the goal is to generate the most complete species lists possible. Alternatively, community characterization inventories use single or few quantitative collection techniques, allow statistical comparison of spatiotemporal quadrats, and are beneficial in monitoring projects concerned with habitat change, pest management, or other ecological questions (Longino and Cowell 1997). While both types of inventories benefit from the comprehensive nature of multiple techniques, the expertise, time, and cost associated with the application of more than one technique are often prohibitive when large numbers of samples are required or complete inventories are not needed or justified. For this reason, many ecological studies that use ants as bioindicator taxa, employ the utility of a single collection method (e. g. Golden and Crist 2000, Wang et al 2001, Mitchell et al 2002, Zettler et al 2004). Although methodological bias can influence the outcome of ecological studies, the nature of sampling bias is relatively unexplored for specific habitats, taxa, and techniques. In studies concerned with richness or relative abundance, the effect of treatments might be obscured by sampling bias. Bias should be

of special concern when a single collection method such as pitfall trapping is used (Melbourne 1999).

This study demonstrated that the effectiveness of pitfall and litter sampling varied among grassland and forest communities in the southern Appalachians, while neither of the single techniques was as effective as their combination. Individual methods generated complementary species lists, with species biased towards each of the collection techniques (Table 4-1).

Average per/station ant abundance, richness, and diversity were significantly less when pitfall trapping was used in the forest habitat of the GSMNP. This deficiency is demonstrated in the total richness captured with this technique (Table 4-1) and a consistently lower richness across subsample sizes (Figure 4-1). In the forest habitats of the GSMNP, there is an unbalanced bias (1-12) toward Winkler litter sampling (Table 4-1). Specifically, several small litter-inhabiting genera including *Tapinoma*, *Brachymyrmex*, *Lasius*, *Paratrechina*, *Pyramica*, and *Stenamamma* were captured significantly more or exclusively with Winkler litter extraction. Additionally, all (5/5) of the Ponerinae species captured in the forest were biased towards or collected exclusively with Winkler litter extraction. These genera include *Amblyopone*, *Hypoponera*, *Ponera* and *Proceratium* (Table 4-1). The only genera bias for pitfall trapping in the forest was for the nocturnal genus *Camponotus* whose peak period of activity falls outside the time frame when Winkler litter extraction was performed (daylight hours).

In the grassland plots of the GSMNP, the average per/station ant abundance, richness, and diversity were not different for pitfall or Winkler litter extraction. However,

the combination of these techniques was statistically better than either of the techniques alone. Although the total species richness for pitfall trapping was higher than Winkler litter extraction, the disparity was the result of a drop in new species accumulation past the 40 subsample size when using the Winkler extraction method (Figure 4-1. B.). Trap bias was equal in the grassland (4/4). Both species of Ponerinae collected in the grasslands were biased towards Winkler litter extraction.

Pitfall sampling is less effective in capturing cryptic ant species that are likely to inhabit specialized habitats in deep litter or other vegetative debris associated with complex forest ecosystems (Marsh 1984, Olson 1991, Fisher 1999, Melbourne 1999). In the tropical wet forests of Costa Rica, litter-sifting samples consistently captured smaller and specialist species more than pitfall trapping. Pitfall trapping was less effective in hardwood hammocks of Florida where litter layers were deeper than at other sites where pitfall trapping performed as well or better than litter sampling (King and Porter 2005). In the hardwood forests and cultivated pine stands of the Cumberland Plateau in southern Tennessee, pitfall traps captured fewer individuals and fewer species, and yielded a reduced frequency of occurrence in most species versus Winkler litter extraction. The Ponerinae also showed a bias for Litter sifting techniques (Martelli et al. 2004).

Seasonal sampling, although greatly reduced in the December – January and March –April time periods, demonstrates that the majority of ant diversity and activity is captured with July – August sampling. The nearly nested nature of the reduced species lists from these time periods shows that uncaptured diversity in the July – August sampling is negligible with only one species, *S. meridionale*, showing a different

abundance pattern. Studies concerned with ant richness or relative abundance should focus on mid-to late-summer sampling.

Summary

Winkler litter extraction and pitfall trapping are effective complementary techniques, each with species biased towards capture, and generating more comprehensive species lists in combination than either of the techniques used alone. However, expertise, time, and resource limitations might require ecologists to select one sampling technique for use in a particular study. In forest habitats of the southern Appalachian Mountains, Winkler litter extraction should be the technique of choice. The majority of species (12/13) showing capture bias in the forest were captured more frequently with Winkler extraction and this technique captured more species (total, 42 vs 33) consistently across all subsample sizes (1-131). However, the *Camponotus*, an ecologically important nocturnal forest genus, was biased towards pitfall trapping. In the grassland habitats, the choice of a single superior sampling technique is not as clear. An equal number (4/4) of species were biased towards both techniques. While pitfall trapping captured more total species (35 vs. 31) after 89 samples, this technique performed less efficiently than Winkler litter extraction if fewer than 40 samples were taken. In addition, species of Ponerinae, an ecologically important litter-inhabiting subfamily, were biased towards Winkler litter extraction in both the forest and the grassland. Sampling during late summer (July-August) produced the most species and most species were captured with a greater percentage frequency (of all collections) during this season compared to December-January or March-April sampling. In addition the

reduced species assemblages from these sampling periods were perfectly nested subsets of the July-August assemblage, with one exception. *Stenamma meridionale* was not present in July-August sampling and had peak frequency of collection in December-January.

SUMMARY AND DISCUSSION

Ecotonal effects in ant communities at forest edges in temperate North America

The ant community of temperate forests in the Great Smoky Mountains National Park (GSMNP) is modified where trees have been cleared and grasslands are maintained. As a result, different ant communities are found on either side of the boundary between these habitats. The forest-ant community, as defined within an ecological distance matrix, is intact within 15 m of the forest edge. These results support the hypothesis that ant species assemblages in forests and grasslands are significantly different. Significant indicator species were identified within four distinct ant assemblages. Ecotonal effects are observed in forests when individual species abundances are compared at different distances into undisturbed forest. These data support the hypothesis that individual ant species have significant indicator value within assemblages across the habitat boundary. Differential abundance with respect to habitat boundaries is seen in significant indicator species in both grassland and forest habitats, while differences in rarely-collected species occurs in the forest habitat only. In accord with theory, landscape-level total species richness is greatest near edge zones in both grassland and forest habitats. However, within-habitat ecotonal effects were not evident in analysis of average per sample species richness or diversity across distances from edges. Average ant abundance (all species) showed an ecotonal effect in the grassland where values increased with distance from the forest edge. Several biotic and abiotic habitat characteristics were identified that correspond with patterns in habitats and ant distributions. These data support the

hypothesis that ant ecotonal effects can be predicted with biotic and abiotic habitat characteristics. Specifically, the abundance of eight ant species that were both significant indicator species and showed within-habitat ecotonal effects were correlated with various environmental characteristics including but not limited to tree species, # of trees, % canopy, % ground cover, slope, elevation, and humus depth. My work does not demonstrate that habitat characteristics are causally related to biotic edge effects. Identifying characteristics that are causally related to patterns in biota should be the basis for future hypothesis testing experiments and might explain some differences in ant communities on a landscape level between the sampling sites Cataloochee Cades Cove/Oconoluftee.

Evaluation of *Pachycondyla chinensis* (Emery) as a Threat in the GSMNP

Pachycondyla chinensis is functioning as an invasive species in South Carolina where it has become well established and dominant in several locations. My work supports the hypothesis that *P. chinensis* is an invasive species with the ability to penetrate naturally vegetated forests in the southeastern United States where it becomes a dominant species. Nests of *P. chinensis* in South Carolina have abundant workers, are polygynous, and possess some of the characteristics of a unicolonial species. The latter of these behavior should be further studied for confirmation and is important because unicoloniality allows a high reproductive potential and characterizes invasive ants capable of dominating arthropod communities. The collections made in 2001 document the first sighting of *P. chinensis* in the forests of GSMNP. Although *P. chinensis* is not well established in GSMNP, the forests are similar, in terms of ant-assemblage

composition, to other more heavily infested forests in the southeastern United States. The establishment of dense populations of *P. chinensis* in GSMNP is likely. The ecological outcomes of *P. chinensis* invasion are only speculative but might be comparable to invasions by *Linepithema humile* (Mayr) and *Solenopsis invicta* (Buren) in the United States and other countries. With ever-increasing global trade and travel, human-assisted transport, and the biological characteristics of the species in North America, the threat of significant range expansions by *P. chinensis* are a legitimate concern.

Verification of Sampling Techniques

In agreement with literature from other geographic locations, Winkler litter extraction and pitfall trapping are effective complementary techniques in the temperate forests and grasslands of the GSMNP. Individual species are biased towards capture with both collection methods, and their combined use generates more comprehensive species lists than either of the techniques used alone. These results support the original hypothesis that the two techniques would differentially capture individual species. Frequently, ecologists face limitations in available expertise or time that can be dedicated to the identification of the large numbers of individuals associated with multiple collection methods. The selection of one sampling technique for use in a particular study is often a necessity. In forest habitats of the southern Appalachian Mountains, Winkler litter extraction is the technique of choice. The majority of species showing capture bias in the forest were captured more frequently with Winkler extraction, and this technique captured more species consistently across all subsample sizes. However, the *Camponotus*, an ecologically important nocturnal forest genus, were biased towards

pitfall trapping. In the grassland habitats an equal number of species were biased towards both techniques, making the choice of a single sampling technique less clear. While pitfall trapping captured more total species by the end of the sampling, this technique performed less efficiently than Winkler litter extraction if fewer than 40 samples were taken. In addition, species of Ponerinae, an ecologically important litter-inhabiting subfamily, were biased towards Winkler litter extraction in both the forest and the grassland.

Sampling during late summer (July-August) produced the greatest species richness, and most species were captured with a greater percentage frequency (of all collections) during this period when compared to December-January or March-April sampling. These results support the hypothesis that summer sampling would capture the majority of ground dwelling ant species. The reduced species assemblages from the latter sampling periods were perfectly nested subsets of the July-August assemblage with one exception. *Stenamma meridionale* Smith was not present in July-August sampling and had peak frequency of collection in December-January.

Discussion

As human-land-use induced environmental change continues to alter habitats, the biodiversity of some communities will continue to be threatened. In nearly every example, there will be species that benefit from the demise of others. For example, the grassland species discussed in this work have benefited from the forest clearing-habits of humans in the southern Appalachians. Ant biodiversity in the GSMNP would be greatly depleted if these human-maintained habitats were allowed to return to a forested climax

community. In this example, the adjacent forest-ant communities are minimally impacted, allowing both communities to coexist within a limited range, further justifying the continued maintenance of these areas. In addition, these results indicate that small forest or grassland preserves are likely to successfully support precinctive ant communities in the southern Appalachians. However, this trend is not globally universal or applicable to other groups of organisms where interior species are severely threatened by edge effects and require expansive undisturbed tracts of habitat.

Adding to the contingency and complexity of community responses across large geographic ranges, the introduction of adventive and invasive species is a phenomenon that goes hand in hand with increased human activity. Adventives that become invasive usually exacerbate reductions in species diversity by decreasing the ability of habitats to support native species. Efficient conservation measures must be based on regional studies that document the effects of habitat boundaries, the impacts of invasive species, and other factors associated with the isolation, and disruption of specific organisms in the land-use mosaics created by human activity. In short, we must understand the ecological requirements of the communities or individual species we wish to preserve. The relatively recent use of ants as bioindicator taxa has led to the refinement of reliable sampling techniques. The continued use of ants as bioindicators will likely benefit the systematics of the group through renewed interest in the skills needed to make identifications, as well as the discovery of new species in sampling-intensive ecological work.

My work is entirely dependent on morphological taxonomy. The limitations of this taxonomic framework are becoming better known as the DNA of populations reveals the complex and subdivided nature of what we have typically considered single-species populations. A pertinent example in the ants is the *Aphaenogaster fulva-rudis-texana* complex (Umphrey 1996). These ants were historically considered a simple group until cytotaxonomic techniques revealed a complex of morphologically similar sibling species. The techniques required to separate these species cannot be applied to worker ants making their use in sample-based ecological studies impractical. There is little doubt that most species will be equally complex when their genetics are studied and our very concept of the “species” will continue to be challenged. As the field of molecular ecology continues to advance, the tools required to answer genetics-based questions in field studies will eventually become commonplace.

The challenge for the molecular ecologists of the future will be to recognize the value of morphology-based studies in their work. Scale is variable of immense importance in ecology and the scale of morphospecies will be an important starting point or pre-filter for genetics-based field studies in the years to come. For example species that exhibit widely variable morphology or ecology might be prime examples of hidden sibling species complexes. The *Tapinoma sessile* (Say) encountered in my work is a good example. While the species is found primarily in forest edge or field habitats in large numbers, it is occasionally found in deep forest habitat where it is present in low numbers. This ecological disparity is also corroborated by morphological polymorphism. The deep forest form is a smaller more lightly sclerotized version of the typical open-

habitat form. Another example is seen in the species *Lasius neoniger* Emery. Two forms were encountered in this study. The first form is typical of the description for the species while the second form is lighter in color and with many more setae on the scapes and fore tibiae. The typical form was found exclusively at Cataloochee while the lighter form was found exclusively at Oconoluftee. Mixed populations were seen at Cades Cove. While differences in both *T. sessile* and *L. neoniger* are not clear enough at this point to be called different species based on morphology, these observations suggest that molecular studies might uncover hidden subdivision and subsequent ecological differentiation.

Community ecology is a field that has many difficulties associated with inconsistencies among ecosystems. The lack of generally applicable rules in this area of research is indicative of the enormous complexity of interactions between organisms and their environment. While the complexity of community ecology is daunting and presents unique challenges to ecologists, it is an appealing field that has generated a rich literature and sophisticated statistical tools. The statistical algorithms historically accessible to a limited esoteric few have become commonplace in software packages and are often freely available via the internet. The facilitated use of these tools in various ecosystems around the globe is producing a wealth of local community data and is increasing our knowledge of organismal ecology in the terrestrial arthropods. The next decade should prove to be a productive period in this field. Future work will continue to define the patterns of community responses to various human-mediated disturbances on a local scale. Future progress will require ecologists to shift from what is currently a largely inductive or exploratory mode to deduction or the specific testing of hypotheses through

experimentally manipulative work. The recent literature does bear some experimental work in this area. However, causal relationships between species and specific measurable habitat characteristics have been overlooked and can only be investigated experimentally. The next step in developing effective conservation strategies will rely on our understanding of the specific causally related effects of invasive species and physical alteration of habitats. The identification of key influences on biodiversity will potentially provide land managers with a new set of controllable criteria on which to focus efforts to preserve biodiversity. Because of the geographically specific nature of these effects and limited resources, conservation ecologists should first focus efforts in critical areas where 1) biodiversity is potentially threatened and 2) infrastructure is in place to allow for the allocation of the resources required in effective management.

The presence of the invasive species *Pachycondyla chinensis* (Emery) in GSMNP should be of concern to land managers. The observations made in South Carolina forests suggest that the species could become widespread and alter the ant community structure of the Park's forests. Efforts to prevent the spread of this species should be based primarily in a monitoring program to ensure early detection in areas prone to infestation such as entrance roadways or areas where infested materials might be deposited. Periodically using the Winkler litter sifting technique in these areas should detect even low level populations. If early infestations are found, spot treating individual nests will be the most practical control measure as there is no other way to specifically target this omnivorous species with baits or other broadcast applications. If large populations of *P. chinensis* become well established outside the Park the task of excluding the ant will

become impractical. In the scenario of a large scale invasion land managers can expect short term reductions in biodiversity but in the long term native communities will probably rebound reaching a new equilibrium as has been seen in *S. invicta* invaded areas.

The data presented here should serve as a stepping stone in other ecological or conservation endeavors in the forests and grasslands of the southern Appalachians. Specifically the establishment of extensive species lists, identification of important indicator species, description of general and species-specific ecotonal effects, identification of possible habitat characteristics associated with ant ecotonal effects, identification of a previously unrecognized invasive species, and validation of collection techniques should prove useful for ecologists and land managers working in this biologically diverse region.

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