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## Ant (Hymenoptera: Formicidae) Assemblages in Three New York Pine Barrens and the Impacts of Hiking Trails

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**ANT (HYMENOPTERA: FORMICIDAE) ASSEMBLAGES IN THREE NEW YORK  
PINE BARRENS AND THE IMPACTS OF HIKING TRAILS**

A Thesis Presented

By

GRACE W. BARBER

Submitted to the Graduate School of the  
University of Massachusetts Amherst in partial fulfillment  
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## **DEDICATION**

To my parents and brothers.

Your strength, creativity, and generosity inspire me.

## ACKNOWLEDGMENTS

I would like to thank my advisors, Aaron Ellison and Paul Sievert, for the opportunity to complete this work and for their guidance and support. In particular, I want to thank Aaron for encouraging me to follow my curiosity, believing in my ability, and setting an exceptional example as a mentor. I am thankful to Aaron also for financially supporting of this work. To Paul, I am thankful for his enthusiastic encouragement and practical guidance throughout, which greatly facilitated my progress, eased my nerves, and improved the quality of my experience in the graduate program.

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## **ABSTRACT**

### **ANT (HYMENOPTERA: FORMICIDAE) ASSEMBLAGES IN THREE NEW YORK PINE BARRENS AND THE IMPACTS OF HIKING TRAILS**

FEBRUARY 2015

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Ants are ecologically important, environmentally sensitive, widespread, and abundant, yet ant assemblages of many habitats remain poorly understood. Ants in inland barrens of New York State (NY) barely have been studied, but the limited data suggest such habitats are likely to support uncommon ant species and high species density for the region. To increase knowledge of these assemblages, I systematically collected ants from three inland barrens systems in NY, to create species lists and measure species density. I also investigated how hiking trails — a common man-made disturbance — may be impacting ant assemblages in these early-successional, disturbance-dependent ecosystems. My data strongly indicate uncommonly high densities of ant species in NY pine barrens, including the most northern known occurrences of some species, and show that ant assemblage composition and species density are altered on hiking trails relative to managed barrens habitat bordering the trails.

In Chapter 1 I compare the species density of my study plots to what has been reported from other nearby habitats and northeastern pine barrens. I also identify environmental variables that best explain variation in species composition among my study plots. My results demonstrate the importance of inland pine barrens for regional ant biodiversity, and show that shrub-level oaks may be an important factor contributing to their rich ant fauna.

In Chapter 2 I investigate the impact of hiking trails on ant assemblages at the Albany Pine Bush Preserve. I find that ant assemblages are altered on hiking trails relative to assemblages in managed habitat bordering the trail. I conclude that monitoring ants on hiking trails could provide valuable information, particularly on disturbance-tolerant species, and an opportunity for visitor participation and citizen science programs that could detect additional rare species.

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## CHAPTER 1

### ANT DIVERSITY IN NEW YORK STATE INLAND PINE BARRENS

#### 1.1 Abstract

Ants are major contributors to ecological processes — including soil development, nutrient cycling, and seed dispersal — in the northeastern United States and around the world. However, distributions of these influential invertebrates in the inland Pitch Pine barrens of New York State are poorly understood. I used quadrat searches and pitfall traps to systematically sample ant assemblages along transects in open habitats at three of these inland barrens. My results demonstrate that (1) inland Pitch Pine barrens in New York support high ant species density, including rare species; (2) shrubland habitats appear to support higher ant species density than grassland habitats in the Northeast, as in other regions; and (3) shrubland and grassland ant assemblages in these barrens are compositionally distinct.

#### 1.2 Introduction

Ants are important contributors to ecosystem function in most terrestrial environments. In the northeastern United States, ants contribute substantially to nutrient cycling and decomposition and are among the most important seed dispersers and soil developers (Del Toro et al. 2012, Folgarait 1998, Frouz and Jilková 2008, Handel et al. 1981, Lyford 1963). Although the ecological importance and potential utility of ants for ecosystem monitoring are widely accepted (Andersen and Majer 2004, Ellison 2012b), ant assemblages of many ecosystems, including some of high conservation concern, have been surveyed only rarely, or in some cases never. Ants are important to monitor and study not only for the purpose of understanding of their many ecological roles, but because ant assemblages and the processes they mediate are susceptible to dramatic change following invasion by non-native ant species, changes in habitat, or changes in

disturbance regimes (Christian 2001, Rodriguez-Cabal et al. 2012). With early detection and understanding of these changes, we stand a better chance of responding to them appropriately.

Although pine barrens ecosystems are well known for their invertebrate diversity (Barnes 2003, Wagner et al. 2003, Wheeler Jr. 1991), most have not been thoroughly or recently surveyed for ants. Evidence from previous surveys in both inland and coastal pine barrens (Barnes 2003, Dindal 1979, Ellison 2012a) suggests that these ecosystems may have high ant species richness relative to other habitat types. A species list of ants from the Albany Pine Bush Preserve (APBP) published in 2003 (Barnes 2003) included 33 species, but the data available from the APBP (on which the Barnes (2003) list is based) do not include large areas and many habitat types occurring in the APBP, nor have ant assemblages been studied at other inland barrens systems in New York State.

Inland Pitch Pine barrens are characterized by well-drained sandy soil, an open canopy of *Pinus rigida* Mill. (Pitch Pine), variable shrub layers, and grassy patches (NatureServe 2014). Within inland pine barrens throughout the northeast, there is variability in the presence and density of shrub-level oak species such as *Quercus ilicifolia* (Wangenh.) (Scrub Oak/Bear Oak) and *Quercus prinoides* (Willd.) (Dwarf Chinquapin Oak). The encroachment of woody plants in grasslands is a phenomenon that has received considerable attention in recent years (Eldridge et al. 2011, Quero et al. 2013), and other authors have shown that this ecosystem change can increase ant species density in other arid and mesic environments in the southwestern United States and in Europe (Bestelmeyer 2005, Kumschick et al. 2009, Wiezik et al. 2013). In the northeastern United States, however, the difference in ant species density between shrublands and grasslands is not known. At northern latitudes in North America, ant richness has been observed to decrease with increasing canopy cover, and other authors have suggested this is likely due to the cooler temperatures of shaded areas being thermally limiting to some species (Banschbach and Ogilvy 2014, Del Toro et al. 2013, Gotelli and Arnett 2000, Jeanne 1979, Ouellette et al. 2010). If this is true, oak-dominated shrublands might be expected to have lower ant species

density than grasslands in northern latitudes, owing to the greater shading-capacity of broad-leaved plants.

I surveyed ant assemblages in two barrens habitat types among three inland Pitch Pine barrens systems: grasslands and shrublands at APBP, and grasslands at the Saratoga Sand Plains (SSP) and the Rome Sand Plains (RSP). Of these three preserves, APBP is the only one where managers actively create shrubland. The objectives of my study were to (1) create or update ant species lists for three inland pine barrens preserves; (2) assess the relative ant species richness of pine barrens compared to other habitat types in the region, and (3) identify environmental variables that best explain patterns in ant assemblage composition and species density among these barrens habitats.

My comparison of ant species density among shrubland and grassland habitats of these inland pine barrens provides a case study from the northeastern United States of how shrub density in open habitats affects ant assemblages. Results from my survey of these inland barrens ecosystems and comparison of shrubland and grassland ant assemblages within the barrens provide new knowledge of ant species distributions and diversity. This knowledge will improve our ability to monitor ant assemblages and develop appropriate conservation strategies for ant biodiversity.

### **1.3 Field-site Description**

The APBP is located between 42.67 and 42.76 °N latitude and 73.82 and 73.94 °W longitude at an elevation of approximately 100 meters above sea level (m.a.s.l.) in Albany County, New York (Figure 1.1), between the cities of Albany and Schenectady. The average annual temperature for the city of Albany is 9.7 °C, and the average annual precipitation is 875 mm (CantyMedia 2014). The preserve includes 1295 ha of protected land and several habitat types, including mixed deciduous and conifer forests, Pitch Pine-Scrub Oak barrens, open grasslands, Scrub Oak thickets, and wetlands. Albany is one of the oldest cities in the United

States, and the region that includes the APBP has been a center of commerce and travel for well over 200 years. The land included in the preserve has a history of agriculture and excavation of sand for glass-making and molding sands. Today, the APBP is maintained by the Albany Pine Bush Preserve Commission (APBPC), which restores and maintains the Pitch Pine-Scrub Oak barrens community through a combination of mowing, herbicide, tree removal, planting, and prescribed burns (APBPC 2010, Bried and Gifford 2010).

The SSP is located between 43.13 and 43.16 °N latitude and 73.72 and 73.68 °W longitude, approximately 50 km north of the APBP, at an elevation of approximately 90 m.a.s.l. in Saratoga County, New York, approximately 9.6 km north of the city of Saratoga Springs. The average annual temperature for Saratoga Springs is 8.9 °C, and the average annual precipitation is 1143 mm (CantyMedia 2014). Most of the protected land is part of the Wilton Wildlife Preserve, which includes approximately 280 ha of oak-pine forests and savannas and wetlands (NYSDEC 2014). The SSP lands are currently monitored and maintained by the Nature Conservancy (TNC), the New York State Department of Environmental Conservation (DEC), and The Wilton Wildlife Preserve & Park through a combination of vegetation clearing, mowing, herbicide treatments, and planting.

The RSP is located between 43.22 and 43.24 °N latitude and 75.56 and 75.58 °W longitude at an elevation of approximately 130 m.a.s.l. in Oneida County, New York, approximately 6.4 km west of the city of Rome. RSP is separated from SSP and APBP by a distance of approximately 150 km. The average annual temperature for the city of Rome is 8 °C, and the average annual precipitation is 1082 mm (CantyMedia 2014). The RSP includes an area of approximately 6475 ha, but much of this has been developed by private land owners. The DEC, Oneida County, TNC, and the Izaak Walton League each owns sections of undeveloped land within the system, and their combined holdings amount to approximately 1568 ha dominated by mixed northern hardwood and pine forests, wetlands, dunes, and occasional open grasslands within the RSP system. It is for these latter areas that a management plan recommends vegetative

management to maintain the Pitch Pine-heath barrens community, however little restoration and management work was underway at RSP at the time of this study (RSPRMT 2006).

### **1.3.1 Study plots**

I surveyed six plots in 2012, and six in 2013, all of which were defined by having short, relatively homogenous vegetation covering areas that ranged from 1.8 to 17.1 contiguous ha (Table 1.1). The 2012 plots were divided among the three field sites — three in the APBP, two in the SSP, and one in the RSP. The 2012 APBP plots were the Discovery Center Field (DC), Apollo Restoration (AR), and Baron's Field (BF). The two at SSP were Camp Saratoga (CS) and Trinity (TR), and the sole plot at RSP was the Rome Sand Plains Field (RS). I selected flat, open areas, dominated by graminoids and heaths, with little or no cover of shrub-level oaks to maximize habitat similarity of plots across the three pine barrens systems. Location, size, and vegetation cover data for these plots are presented in Table 1.1.

All plots sampled in 2013 were at ABPB, and included Blueberry Hill West (BH), Draperies (DP), Great Dune (GD), Karner Barrens East (KE), Karner Barrens West (KW), and King's Road Barrens (KB); none of the 2012 plots were resampled in 2013. The 2013 plots were under active management aimed at creating and maintaining Pitch Pine-Scrub Oak habitat, which is characterized as being dominated by shrub-level oaks, herbs and heaths, and having a sparse over-story of Pitch Pine and oak species (Table 1.1). All of the 2013 plots were bisected by a hiking trail, and, except for KE, all contained a substantial dune and correspondingly steep topography over portions of the plot.

The soil underlying most of the study plots at the three sites is loamy fine sand that is well to excessively drained, rapidly permeable, with strong to medium acidity, and lacking gravel (Barnes 2003, SSSNRCS 2014). However, the three APBP plots surveyed in 2012 were located on areas that had been heavily impacted by human activity, and the soils at these sites are classified as Udipsamments (AR and DC) and Udorthents (BF) (SSSNRCS 2014). The



Udipsammments soils of AR and DC differed from all other plots in that the top layer of soil was coarse sand rather than loam or loamy fine sand. The Udorthents soil of BF has an upper layer of loam, which is similar to most other plots, but is somewhat less well drained. Both of the SSP plots were on Oakville loamy fine sand, the RSP soil type was Windsor loamy fine sand, and the other APBP plots were primarily located on Colonie loamy fine sand (SSSNRCS 2014) (Table 1.1).

## **1.4 Methods**

### **1.4.1 Sampling design**

From May through August of 2012, I surveyed ants along transects summing to 140 m in length per plot. For plots that were <140-m long in any direction I used multiple, smaller transects, laid out in parallel across the plots and separated by a distance of 30 m so that the same total length of transect was sampled in every plot. All transects (or transect segments) were at least 10 m from the edges of the plot and the exact placement of the transect (or first transect segment from which the placements of all other transects in the plot were determined) was determined randomly. I placed twelve 1-m<sup>2</sup> quadrats at 11-m intervals (10 m for the space between quadrats, plus 1 m for the quadrat) along each transect, and at the midpoint between each of the quadrats I placed a pitfall trap.

In 2013, I placed a single 120-m transect within each plot. These transects were aligned roughly parallel to the trail that bisected the plot and were 35-45 m from the trail. These transects were at least this far from any of the other habitat edges, except at their ends, which I allowed to be as close as 20 m from the habitat edge when necessary. As in 2012, I randomly determined the exact placement of the transect. Ten 1-m<sup>2</sup> quadrats were placed along the transect at 11-m intervals and the distance from one end of the transect to the first quadrat also was determined randomly. Each of the 2013 transects was surveyed twice: once in May–June, and again in July–

August. The order of plot sampling was randomized during both surveys. The ten quadrats sampled along each transect during the second survey were offset from the ten sampled during the first survey by a distance of one meter (a full meter between the two proximate edges of the first- and second-survey quadrats) to reduce the effects of disturbance from the first survey.

## **1.4.2 Ant collection methods**

### **1.4.2.1 Pitfall traps**

In 2012 I sampled quadrats with pitfall traps consisting of 118-ml polypropylene cups (6-cm diameter) filled with  $\approx 80$  ml of a dilute solution of water and unscented, biodegradable detergent. I buried the cups in the ground so that the lip of the cup was level with the soil surface, and left the cups in the field with the lids on for three days of settling time to reduce the effect of disturbance on ant captures (the “digging-in effect”: Greenslade (1973)). After this period, I removed the lids and left the traps open to collect specimens for 48 hours during dry, warm weather. I then collected the traps and transferred the specimens to 95% ethyl-alcohol. I did not use pitfall traps in 2013 due to both time constraints and concerns about inadvertently trapping endangered *Lycaeides melissa samuelis* Nabokov (the Karner Blue Butterfly) larvae, among other rare and non-target species.

### **1.4.2.2 Timed, quadrat searches**

In 2012 I searched each of the twelve  $1\text{-m}^2$  quadrats per transect (one transect per plot) for 15 minutes; in 2013 I used 8-minute searches for ants in the twenty  $1\text{-m}^2$  quadrats per transect (one transect per plot). The 2013 quadrat searches were done over two survey periods so that ten quadrats per plot were searched during each of the two surveys. My method was similar to that described as “quadrat sampling” in Agosti et al. (2000), except that I did not attempt to collect every ant observed, only representatives from each species and colony observed. I recorded which ants were clearly collected from colonies within the quadrats and which were not. Time

spent recording and transferring specimens was not included in the search time. Visual searching and pitfall trapping both were done during dry weather, but were not done simultaneously.

### **1.4.2.3 Litter sifting**

Thorough quadrat searches provided a snapshot of all ants foraging and nesting within a given area, thereby generating a good estimate of species density. My quadrat searches were standardized by size across both years, and by time within years. However, most of the 2013 plots were in areas of high shrub-level oak density, and had correspondingly high quantities of leaf litter. The 2012 plots, conversely, had little leaf litter in most cases, or litter that consisted mainly of dead grasses and sedges. This difference in litter composition among quadrats in 2013 and between 2013 and 2012 quadrats affected the ease of searching for ants during the allotted time. The leaf litter from shrub-level oaks tended to provide more nesting and hiding opportunities for ants than did no litter or litter made up of dead grass, which meant that ants were more likely to be overlooked in the quadrats beneath shrub-level oaks. To maintain a similar level of search completeness across quadrats and habitat types, I added litter-sifting to the quadrat searches in 2013.

During the 8-min quadrat searches in 2013, I collected all of the leaf litter from each quadrat and placed it into a wire-mesh, waste-paper basket set inside a white bucket. The mesh holes were parallelograms with corner-to-corner distances of 30 and 50 mm, which was large enough for the largest species (*Camponotus americanus* Mayr (The American Carpenter Ant), *Camponotus pennsylvanicus* (DeGeer) (The Black or Eastern Carpenter Ant) and *Camponotus novaeboracensis* (Fitch) (The New York Carpenter Ant)) to pass through. At the end of the search time, I took the mesh basket out of the white bucket, collected any ants in the bucket, shook the material in the mesh basket over a white drop-cloth until a thin layer of material covered the cloth, and collected any ants that had fallen onto the cloth. I repeated this process of shaking the mesh basket and collecting ants three times per litter sample, and before each shaking event I

mixed the litter by hand and broke apart sticks and stems when they were present. Ants collected through this process were kept separate from ants collected through the timed visual searches.

#### **1.4.2.4 Baiting**

I used limited bait sampling at most of the study plots during both years, but these data were excluded from the analyses due to baits being strongly biased toward some species. No species were collected through bait sampling that were not also collected by other methods during the study. However, within individual plots, bait sampling did occasionally yield the only record of a species for that plot.

#### **1.4.3 Environmental measurements**

I measured vegetation structure along each transect, at 24 evenly spaced points (5.5-m spacing) in 2012, and 30 evenly spaced points (4-m spacing) in 2013. At each sampling point, I estimated the vegetation cover within three height classes (under 0.5 m, between 0.5 and 1 m, and between 1 m and 2 m) by recording whether or not vegetation contacted a 2.7-cm diameter pole placed vertically on the ground. I also recorded whether there was vegetation present above the 2 m pole. I recorded the proportion of sampling points on each transect at which specific types of vegetation (grasses/sedges and shrub-level oaks) contacted the pole. Finally, I classified the ground cover at the base of the pole as “bare”, “green” or “dead”, based on whether the ground within 20 cm of the base of the pole was primarily bare soil (bare), living plant material (green), or dead plant material (dead). Although “bare” was mutually exclusive of the other two classes, the area surrounding the pole could be covered by both living material and dead material, as was often the case when living plants were growing above a layer of leaf litter.

I used a spherical densiometer (Robert E. Lemmon, Forest Densiometers, Model-A) to estimate the percent cover of vegetation around each ant-sampling quadrat. Four densiometer readings were taken at each quadrat, one facing outward from each side of the quadrat,

approximately 0.5 m above the ground. Finally, I measured the litter depth in the center of each quadrat to the nearest full centimeter beneath the litter surface.

Soil type and plot area were not measured at the time of the ant surveys. I obtained soil data for each of my study plots from the online database [websoilsurvey.sc.egov.usda.gov](http://websoilsurvey.sc.egov.usda.gov) (SSSNRCS 2014), but did not include it as a possible variable explaining variation in ant assemblages due to the data being unreplicated categorical variables. I defined the area of each study plots as the extent of contiguous, open, barrens habitat, and estimated the total area of these plots by drawing polygons over satellite images with the software Google Earth Pro (version 7.1.2.2041).

#### **1.4.4 Habitat classification**

Much of the APBP has open habitat dominated by shrub-level oaks, whereas open habitats at SSP and RSP tend to be dominated by graminoids. The APBPC defines the shrub-covered areas of the preserve as either Pitch Pine-Scrub Oak barrens if the shrub-level oaks constitute 30%-60% cover, or as Pitch Pine-Scrub Oak thicket if the shrub-level oaks cover >60% of the ground area. The APBPC is seeking to increase the percentage of the preserve falling into these habitat types (APBPC 2010), but Pitch Pine-Scrub Oak barrens is preferred over Pitch Pine-Scrub Oak thicket, because it allows for the persistence of *Lupinus angustifolius* L. (Wild Blue Lupine) and the Karner Blue Butterfly (Bried and Gifford 2010).

I classified the plots as either grassland or shrubland based on the percentage of my sampling points at which shrub-level oaks intersected the point (i.e. contacted the pole). Any plot in which at least 30% of the sampling points were intersected by shrub-level oaks was classified as shrubland, and the plots that had less than this percentage were classified as grassland (in all plots, graminoids intersected at least 50% of the sampling points). The shrubland plots included four of the six plots from 2013. One of the grassland plots (GD) from 2013 had been restored from a woodland in 2008, and another (DP) was burned in 2011. The latter had a strong shrub-

level oak component, but the plants were small at the time of the survey, resulting in just 13% cover by my measurements (Table 1.1).

#### **1.4.5 Specimen identification**

I identified the ant specimens, relying almost exclusively on the dichotomous keys in Ellison et al. (2012), and aided by data and images from Antweb.org. A subset of the ants were pinned and identifications confirmed by Aaron M. Ellison (Harvard Forest, Petersham, MA). Identifications of rare and particularly challenging specimens were confirmed by Stefan Cover at the Museum of Comparative Zoology in Cambridge, MA. Voucher sets have been sent to the Albany State Museum, Albany, NY, and the Museum of Comparative Zoology in Cambridge, MA.

Distinguishing specimens of *Aphaenogaster rudis* Enzmann (The Rough *Aphaenogaster*) and a closely related species *Aphaenogaster picea* (Wheeler) (The Pitch-black *Aphaenogaster*) is difficult and these are some of the most abundant species in eastern woodlands. Due to my uncertainty in identification of these common ants, I lumped all of the specimens of these species under the name of the more common species, *A. picea*, for the analyses described below. However, one specimen from a study plot in the APBP was positively identified as *A. rudis* by Bernice DeMarco (Department of Entomology, Michigan State University, East Lansing, MI) and this specimen along with one from SSP plot TR were confirmed by Stefan Cover, so *A. rudis* appears in the species lists for the APBP and SSP (Table 1.2).

#### **1.4.6 Data Analysis**

##### **1.4.6.1 Interpreting ant numbers**

Many authors have emphasized the importance of not basing relative species abundance estimates on the numbers of individual ants, but rather on colony numbers (reviewed by Gotelli et al. 2011). For plot-level comparisons, I used the instances of species occurrence (termed

“species incidence”) in distinct sub-samples (i.e. quadrats or pitfall traps), which I consider a valid surrogate for colony frequency, rather than worker numbers or direct colony observations. This decision was supported by a highly significant correlation in the rank order of the overall incidences of detection and the incidences of colony detection for each species (Spearman’s rho) ( $\rho = 0.87, P \ll 0.0005$ ) (Figure 1.2). Species-specific differences in nest structure (i.e. polydomy vs. monodomy), which influence probability of nest detection, and the fact that one species (*Monomoreum emarginatum* DuBois (The Furrowed *Monomorium*)) was more readily collected in pitfall traps and always counted as strays when collected by this method, likely contribute to the variance in this relationship.

#### **1.4.6.2 Species density**

Species density is defined as the number of species per unit area, whereas species richness is the total number of species in a habitat or ecosystem. Since samples in the current study are area-based, they can be used to estimate the species density of ants in my study plots (Gotelli and Colwell 2001). I compared species density across plots by rarefying my data to adjust for unequal sample sizes and examining the species accumulation curves and estimates of the true species density of the plots and of the habitat types. I used the software EstimateS (Colwell 2013) to rarefy the data and generate the Chao2 estimates of true density. The Chao2 formula is recommended for making comparisons across samples for incidence-based data (Chao et al. 2014) and provides more reliable estimates of the true species density by taking into account the completeness of the sample based on the number of species recorded only once or twice in the sample.

To more reliably compare species density across plots, I minimized the effect of sampling method by using only the data from ants collected through quadrat searches. Furthermore, I used only the first survey from the 2013 data because the quadrats from the first and second surveys were not necessarily sampling independent colonies due to their spatial proximity. The decision

to use the first rather than the second survey from 2013 was based on the first survey having a higher degree of seasonal overlap with the 2012 survey. Thus, all twelve 1-m<sup>2</sup> quadrat searches were included in the analysis for each of the 2012 plots, and ten 1-m<sup>2</sup> quadrat searches per plot were used from the 2013 data. I then compared the estimates of rarefied species density for ten quadrats per plot, the largest number for which Chao2 estimates were able to be calculated for all plots.

In nine of the twelve sites (BF, BH, DC, GD, KB, KE and KW at APBP; CS and TR at SSP), the coefficient of variation of the incidence distribution was >0.5. Under these circumstances, it is recommended to use the larger of the Chao2 estimates calculated using either the bias-corrected or classic formula (Colwell 2013). In every case, the estimate from the classic formula was larger for these sites, so I used that estimate in all analyses involving species density. For the other three sites (AR, DP, and RS), the bias-corrected formula was used.

#### **1.4.6.3 Compositional differences**

To identify patterns in ant assemblage composition across my sites and simultaneously identify the measured environmental variables most closely correlated with differences in assemblage composition, I used redundancy analysis (RDA) (Gotelli and Ellison 2012). I used RDA for the constrained ordination because detrended correspondence analysis axis lengths for the data were <3, indicating that the species responses across the samples were likely to be linear, rather than unimodal (Jongman et al. 1995). Furthermore, environmental gradients within the sites are quite small (i.e. changes from graminoid-dominated to shrub-dominated open habitat with climatic, latitudinal, and soil characteristics being very similar for all plots), making linear relationships over this gradient plausible (McGarigal et al. 2000). The data used in this analysis were ant species incidences (occurrence in pitfall traps or quadrats) for each plot, and included only species that were detected in two or more plots (McCune and Grace 2002). Species incidence data were Hellinger-transformed to reduce the influence of extreme values and increase



the linearity of relationships between species (Legendre and Gallagher 2001). The measured environmental variables were used as constraining variables. When the absolute correlation value was  $>0.7$  between any two variables, the variable that better explained the variance in the species data based on their constrained eigenvalues from partial RDAs was kept and the other was dropped. Of the variables that remained, only those whose inclusion in the model lowered the AIC value by  $\geq 2$  — as determined through forward step-wise selection — were included in the final ordination.

I included data from pitfall traps and all of the quadrat samples in this analysis to increase the data available for the RDA. However, data from same-transect quadrats spatially separated by just one meter, but temporally separated between the first and second surveys were combined so that if a species was observed in both quadrats, it was counted as a single incidence of that species. Three observations provide support for including the data from both 2013 surveys and both methods in 2012: (1) results of an RDA using the quadrat data alone were qualitatively similar to the RDA done using all the data; (2) all of the species collected by pitfall traps in this study were also collected during quadrat searches, though not always in the same plot; and (3) evidence of consistent, strong biases for particular species by either pitfall trapping or quadrat sampling was nearly absent, except perhaps for *Monomorium emarginatum*, which was consistently collected more frequently in pitfall traps. Although six species were detected through pitfall traps or at baits in 2012 that were not also detected in quadrat searches that year, they occurred in very few samples overall, so their detection by a single method does not necessarily indicate differences in detection probability based on method, but may simply reflect the benefit of increased sampling effort in general.

#### **1.4.6.4 Data and code availability**

I used the R software and programming language (R Core Team 2014) for nearly all data manipulations, analyses, and figures. I used the R libraries “car” (Fox and Weisberg 2011),

“reshape2” (Wickham 2007), “ggplot2” (Wickham 2009), “vegan” (Oksanen et al. 2013), and “knitr” (Xie 2014), and a compilation of R functions written by Kevin McGarigal (Department of Environmental Conservation, University of Massachusetts, Amherst, MA) (“biostats.R” available online at [http://www.umass.edu/landeco/teaching/ecodata/labs/ecodata\\_labs.html](http://www.umass.edu/landeco/teaching/ecodata/labs/ecodata_labs.html)). Rarefaction and calculation of species density estimates were the only analyses for which I used additional software: EstimateS (Colwell 2013). The data from this study and R code will be available online in the Harvard Forest Data Archives (<http://harvardforest.fas.harvard.edu/data-archive>).

## 1.5 Results

I collected and identified 16,851 specimens, which included 53 species in 21 genera and 4 subfamilies, over two years of sampling from the three study sites (Table 1.2). These included 49, 26, and 20 species collected from APBP, SSP, and RSP, respectively. Twenty-eight species were detected through the study methods alone at the 2012 plots, and forty-one through the study methods alone at the 2013 APBP plots. The forty-one species collected from quadrats in 2013 were collected from just 120 square meters of ground at the APBP during 57 total hours of active sampling time (8 or 15 minutes per square meter). The most frequently collected ant species in 2012 were The Furrowed Monomorium (95 incidences) and *Lasius neoniger* Emery (The Labor Day Ant) (91 incidences). In 2013, an undescribed species of *Myrmica*, designated by André Francoeur as *Myrmica* sp. AF-smi, was collected most commonly (52 incidences), followed by *Ponera pennsylvanica* Buckley (The Pennsylvania *Ponera*) and *Aphaenogaster picea* (each with 38 incidences).

The 49 ant species I collected over two years of sampling at the APBP and the existing species list for the preserve (Barnes, 2003) (32 species after updates to the taxonomy), resulted in a combined total of 53 species recorded at the preserve. This represents a 66%, or 21 species, increase over the 2003 list. Species present in historical records, but not in my surveys, were *Myrmica fracticornis* Forel (The Broken-horned Ant), *Lasius interjectus* Mayr (The Large

Yellow Ant), *Formica difficilis* Emery (The Troublesome Ant) and *Formica querquetulana* Kennedy and Dennis (The Oak-grove Ant).

Two particularly uncommon species for the region that I collected during this study effort were *Forelius pruinosus* (Roger) (The High Noon Ant) and *Formica knighti* Buren (Knight's Ant). *Forelius pruinosus*, though common in the southern United States, rarely has been collected in the Northeast, and the record of it at APBP may be the most northern record for the eastern United States (AntWiki). *Formica knighti* is a rarely collected species that had been recorded previously only in Iowa, Missouri (MacGown 2003), Plymouth County, MA; Martha's Vineyard, MA; and Long Island, NY. Its presence in the SSP in a small clearing dominated by grasses and *Comptonia peregrina* (L.) J.M. Coult. (Sweet Fern) is the northernmost known record.

### **1.5.1 Grassland vs. shrubland species density**

In all comparisons of grassland and shrubland plots, the shrubland plots had an equal or greater number of species detected and estimated than did the grassland plots. I collected 39 species from the shrubland plots and 33 from the grassland plots if only data from quadrat samples and pitfall traps were considered (44 and 35 species respectively when all samples were included). The Chao2 point estimates of species density within ten 1-m<sup>2</sup> quadrats per plot were higher for all of the shrubland plots ( $33 \pm 9$ ) than they were for the grassland plots ( $14 \pm 4$ ) (Figure 1.3). A similar pattern was seen based simply on the rarefied species data at the level of ten quadrats sampled per plot (shrubland plots:  $19 \pm 3$ [sd]; grassland plots:  $11 \pm 3$ [sd]). However, since the Chao2 formula takes into account the completeness of the survey based on the numbers of singletons (species collected only once in a plot) and doubletons (species collected just twice in a plot), it is considered the better metric for making comparisons across plots. A Welsh Two Sample t-test indicated that there was a significant difference in Chao 2 mean estimates of species density between the two habitat types ( $t = 3.9$ ,  $df = 3.7$ ,  $P = 0.02$ ). Additionally, the species accumulation curves from the rarefied quadrat data have steeper slopes at the level of ten samples

for the shrubland plots than for the grassland plots, indicating that the sampling effort was less adequate for capturing the full assemblage in the shrubland than grassland plots and that the Chao2 estimates should be considered a lower-bound estimate (Figure 1.3).

AR (a grassland plot) was significantly less species-dense than all of the shrubland plots, and was also significantly less species-dense than the grassland plot having the highest incidence of shrub-level oaks (DP). The two plots with the highest estimates of mean species density (KB and BH) were both shrubland plots and had significantly more species than multiple grassland plots (Figure 1.4). Increased canopy above 0.5 m was associated with shrub-level oak density and strongly correlated with increases in estimated ant species density ( $r^2 = 0.73$ ,  $P < 0.0005$ ) (Figure 1.3).

### **1.5.3 Grassland vs. shrubland assemblage composition**

The separation of shrubland and grassland plots along the first principle axis of the RDA, which explained 47% of the variance among the transect assemblages, indicated that there were compositional differences among ant assemblages occurring in the different habitats (Figure 1.4). The results of the RDA also revealed that two constraining variables, one related to shrub-level oak coverage and the other to the proportion of ground covered by dead material, explained 59% of the variation in the species data based on a permutation test (199 permutations;  $P = 0.005$ ). Beyond the clustering of the shrubland plots in the RDA, the APBP sites also separated slightly from the SSP and RSP sites along the second axis, suggesting possible regional differences. However, the low proportion of the variance explained by this axis (12%) and the low replication in SSP and RSP (none in the case of RSP) result in little statistical power to detect regional or latitudinal differences.

*Lasius neoniger* and *Tetramorium caespitum* (Linnaeus) (The Pavement Ant) are common species of open and highly disturbed habitats in the northeastern United States, and in the current study were much more common in the grassland than shrubland plots, having among

the most negative loadings on the first axis of the RDA and highest goodness-of-fit values (0.87 and 0.85, respectively). Many other species were somewhat shifted toward the shrubland plots in the ordination space. Of these, *Ponera pennsylvanica*, *Myrmica pinetorum* Wheeler (The Ant of the Pines), and *Dolichoderus taschenbergi* (Mayr) (Taschenberg's *Dolichoderus*) appeared to be the most strongly associated with the shrubland plots in the ordination space of the RDA and had high goodness-of-fit scores relative to the other species (goodness of fit values = 0.74, 0.82, and 0.95, respectively) (Figure 1.4).

## 1.6 Discussion

The results of this study add to our understanding of ant species distributions in the northeastern United States. They reveal high overall species density in inland Pitch Pine barrens, with higher species density in shrubland than in grassland habitats. The higher richness in shrubland habitats was accompanied by some species being more strongly associated with this habitat type. The described differences in species composition that I was able to detect involve abundant species at the plots. These habitat types may be influencing less common or rare species that occur in pine barrens as well, but more extensive sampling is needed to identify such relationships. At the current state of understanding, conserving pine barrens and both these habitat types within pine barrens is recommended for the conservation of regionally, and perhaps globally, rare ant species.

In the Northeast, similar densities of ant species to those found in the APBP (41 species from 120 m<sup>2</sup> in 25 person-hours) are rarely encountered, and similar ant species richness (53 species at the APBP) in a preserve or other similarly sized landscape have been reported only after much more extensive sampling or in other pine barrens. For example, a survey of ants across nine habitat types within Acadia National Park, conducted by 34 volunteers for a time period of up to 5 hours (170 person-hours) produced 42 species (Ouellette et al. 2010), and ten years of exhaustive sampling in an Albany County woodland yielded just 14 species from 2512 m<sup>2</sup> of

ground searched (Herbers 2011). Extensive sampling of blueberry fields in Maine over a six-year period yielded a maximum of 27 species in any single field-type for any given year (Choate and Drummond 2012). In comparison, five of the twelve APBP plots yielded >30 species when including data from all collection methods, with 44 being the maximum number of species observed at any single plot (this was observed at BH). Finally, 53 is more species than have been recorded from all but 16 of 67 counties in New England (Ellison and Gotelli 2009).

Other well-surveyed pine barrens systems in the Northeast also show high ant species richness. Seven years of intensive collecting across Nantucket Island resulted in the collection of 58 species, 54 of which occurred in sandy barrens habitats (Ellison 2012a). In the Montague Sandplains in Massachusetts, another inland pine barrens system at approximately 100 m.a.s.l. and similar latitude (41.56°N), 42 species have been recorded (Ellison and Gotelli 2009). Considered together, these findings suggest that the high species richness at the APBP is not idiosyncratic, but rather is characteristic of the pine barrens habitat.

I also found evidence of higher ant species density associated with shrublands than grasslands in northeastern United States inland Pitch Pine barrens. Not only did I observe more species in each of the shrubland plots than in any of the grassland plots, but the combined shrubland plots yielded more species than the combined grassland plots. This is true despite there being twice as many grassland plots as shrubland plots and the grassland plots being distributed over a broader longitudinal (but narrow latitudinal) range. The extent to which it is possible to draw inferences about the relative species richness of ants in grasslands and shrublands based on these results is limited by the small sample size, geographic range and number of habitats considered. However, my results are similar to those of studies from other regions and ecosystems (Bestelmeyer 2005, Ellison 2012a, Kumschick et al. 2009, Wiezik et al. 2013). At the APBP, where shrubland is intentionally created, the differences between grassland and shrubland invertebrate assemblages and related ecosystem processes merit further investigation.

The findings of this study suggest that pine barrens, and shrub-level oak-dominated shrubland habitats in particular, should be considered areas likely to have high ant biodiversity in the northeastern United States. However, increasing shrub density may lead to increasing ant species density only up to a point. Ant species density tends to decrease in forests at this latitude, presumably due to the cooler temperatures under shade (Gotelli and Ellison 2002). Therefore, shade-producing canopy cover would be expected to increase with increasing shrub density and could eventually lead to some ant species being thermally excluded from areas of denser shrub vegetation.

The reasons behind the higher species richness in shrubland plots are not resolved in this study and could be attributable to many factors. These include the availability of food resources, particularly the abundance of honey-dew-secreting hemipterans (Choate and Drummond 2012, Wheeler Jr. 1991); higher habitat heterogeneity on the ground (Graham et al., 2009), allowing both forest and field species to find suitable nesting sites (Bestelmeyer 2005, Dangerfield et al. 2003, Wiezik et al. 2013); and the type and frequency of disturbance. Understanding to which of these factors the ant assemblages are responding could be useful in tracking ecosystem recovery and guiding management decisions.

There is great potential to gain insight into factors mediating ant assemblage structure in the northeastern U.S. through studying their dynamics in pine barrens systems. These systems experience a wide range of daily and annual temperature variation, contain a variety of plant communities, and occur on fairly consistent substrate. Ants have been used as indicator species in other parts of the world, but most of these cases are restricted to warm regions with high diversity in species and functional groups (Ellison 2012*b*). In the northeast, ant assemblages may peak with respect to species richness in pine barrens, and should therefore be investigated for their potential as indicators in these habitats. As pine barrens continue to be restored through management, monitoring changes in the ant assemblages could provide useful insights into how this important

taxon might be expected to respond to the rising temperatures expected with climate change in the context of a northern temperate biome and its current suite of biota.

The high ant species richness that currently exists in pine barrens may benefit the region as a whole as the regional climate changes. One concern regarding climate change is that many species will not be able to disperse rapidly enough to keep pace with the northward-shifting climate (Schloss et al. 2012). Because pine barrens currently serve as northern range extensions for some southern and more heat-tolerant species, these habitats could help to maintain overall ant species density by providing northern occurrences of heat-tolerant species to replace heat-intolerant species that may be lost. The incidence of *Forelius pruinosus* and *Formica knighti*—both of which experience their northern-most known occurrences in these inland pine barrens systems—points to the value of these habitats in terms of regional ant biodiversity.

## **1.7 Acknowledgements**

This work would not have been possible without the tremendous help and support of Aaron Ellison (Harvard Forest, Petersham, MA) and Paul Sievert (Department of Environmental Conservation, University of Massachusetts, Amherst, MA). I thank The Nature Conservancy (TNC), The New York State Department of Environmental Conservation (DEC), and the APBPC, who granted me permission to collect specimens in these New York State pine barrens. Staff at the APBP, including Chris Hawver, Neil Gifford, Joel Hecht, Amanda Dillon, Jesse Hoffman, and Erin Kinal, and others, including Chis Zimmerman (TNC), Kathleen O'Brien (DEC), and Bernard Davies provided a great deal of feedback and knowledge of the barrens systems investigated in this study. Claudia Knab-Vispo and Conrad Vispo of Hawthorne Valley Farm and the Farmscape Ecology Program, Jesse Hoffman, and Amanda Dillon provided valuable assistance with plant identifications, and Amanda Dillon contributed many hours of assistance sorting and identifying ant specimens. Aaron Ellison, Stefan Cover (Museum of Comparative Zoology in Cambridge, MA) and Bernice DeMarco (Department of Entomology, Michigan State



University, East Lansing, MI) assisted with ant specimen identifications. This research was supported by the Department of Environmental Conservation at the University of Massachusetts Amherst, and grant number DE-FG02-08ER64510 from the US Department of Energy, awarded to Aaron Ellison.

**Table 1.1:** Study plot characteristics. The texture of the upper 18 cm of soil is denoted by the abbreviations “CS”: coarse sand, “L”: loam, and “LFS”: loamy fine sand. Drainage class is denoted by the abbreviations “W”: well drained, “M”: moderately well drained, “S”: somewhat excessively drained, “E”: excessively drained. Habitat type is denoted by “S” and “G” for shrubland and grassland, respectively. Incidence of graminoids and scrub-level oaks refers to their frequency along the transect, and median cover was determined with a densiometer.

Locality	Plot	Latitude (°N)	Longitude (°W)	Area (ha)	Year Sampled	Habitat	Incidence of graminoids (%)	Incidence of shrub-level oaks (%)	Median canopy cover	Upper 18 cm of soil	Drainage class
APBP	<b>AR:</b> Apollo Restoration	42.72235	-73.86834	1.8	2012	G	65.2	4.3	0.4	CS	W
APBP	<b>BF:</b> Barons Field	42.73772	-73.89195	6.2	2012	G	54.5	9.1	7.2	L, LFS	M
APBP	<b>BH:</b> Blueberry Hill West	42.70064	-73.86961	18.5	2013	S	53.3	50.0	65.3	LFS	S
APBP	<b>DC:</b> DC Field	42.71952	-73.86365	3.7	2012	G	73.9	0.0	4.7	CS	W
APBP	<b>DP:</b> Draperies	42.71830	-73.88420	4.4	2013	G	60.0	13.3	21.3	LFS	S
APBP	<b>GD:</b> Great Dune	42.70600	-73.89779	17.1	2013	G	53.3	0.0	16.0	LFS	S
APBP	<b>KB:</b> Kings Road Barrens	42.72390	-73.87666	9.7	2013	S	90.0	53.3	51.5	LFS	S
APBP	<b>KE:</b> Karner Barrens East	42.71402	-73.86525	6.8	2013	S	80.0	70.0	38.7	LFS	S
APBP	<b>KW:</b> Karner Barrens West	42.71904	-73.87059	11.3	2013	S	93.3	53.3	31.5	LFS	W
RSP	<b>RS:</b> RSP Field	43.23065	-75.57895	1.8	2012	G	87.5	0.0	0.0	LFS	E
SSP	<b>CS:</b> Camp Saratoga	43.15621	-73.69557	5.6	2012	G	83.3	0.0	4.4	LFS	W
SSP	<b>TR:</b> Trinity	43.16033	-73.70377	2.1	2012	G	87.0	0.0	2.0	LFS	W

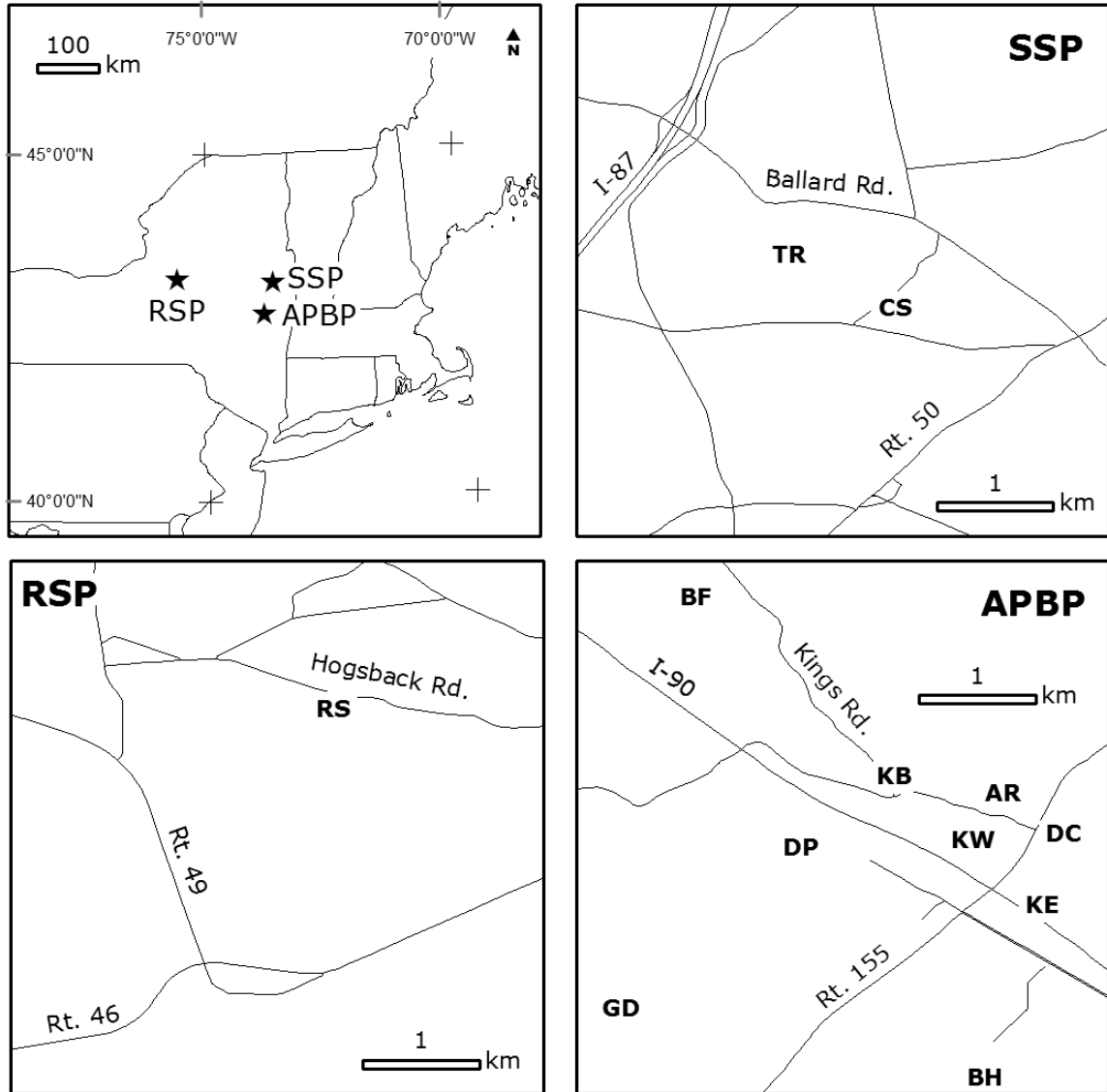
**Table 1.2:** List of ant species collected from the three barrens sites and two habitat types.

<b>Species</b>	<b>APBP</b>	<b>RSP</b>	<b>SSP</b>	<b>Grassland</b>	<b>Scrubland</b>
<i>Aphaenogaster rudis</i> Enzmann, 1947	x		x		x
<i>Aphaenogaster picea</i> (Wheeler, 1908)	x	x	x	x	x
<i>Aphaenogaster treatae</i> Forel, 1886	x			x	x
<i>Brachymyrmex depilis</i> Emery, 1893	x			x	x
<i>Camponotus americanus</i> Mayr, 1862	x			x	x
<i>Camponotus nearcticus</i> Emery, 1893	x				x
<i>Camponotus novaeboracensis</i> (Fitch, 1855)	x		x	x	x
<i>Camponotus pennsylvanicus</i> (DeGeer, 1773)	x		x	x	x
<i>Crematogaster cerasi</i> (Fitch, 1855)	x	x		x	x
<i>Crematogaster lineolata</i> (Say, 1836)	x			x	x
<i>Dolichoderus plagiatus</i> (Mayr, 1870)	x				x
<i>Dolichoderus pustulatus</i> Mayr, 1886	x		x	x	x
<i>Dolichoderus taschenbergi</i> (Mayr, 1866)	x			x	x
<i>Formica argentea</i> Wheeler, 1901	x	x		x	x
<i>Formica dolosa</i> Buren, 1944	x	x	x	x	x
<i>Formica exsectoides</i> Forel, 1886	x			x	x
<i>Formica incerta</i> Buren, 1944	x	x	x	x	x
<i>Formica integra</i> Nylander, 1856		x	x	x	
<i>Formica knighti</i> Buren, 1994			x		
<i>Formica lasioides</i> Emery, 1893	x	x	x	x	x
<i>Formica neogagates</i> Viereck, 1903	x	x		x	x
<i>Formica obscuriventris</i> Mayr, 1870	x			x	x
<i>Formica pallidefulva</i> Latreille, 1802	x			x	x
<i>Formica pergandei</i> Emery, 1893	x		x	x	x
<i>Forelius pruinosus</i> (Roger, 1863)	x				x
<i>Formica rubicunda</i> Emery, 1893	x		x	x	x
<i>Formica subsericea</i> Say, 1836	x	x	x	x	x
<i>Lasius alienus</i> (Foerster, 1850)	x	x		x	x
<i>Lasius claviger</i> (Roger, 1862)	x				x
<i>Lasius latipes</i> (Walsh, 1863)	x				x
<i>Lasius nearcticus</i> Wheeler, 1906	x				x
<i>Lasius neoniger</i> Emery, 1893	x	x	x	x	x
<i>Monomorium emarginatum</i> DuBois, 1986	x		x	x	x
<i>Myrmica</i> (sp. AF-eva) sensu Francoeur			x	x	
<i>Myrmica</i> (sp. AF-smi) sensu Francoeur	x	x	x	x	x
<i>Myrmica americana</i> Weber, 1939	x	x	x	x	x
<i>Myrmica detritinodis</i> Wheeler, 1917		x		x	
<i>Myrmecina americana</i> Emery, 1895	x			x	x
<i>Myrmica pinetorum</i> Wheeler, 1905	x			x	x
<i>Myrmica punctiventris</i> Roger, 1863	x	x	x	x	x
<i>Nylanderia parvula</i> (Mayr, 1870)	x	x	x	x	x

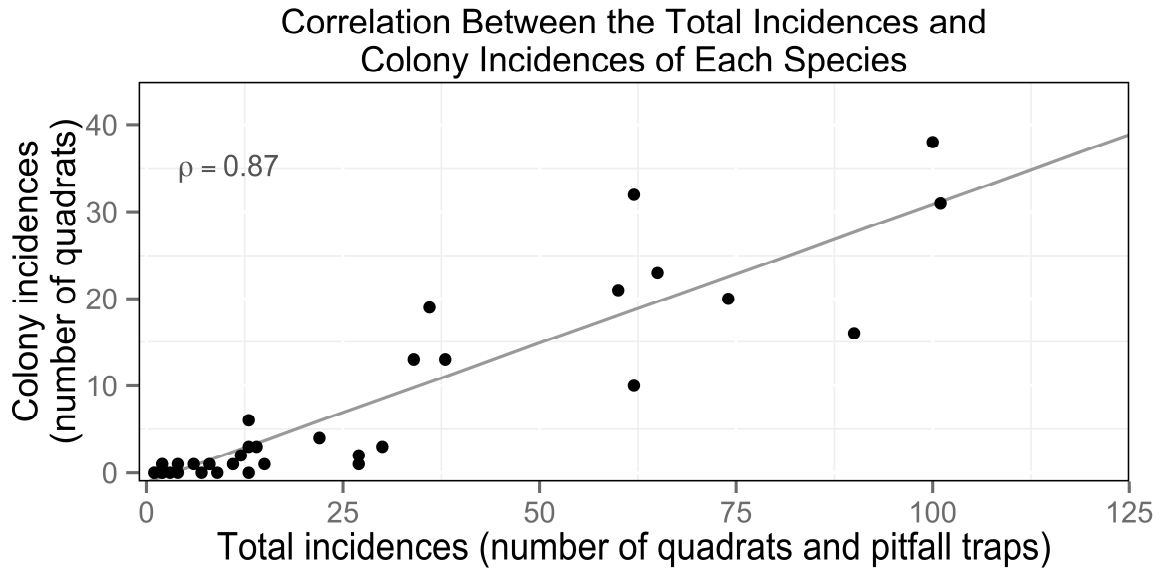
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Table 1.2, continued

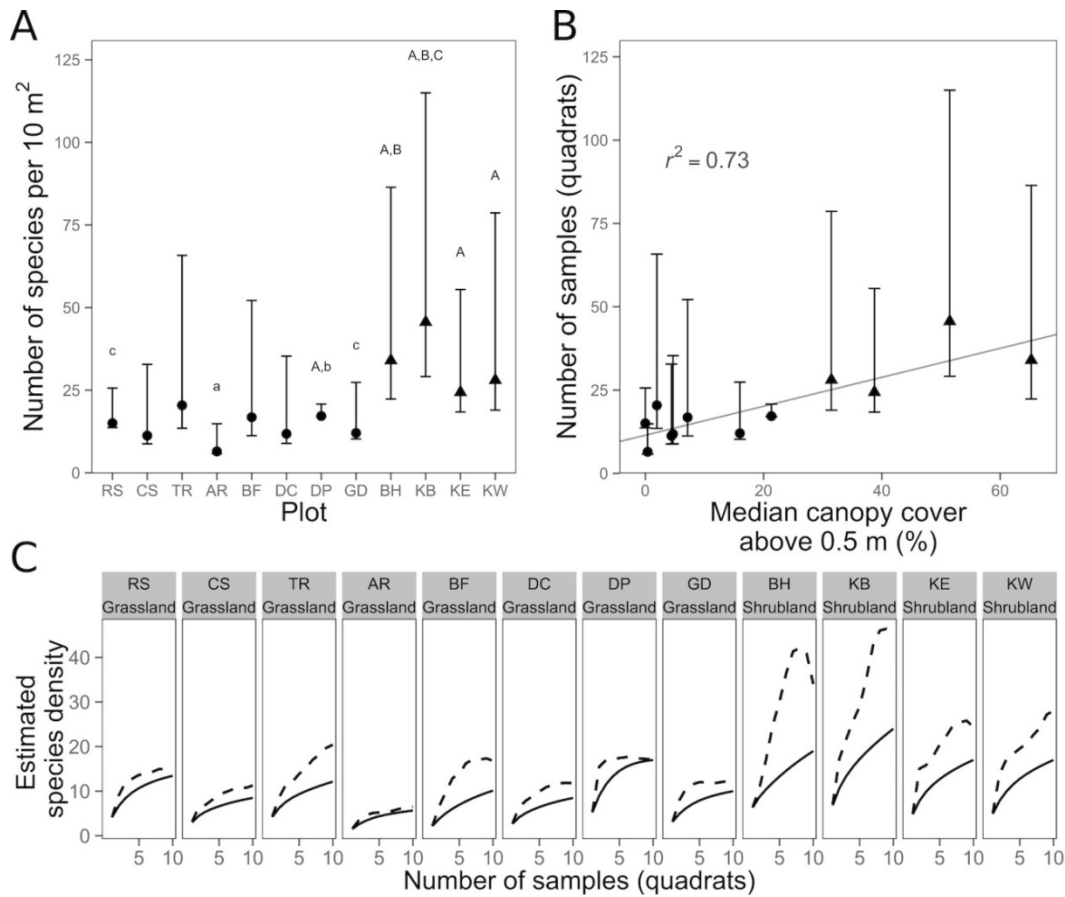
<b>Species</b>	<b>APBP</b>	<b>RSP</b>	<b>SSP</b>	<b>Grassland</b>	<b>Scrubland</b>
<i>Pheidole pilifera</i> (Roger, 1863)	x		x	x	x
<i>Polyergus lucidus</i> Mayr, 1870	x				x
<i>Ponera pennsylvanica</i> Buckley, 1866	x		x	x	x
<i>Prenolepis imparis</i> (Say, 1836)	x			x	x
<i>Solenopsis molesta</i> (Say, 1836)	x	x	x	x	x
<i>Stenammas impar</i> Forel, 1901	x			x	x
<i>Tapinoma sessile</i> (Say, 1836)	x	x	x	x	x
<i>Temnothorax ambiguus</i> (Emery, 1895)	x	x	x	x	x
<i>Temnothorax curvispinosus</i> (Mayr, 1866)	x			x	x
<i>Temnothorax longispinosus</i> (Roger, 1863)	x				x
<i>Temnothorax schaumii</i> (Roger, 1863)	x				x
<i>Tetramorium caespitum</i> (Linnaeus, 1758)	x	x	x	x	x
<b>Totals:</b>	<b>49</b>	<b>20</b>	<b>26</b>	<b>42</b>	<b>49</b>



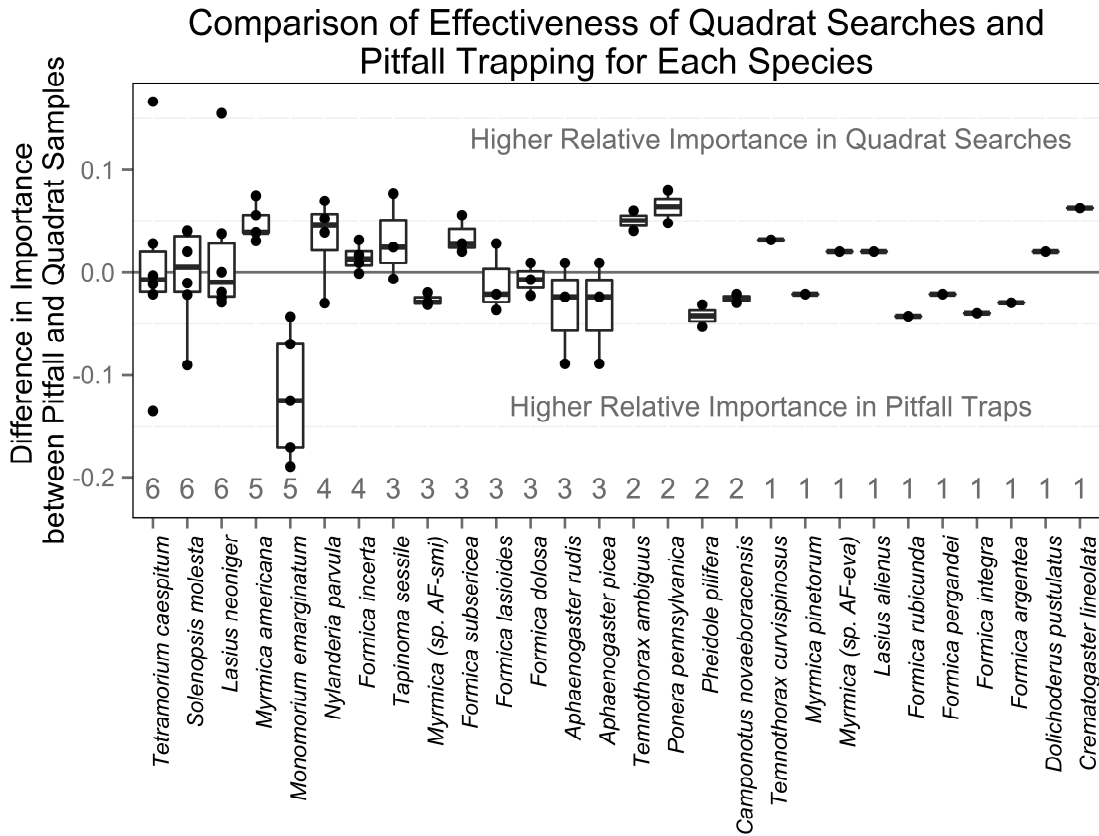
**Figure 1.1:** Maps of the study sites and plots. The location of the study sites are indicated by their abbreviations, (RSP, SSP, and APBP) in the map in the upper left panel. The other three panels show study plot locations (indicated by their abbreviations) within the study sites.



**Figure 1.2:** Correlation between the total incidences of species in quadrats and pitfall traps and the incidences of detection where the species were collected from a nest within a quadrat (colony incidence). The points on the graph each represent the relationship between colony and total incidence for a single species. The correlation value presented in the upper left is Spearman’s  $\rho$  (correlation for rank transformed data), but the data depicted, to which a linear model (gray line) is fitted, are not rank transformed. Spearman’s  $\rho$  is presented rather than Pearson’s  $r$  because the assumptions of linear regression, homoscedasticity in particular, are violated. 10,000 permutations of the data did not yield a single instance with the absolute value of  $\rho$  greater than that 0.86. The deviation of points from the trend line indicate that observations of some species were more or less commonly made at the nest-site (points falling above or below the line, respectively). Overall, the total incidence is closely correlated with the colony incidence, but provides more information, particularly for less common species.



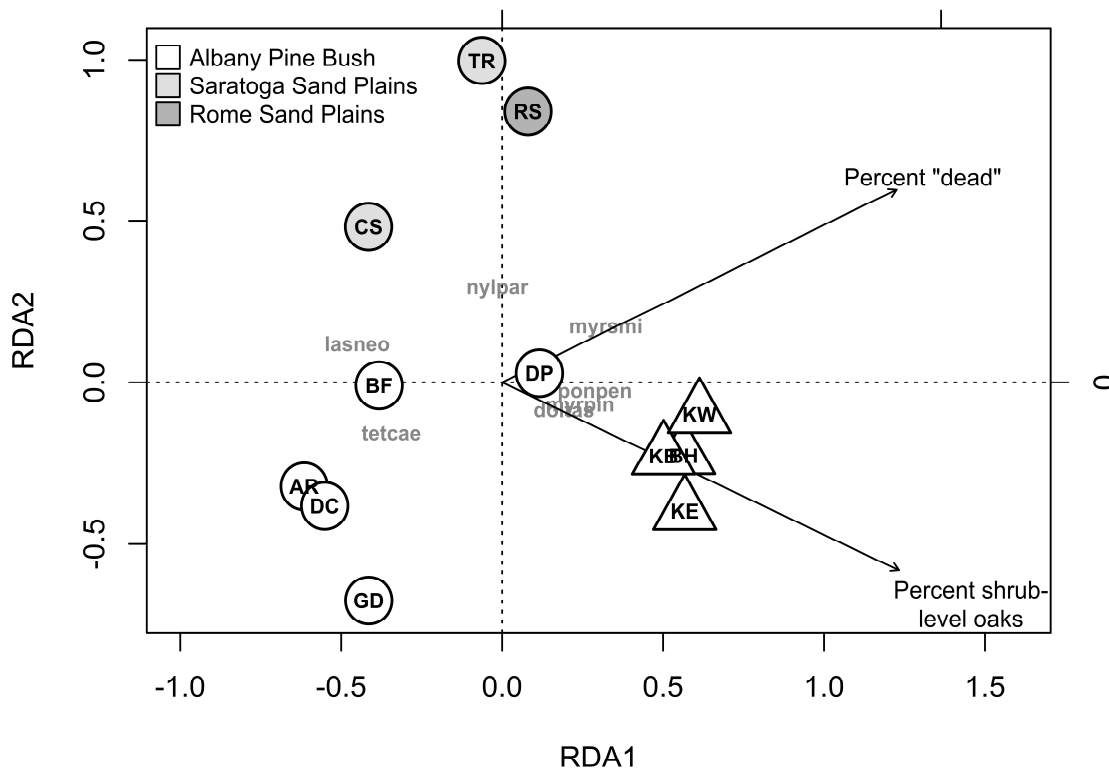
**Figure 1.3:** Species density across study plots. In panels A and B, circles represent grassland plots and triangles represent shrubland plots. In both panels A and B, the point estimates for species density and 95% confidence intervals (error bars) based on the Chao2 formula are shown. In panel A, significant differences as determined by non-overlapping error bars are indicated by different letters above the error bars. A lowercase letter signifies the plot had significantly lower species density than plots labeled with the corresponding uppercase letter. The plot identities are indicated on the x-axis. In panel B, the same data are shown regressed against the median canopy cover for the plot (transect) on the x-axis. The coefficient of determination is indicated in the upper left. Panel C shows the species accumulation curves (solid lines) and Chao2 estimates (dashed lines) with increasing sample size (1-10 quadrats) based on the rarefied data from the plots.



**Figure 1.4:** Comparison of effectiveness of quadrat searches and pitfall trapping for each species. The data presented are the difference in relativized species incidences detected by each survey method (i.e. the number of incidences of each species captured by one or the other of the sampling methods, divided by the combined species incidences detected by that method at each 2012 plot. The relative species values detected by pitfall traps were then subtracted from the relative species values detected by quadrats and those data are plotted). Each point represents the value for the corresponding species at one of the six 2012 plots. In cases where a species was not detected in a plot at all, by any method, there is no point for that plot × species combination. The number of points (plots) for each species is indicated by the gray numbers above the x-axis. The points falling below 0 on the y-axis are instances where that species’ abundance as detected by pitfall traps was relatively higher for that plot than it was as detected by quadrat searches, and the points above 0 show instances of the opposite relationship.



### Redundancy Analysis of Ant Incidence Data



**Figure 1.5:** Redundancy analysis (RDA) of species data consisting of Hellinger-transformed species incidence from pitfall traps and quadrat searches. The vectors indicate the environmental variables that contributed to a plausible model (Percent “dead”: the percent of points along a transect where the ground was at least 50% covered in dead material, and Percent Shrub-level Oaks: the percentage of sampling points intersected by shrub-level oaks). The centroid of ant species having goodness-of-fit values >0.70 are indicated by their species code written in gray; see the Results section for further details. Initials inside the symbols indicate the plot identity.

## CHAPTER 2

### HIKING TRAILS IN A NY PINE BARRENS: IMPACTS ON ANT ASSEMBLAGES (HYMENOPTERA: FORMICIDAE)

#### 2.1 Abstract

Anthropogenic habitat disturbance threatens the persistence of many ecosystems, but disturbance-dependent systems may benefit from some types of human-generated disturbance. The Albany Pine Bush Preserve (APBP) is an inland pine barrens requiring a relatively high intensity or frequency of disturbance to maintain its characteristic habitat and biota. The maintenance and use of hiking trails is a widespread form of disturbance in many ecosystems, including the APBP. The effect of these trails on most species is unknown, but anecdotal evidence suggests that some thermophilic species may benefit from the trails' presence. Ants are ecologically important invertebrates that are easy to sample and show strong responses to habitat variation and changes in temperature at the ground level. Virtually nothing is known, however, about how ant assemblages respond to hiking trails in any environment. I sampled ant assemblages along hiking trails and in the interior of managed shrubland in the APBP with timed quadrat searches, and used ordination techniques to explore the data for patterns in ant species distributions related to these features and associated environmental variables. The results indicated associations of some ant species with hiking trails in this ecosystem. Furthermore, the results revealed that it is not hiking trails per se, but the often-associated changes in environmental variables that drove differences in ant species assemblage. The environmental variability along hiking trails and the habitats through which they pass provide opportunities to observe how species respond to increased disturbance and a variety of other variables. Hiking trail ant assemblages also could be informative when monitoring rates of recovery in ant fauna following management or by providing early warning of the arrival and spread of non-native species. Sampling ant assemblages along hiking trails is relatively convenient, safe, and results in

little added environmental impact, and could feasibly be incorporated into community-supported- or citizen-science programs.

## 2.2 Introduction

The Albany Pine Bush Preserve (APBP) is an example of globally rare inland Pitch Pine-Scrub Oak barrens (Barnes 2003). The preserve is known for having high invertebrate species richness (Barnes 2003) and as a northern range extension for some southern species including *Scaphiopus holbrookii* (Harlan, 1835) (the Eastern Spadefoot), and *Carphophis amoenus* (Say, 1825) (the Eastern Worm Snake) (Stewart and Rossi 1981). Previous studies in other pine barrens and at the APBP have revealed uncommonly high ant species density and the presence of at least one southern species (*Forelius pruinosus* (Roger) (the High Noon Ant) (Chapter 1)). In the APBP, ant species density appears to be higher in shrubland habitats than in areas with shorter and sparser vegetation, a phenomenon that has been observed in other arid and mesic ecosystems (Bestelmeyer 2005, Wiezik et al. 2013) and for other invertebrate groups, including ant-mimicking Heteroptera (Wheeler Jr. 1991). As part of its mission, the Albany Pine Bush Preserve Commission (APBPC) maintains pitch pine-scrub oak habitat, and a trail system that is open to the public. The effects of these hiking trails on wildlife is a concern of preserve managers, who rerouted large sections of some of the most popular trails in 2013 in order to create larger patches of contiguous, interior habitat that will experience less disturbance from recreational use of the trails.

Although the impacts of hiking trails on several groups of organisms have been repeatedly evaluated (birds: (Deluca and King 2014, Immitzer et al. 2014), plants: (Bright 1986, Törn et al. 2009, Tysler and Worley 1992), birds and plants: (Wolf et al. 2013)), virtually nothing is known about how they affect ant assemblages or other insects (but see Chow et al. 2014). This is surprising for several reasons, among which are the ubiquity and ecological importance of ants (Del Toro et al. 2012), the relative ease of sampling ants (Agosti et al. 2000),

and the fact that hiking trails are known to affect soil compaction, temperature, moisture, and resource availability, all of which in turn influence ant assemblages (Barrow and Parr 2008). Indeed, some species of ants have been observed to found, or attempt to found, colonies preferentially on dirt roads (Vasconcelos et al. 2006), and both high levels of disturbance and habitat fragmentation, have been shown to alter ant species assemblages (Ślipiński et al. 2012, Vasconcelos et al. 2000).

Hiking trails often are thought of as an ecologically damaging form of anthropogenic disturbance, but in disturbance-dependent ecosystems they may provide valuable habitat or resources to some species (Cornelisse and Duane 2013). On the other hand, highly disturbed environments and areas with more human activity may be particularly susceptible to invasion by non-native species. The purposes of this study were to evaluate the effects of hiking trails on ant assemblages in the APBP and shed light on the relationships between the ant assemblages of interior habitat and those of the trails that pass through these habitats. I investigated these relationships through comprehensive sampling of ant assemblages along transects in the interior of managed pine barrens habitat at the APBP, along the edge of this managed habitat bordering hiking trails, and on the margins of hiking trails, and compared species assemblages based on species density, colony density, and assemblage composition.

### **2.3 Field Site Description**

The Albany Pine Bush Preserve is located in New York State and encompasses approximately 1,110 hectares of land in the towns of Colonie and Guilderland and the city of Albany. The average annual temperature for the City of Albany is 9.7 °C with an average annual precipitation of 875 mm (CantyMedia Accessed 19 April 2014). The landscape consists of a system of stabilized inland dunes comprised of sand deposited at the end of last glacial period in a delta of glacial Lake Albany. Rain and wind have stripped additional silts and clays from these

glacial deposits, creating the dune system of sands and sandy loams that exists today (Barnes 2003).

These well-drained sand dunes create hot, dry conditions and the potential for frequent and intense wildfires. Such fires are believed to have played an important role in maintaining early-successional, fire tolerant vegetation for much of the post-glacial history of the ecosystem (Barnes 2003). Since European settlement, the pine barrens have been developed, excavated, farmed, and grazed, but due to the poor quality of the soil and the risk of frequent fires, the area was subjected to comparatively less development and agricultural use than much of the surrounding landscape (Barnes 2003). Nevertheless, it is likely that at least a third of the APBP was put to agricultural use during the 19th and 20th centuries (Motzkin et al. 1999).

The APBPC was established in 1988 with a mission to restore the pitch pine-scrub oak barrens habitat in the preserve, which had been substantially degraded due to fire suppression and the resulting encroachment of hardwood species. Today, the APBP is a patchwork of open, shrubland, woodland, and forested habitats, throughout which more than 29 km of official hiking trails are maintained. The preserve includes a Discovery Center and regularly offers guided tours to school groups, attracting over 30,000 visitors each year. In 2014, the preserve was designated a National Natural Landmark and an Important Bird Area because of its unusual geological and biological characteristics. Although the APBP has made significant gains in popularity since the 1980's, development pressures and other conflicts of interest are likely to lead to further degradation of the ecosystem should public support and funding for the preserve not keep pace. For this reason, public involvement and educational outreach are central to the work being done by the staff at the APBPC, and opportunities for visitor-supported research should be expanded.

## **2.4 Methods**

### **2.4.1 Plot selection**

I selected study plots that contained a hiking trail bordered on both sides by managed barrens. The trail and adjacent barrens habitat each were enough to accommodate 120 m × 1 m transects running along the trail and roughly parallel to it but at least 35 m from the trail and other habitat edges. I was able to identify six plots that met these criteria at the APBP: Blueberry Hill West (BH), Draperies (DP), Great Dune (GD), Karner Barrens East (KE), Karner Barrens West (KW), and King's Road Barrens (KB) (Figure 2.1).

### **2.4.2 Sampling design**

In 2013, I placed three 120 m × 1 m transects within each plot. Each transect was placed so that it would fall under one of three conditions, “trail”, “edge”, or “interior”. These conditions were defined based on physical location relative to a hiking trail. The interior transects were oriented roughly parallel to the trail, but placed away from it by a distance of 35-45 m into the managed habitat. Dauber and Wolters (2004) considered “center” habitat in agricultural fields to be any area separated from the field boundary by a distance of at least 2 m, whereas, in a study of ant assemblages in Maine low-bush blueberry fields, Choate and Drummond (2012) used a distance of 30 m from field boundaries to classify habitat as the “middle” of fields. The distance of 35-45 m that I used in this study is enough to reasonably assume low probability of collecting foraging ants belonging to colonies located along hiking trails on the interior transects. The edge transects were located in the same managed habitat patch as the interior transects, but were placed 10 to 25 cm from the boundary between the habitat patch and the trail, such that the entire width of the transect was inside the managed habitat and at least 10 cm from the trail boundary. The boundary of the managed habitat was determined visually, based on vegetation height, which almost always increased suddenly and drastically at the trail edge (see Figure 2.2). The trail

transects were placed along the margin of the hiking trail, so that one edge of the transect abutted the determined edge of the trail. I used a random number generated in Microsoft Excel 2010 (Microsoft Corporation, Redmond, WA) to determine the exact placement of the start of the trail transect. The edge and interior transects were then placed relative to it.

### **2.4.3 Quadrat sampling for ants**

Ten, 1-m<sup>2</sup> quadrats were sampled along the transects at 11-m intervals, so that there was 10 m of space separating the 1 m<sup>2</sup> quadrats on an individual transect. The distance from the transect end to the first quadrat on the trail and interior transects also was determined by a random number, and the edge quadrats were placed adjacent the midway point between the quadrats on the trail to ensure a distance of at least 4.5 m between trail and edge quadrats. Each of the 2013 transects was surveyed twice: once in May – June, and again in July – August. The order of plot sampling was randomized during both surveys. The ten quadrats sampled along each transect during the second survey were offset from the ten sampled during the first survey by a distance of one meter (a full meter between the two proximate edges of the first- and second-survey quadrats). This was to reduce the effects of disturbance resulting from the first survey.

I surveyed ants along each transect through 8-minute quadrat searches. During each survey, I sampled ten quadrats spread out along each transect. My method was similar to that described as “quadrat sampling” in Agosti et al. (2000). I recorded which ants were clearly collected from colonies within the quadrats and which were not. Time spent recording and transferring specimens was not included in the search time.

During the 8-min quadrat searches, I also collected all of the leaf litter from each quadrat and placed it into a wire-mesh, waste-paper basket set inside a white bucket. The mesh holes were not rectangles, but parallelograms, having diagonal, corner-to-corner distances of 30 and 50 mm, which was large enough for the largest species (*Camponotus americanus* (Mayr) (The American Carpenter Ant), *Camponotus pennsylvanicus* (DeGeer) (The Black or Eastern Carpenter Ant) and

*Camponotus novaeboracensis* (Fitch) (The New York Carpenter Ant)) to pass through. The white bucket prevented the escape of ants from the litter sample until the timed quadrat search was completed. At the end of the search time, I took the mesh basket out of the white bucket, collected any ants in the bucket, shook the material in the mesh basket over a white drop-cloth until a thin layer of material covered the cloth and collected the ants that fell through the mesh onto the cloth. I repeated this process of shaking the mesh basket and collecting ants three times per litter sample, and before each shaking event I mixed the litter by hand and broke apart sticks and stems when they were present. Ants collected through this process were kept separate from ants collected through the timed quadrat search.

The order in which plots were searched was randomized for each survey period. The order in which the quadrats were searched was also partially randomized, but the randomization was constrained to avoid temporal biases as much as possible. At each plot, I sampled a total of thirty quadrats during each survey (10 per transect). I was usually able to search half this number in a single day. To avoid confounding temporal biases, I always searched, consecutively, a full set of one trail, one edge, and one interior quadrat, before moving on to the next set, but the order of searching these quadrats were randomized. Furthermore, I sampled only odd or even numbered quadrats on any given day, to ensure that each day's samples would be distributed over the entire length of the transects.

#### **2.4.4 Vegetation sampling**

Within each sampling quadrat I took a series of environmental measurements. These included the litter depth in the center of the quadrat; the percent canopy cover over the quadrat, measured at a height of 0.5 m in four directions around the quadrat with a spherical densiometer (Robert E. Lemmon, Forest Densimeters, Model-A), and the percentage of the quadrat that was bare ground. I also identified and recorded any plant species that covered at least 25% of the quadrat area.



### **2.4.5 Habitat classification**

I classified the plots as either grassland or shrubland based on the percentage of 30 sampling points that were intersected by shrub-level oaks. The APBPC defines the shrub-covered areas of the preserve as either pitch pine-scrub oak barrens if the shrub-level oaks constitute 30%-60% cover, or as pitch pine-scrub oak thicket if the shrub-level oaks cover > 60% of the ground area (APBPC 2010). Therefore, any plot in which at least 30% of the sampling points were intersected by shrub-level oaks was classified as shrubland, and the plots that had less than this percentage were classified as grassland (in all plots, grasses or sedges intersected at least 50% of the sampling points).

The sampling points were spaced out along the interior transect at 4-m intervals, and at each point, I placed a 2.7-cm diameter pole vertically on the ground. The point was counted as intersected by shrub-level oaks if oak leaves or branches touched the pole.

The shrubland plots included four of the six plots. One of the grassland plots (GD) had been restored from a woodland in 2008, and another (DP) was burned in 2011. The latter had a strong shrub-level oak component, but the plants were small at the time of the survey, resulting in just 13% cover by my measurements (Table 1.1).

### **2.4.6 Data Analysis**

#### **2.4.6.1 Identifying differences between trails and interiors and edges**

Hiking trails are distinguishable from managed barrens in the APBP by visible differences in vegetation between the trail and the edges of the managed habitat. However, there is considerable variation among hiking trails and also among managed habitat with regard to vegetation variables, and vegetation in recently managed barrens can be similar in many respects to that on hiking trails. As such, it was necessary to determine whether the condition of the

transect (trail, edge, and interior) had a consistent relationship with the measured environmental variables.

I used Principal Components Analysis (PCA) to summarize the transect conditions as a function of litter depth, the percent canopy cover, the percent of the quadrat that was bare ground, and the percent of quadrats dominated by the four most common plant types: *Centaurea stoebe* subsp. *micranthos* (Gulger) Hayek (Spotted Knapweed), *Rubus* spp., shrub-level oaks (*Quercus ilicifolia* Wangenh. (Scrub Oak/Bear Oak) or *Quercus prinoides* Willd. (Dwarf Chinquapin Oak)), and graminoids. I tested for significant differences among the condition types using a randomized-block analysis of variance (RB-ANOVA) of the principal component scores with plot as the random effect and condition as the fixed effect. I only tested for difference using the principal component scores from axes that accounted for > 30% of the variance in the data.

#### **2.4.6.2 Species density and hiking trails**

For estimating species density, each quadrat was considered to be a sample, and the occurrence of a species in a quadrat, whether as stray foragers or an established colony, was counted as a single incidence of that species. This is a common adjustment for ant abundance data because strict colony counts can underestimate species that form inconspicuous colonies, while raw forager counts can dramatically overestimate colony density for particularly active species or species whose colonies happen to be close to sampling units (Gotelli et al. 2011). Because pairs of quadrats from the first and second surveys were separated from each other by only one meter, which is almost certainly less than the foraging range of most species, it was probable that individuals from a single colony could occasionally be collected from both of these proximate quadrats, despite their temporal separation. Therefore, I combined observations from adjacent quadrats sampled at the two time periods so that each species could have only one incidence of detection from the combined quadrats.

Species density for each transect was calculated using the free, online software, EstimateS (Colwell 2013). The data for the ten samples (composite quadrats) were rarefied and extrapolated to twenty samples. Species density mean estimates and 95% confidence intervals were calculated using the Chao2 formula, based on the rarefied data for 10 samples. I used the mean estimates generated by this method to test for significant differences in ant species density related to condition with a RB-ANOVA where the plot was the random effect.

### **2.4.6.3 Ant assemblage composition**

The trail and edge transects in my study were separated by less than half a meter, so foragers from colonies along the edge easily might have been collected on the trail and vice versa. However, nest site selection is often specific to a particular environment and is more critical to a colony's survival than foraging site selection by individual workers. Thus, colony occurrence is likely to be more useful for identifying habitat preferences for different species and thereby identifying the probable effects of hiking trails. I therefore compared ant assemblage composition among interior, edge, and trail transects with a PCA using ant colony data alone. I eliminated species from the analysis that seemed likely to be uninformative by restricting the number of species considered to those that appeared on at least 2 transects (McCune and Grace 2002). I also Hellinger-transformed the colony incidence data to make it more suitable for PCA (Legendre and Gallagher 2001). As with the environmental data, I tested for a significant effect of transect condition on ant species assemblage with an RB-ANOVA of the principal component scores of axes that accounted for > 30% of the variance in the data. I also compared the findings of the PCA with indicator species analyses of the trail and interior species assemblages, based on colony incidences alone and colony and forager incidences combined.

All analyses were implemented using the open source software and programming language R. The data and code are available through the Harvard Forest Data Archive (<http://harvardforest.fas.harvard.edu/data-archive>), dataset HF-2XX.

## 2.5 Results

Forty-nine species of ants were collected from the sampled plots at the APBP in 2013 (Table 2.1). Of these, six were not collected from the methods described, but were collected by other methods that were not part of this study, including plot-wide direct sampling and opportunistic collecting. Five species were collected only once by any method, and one species, *Polyergus lucidus* Mayr (The Shiny *Polyergus*), was collected from two locations spaced > 80 meters apart, but could have been from a single colony, as it is a very far-ranging species. The six most commonly collected species at the study plots accounted for 51% of the total observations from the study methods (813 of 1586 observations) (Table 2.1). All but two of the species collected through quadrat searches (*Myrmica americana* Weber (The American Ant) and *Formica dolosa* Buren (The Sly Ant)) were collected along interior transects, whereas 4 and 13 species collected on interior transects did not appear on any of the edge or trail transects, respectively. The most abundant species were also the most widely distributed: the species having the highest number of observations also appeared on the most transects.

### 2.5.1 Identifying differences between transects

In the PCA of the environmental data, only the first principal component axis was significant, and it accounted for 58% of the variance in the transect data. The RB-ANOVA of the conditions by their scores on the first principal component axis found a highly significant effect of transect condition ( $P \ll 0.005$ ). A post-hoc Tukey's honestly significant difference test (Tukey's HSD) further showed that the relationships responsible for this overall significance were those between the trail and the other two condition types, but that the edge and interior conditions were not significantly different from one another. Unsurprisingly, the interior and edge transects tended to have more over-story cover, leaf litter, and higher frequencies of shrub-level oaks than did the trail transects, which tended to have more bare ground (Figure 2.3).

### 2.5.2 Species density and hiking trails

The trail transect always had the lowest number of ant species directly observed and the interior transect almost always had the highest number observed. The exception was in the case of DP, where the most species were observed on the edge transect (Figure 2.4).

Estimates of species density generated with the Chao2 estimator had large confidence intervals, but some patterns were still apparent (Figure 2.5). A RB-ANOVA of the mean density estimates, with the transect-trail relationship as the fixed effect and the plot identity as the random effect, yielded significant p-values for both factors (relationship to trail:  $P = 0.020$ ; plot identity:  $P = 0.0007$ ). Tukey's HSD test revealed that the difference between the interior and trail transects was the only significant difference ( $P = 0.019$ ) among the pairs of conditions.

### 2.5.3 Ant assemblage composition

In the PCA of ant colony data, the first axis accounted for 37% of the variance in the ant assemblage data. As with the environmental data, the RB-ANOVA of the PC1 scores of the transects from the colony data PCA showed a significant effect of condition ( $P < 0.001$ ), and Tukey's HSD revealed this significance to again lay in the relationships between the trail and the other two conditions, but not between the edge and interior conditions (Figure 2.6). Graphs of the transects spread across the PC1 of the ant colonies and the PC1 of the environmental data are qualitatively similar, suggesting strong links between the measured environmental variables and the ant assemblage composition along the transects, at least with respect to colonies. The trail transects, and those located in grassland habitat, tended to have more colonies of *Lasius neoniger*, while the interior and edge transects were more populated by *Ponera pennsylvanica* Buckley (The Pennsylvania Ponera), *Aphenogaster picea* (Wheeler) (The Pitch-black *Aphaenogaster*) and an undescribed species of *Myrmica*, designated by André Francoeur as *Myrmica* sp. AF-smi (these are the species for which the absolute value of their axis loadings was greater than 3). This

association is made clear by the tight correlation ( $r = 0.90$ ,  $P \ll 0.001$ ) between the transects' scores from both the environmental- and colony-based PC1 axes in Figure 2.7.

The indicator species analysis found significant indicators of both trail and interior transects. When the analysis included all of the incidence data, *Brachymyrmex depilis* Emery (The Little Hairless Ant) came out as an indicator of the interior and *Lasius neoniger* Emery (The Labor Day Ant) appeared as an indicator of the trail. When colony data alone were considered, however, *A. picea* replaced *B. depilis* as an indicator of the interior, while *Solenopsis molesta* (Say) (The Thief Ant) was added as an indicator of the trail (Table 2.2).

## 2.6 Discussion

My results demonstrate that hiking trails in pine barrens are sufficiently altered from the surrounding habitat to affect ant assemblages along the trails themselves. Despite the close proximity of the trail and edge transects (separated by less than half a meter), the edge of the managed barrens habitat was more similar to the interior than to the trail itself, as indicated by the results of post-hoc Tukey's HSD tests of both environmental and ant assemblage composition. The closely corresponding differences between the measured environmental variables and ant assemblages demonstrates the strong influence vegetation has on ant nesting site selection, highlighting the importance of considering the secondary impacts of changes to vegetation resulting from the presence of hiking trails.

Studies on the effects of hiking trails in the literature tend to focus on the impacts of human presence on wildlife that is sensitive to the sights, sounds, and smells of human activities. There is a large suite of ecologically important organisms, however, that are probably much more influenced by changes in habitat structure than to the presence of humans per se. For these species, the level of impact of hiking trails is more likely to be closely linked to the environmental context of the trail. In pine barrens, the characteristic vegetation is short enough, yet also productive enough, that the space created by hiking trails can significantly increase the

amount of sunlight reaching the ground. This might not be true for trails in all environments. In forests, for instance, the tree canopy may fill in above the trail, maintaining a similar level of shade to that in the forest interior, and in extremely rocky terrain, where vegetation is sparse, the presence of a hiking trail may not result in much of a change in vegetation cover because there was little cover to begin with.

The results of the PCAs of environmental variables and species data show that the interior of recently disturbed areas — GD was restored from a wooded area in 2008 and DP was burned in 2011 — are similar to trails in both vegetation structure and ant species assemblages. One advantage to monitoring ants on hiking trails, therefore, is that they may provide a good indication of what species could be present in the habitat under highly disturbed conditions. Additionally, recovery from disturbance among interior ant assemblages may be measured against the ant assemblages on nearby trails. It is also important to note that, although the interior transects of these plots were similar in composition to hiking trails, both still hosted a larger suite of species than the corresponding trail transect. In GD in particular, one of the ants found in abundance in the interior was *Formica argentea* Wheeler (The Silver Ant), which is associated with pine barrens habitat. This may indicate that, although the interior of GD currently supports a large number of disturbance-tolerant species, it is also providing good habitat for some less common and habitat-specific species. Furthermore, monitoring trail ant assemblages could allow for early detection of the arrival of non-native and/or disturbance-tolerant species into an ecosystem. The high prevalence of *Tetramorium caespitum* (European Pavement Ant), which was introduced in the 1700s, and *Lasius neoniger* (the native Labor Day Ant) along hiking trails in the APBP indicates that trails could serve as reliable habitat and dispersal corridors for disturbance-tolerant ants to enter the interior barrens habitat. Give this, it is easy to imagine that trails could play a role in the colonization order of newly restored habitats by contributing disturbance-tolerant propagules.

Degraded land can have conservation value (Bestelmeyer and Wiens 1996; Catling and Kostiuk 2011), and other studies in similar ecosystems have shown that hiking trails are used preferentially by some thermophilic, habitat-restricted, invertebrate species (Cornelisse and Duane 2013). Anecdotal observations in the APBP indicate that some trails support rare species and species not typically found so far north (i.e. *Polyergus lucidus* and *Forelius pruinosus*). To what extent hiking trails provide suitable habitat for these species remains unknown and difficult to determine precisely because the species are rare. The results of this study demonstrate that hiking trails are meaningfully different habitat to ants compared to the shrubland habitats and, as such, deserve attention to determine whether they are providing habitat to pine barrens species, providing points of access for non-native and disturbance-tolerant species, or both.

This investigation of the impact of hiking trails on ant assemblages is an initial step toward understanding the major patterns in a complex system. Although statistical tools including PCA, indicator species analysis, and RB-ANOVA were employed to identify the most obvious and probable trends in the data, the small number of independent samples in this study reduces the power of the tests and cautions against overinterpreting the results. Nevertheless, all of the results were consistent with what is known about the natural history of the most common ant species or expected based on a mechanistic understanding of differences among conditions. Additional samples collected from these and other hiking trails and interiors would greatly enhance our ability to identify more subtle patterns or capture additional rare species. Community supported citizen-science, where visitors to the APBP and other preserves would be welcomed to collect ants and some associated environmental data along hiking trails, could provide both useful data for management and opportunities for outreach, education, and enhanced community investment in conservation. Such community involvement with ant sampling has already been employed successfully in The School of Ants project (<http://schoolofants.org>) to map the distribution of ant species in schoolyards across the country.



**Table 2.1:** Ant species incidences on transects of the three conditions. In all columns except that titled “Number of Transects”, the values in the above table correspond to the number of independent observations (instances) of the species (rows) in the transect condition or collection method (columns). For the “Number of Transects” column, the values give the number of transects on which the corresponding species was observed.

<b>Species</b>	<b>Interior</b>	<b>Edge</b>	<b>Trail</b>	<b>Number of Transects</b>	<b>Quadrat Search</b>	<b>Other Method</b>
<i>Myrmica</i> (sp. AF-smi) sensu Francoeur	75	64	49	5	188	16
<i>Solenopsis molesta</i> (Say, 1836)	36	55	72	6	163	6
<i>Tapinoma sessile</i> (Say, 1836)	51	54	26	6	131	12
<i>Ponera pennsylvanica</i> Buckley, 1866	55	45	12	5	112	2
<i>Tetramorium caespitum</i> (Linnaeus, 1758)	27	43	42	6	112	16
<i>Aphaenogaster picea</i> (Wheeler, 1908)	52	37	18	5	107	14
<i>Myrmica pinetorum</i> Wheeler, 1905	29	40	27	5	96	4
<i>Lasius alienus</i> (Foerster, 1850)	35	26	16	6	77	4
<i>Formica subsericea</i> Say, 1836	24	33	18	6	75	14
<i>Monomorium emarginatum</i> DuBois, 1986	14	24	35	6	73	15
<i>Formica incerta</i> Buren, 1944	19	11	15	6	45	24
<i>Lasius neoniger</i> Emery, 1893	10	7	28	6	45	12
<i>Temnothorax curvispinosus</i> (Mayr, 1866)	14	24	4	5	42	5
<i>Camponotus novaeboracensis</i> (Fitch, 1855)	11	17	13	5	41	6
<i>Formica lasioides</i> Emery, 1893	11	13	14	5	38	5
<i>Temnothorax ambiguus</i> (Emery, 1895)	8	15	5	4	28	1
<i>Dolichoderus taschenbergi</i> (Mayr, 1866)	12	9	5	5	26	3
<i>Formica argentea</i> Wheeler, 1901	8	3	7	6	18	
<i>Dolichoderus plagiatus</i> (Mayr, 1870)	13	3		3	16	6
<i>Pheidole pilifera</i> (Roger, 1863)	8		8	5	16	6
<i>Camponotus pennsylvanicus</i> (DeGeer, 1773)	6	4	3	4	13	2
<i>Formica pallidefulva</i> Latreille, 1802	8	2	2	5	12	6
<i>Formica obscuriventris</i> Mayr, 1870	4	5	2	2	11	8
<i>Brachymyrmex depilis</i> Emery, 1893	8	2		6	10	
<i>Myrmica punctiventris</i> Roger, 1863	1	9		4	10	
<i>Crematogaster cerasi</i> (Fitch, 1855)	3	4	2	3	9	3
<i>Nylanderia parvula</i> (Mayr, 1870)	8	1		3	9	5
<i>Stenamma impar</i> Forel, 1901	2	6		2	8	
<i>Camponotus americanus</i> Mayr, 1862	2	2	3	4	7	6
<i>Crematogaster lineolata</i> (Say, 1836)	6			3	6	3
<i>Formica neogagates</i> Viereck, 1903	2	2	2	4	6	2

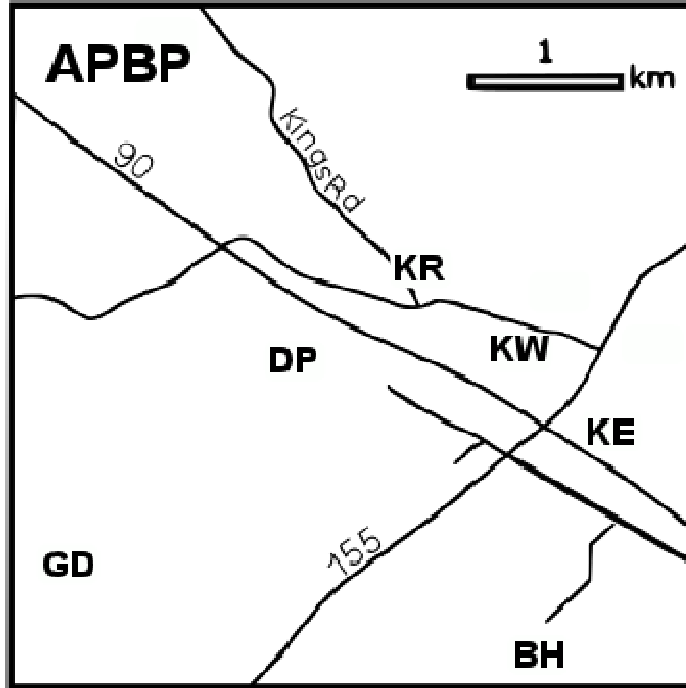
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Table 2.1, continued

Species	Interior	Edge	Trail	Number of Transects	Quadrat Search	Other Method
<i>Myrmica americana</i> Weber, 1939		2	4	2	6	4
<i>Formica exsectoides</i> Forel, 1886	2	3		1	5	7
<i>Formica pergandei</i> Emery, 1893	1	2	1	2	4	6
<i>Formica rubicunda</i> Emery, 1893	2	2		3	4	5
<i>Lasius claviger</i> (Roger, 1862)	2	2		3	4	1
<i>Myrmecina americana</i> Emery, 1895	2	2		3	4	1
<i>Aphaenogaster treatae</i> Forel, 1886	1	1	1	3	3	2
<i>Prenolepis imparis</i> (Say, 1836)	2	1		3	3	2
<i>Camponotus nearcticus</i> Emery, 1893	1			1	1	3
<i>Dolichoderus pustulatus</i> Mayr, 1886	1			1	1	
<i>Formica dolosa</i> Buren, 1944		1		1	1	5
<i>Forelius pruinosus</i> (Roger, 1863)						3
<i>Lasius latipes</i> (Walsh, 1863)						2
<i>Lasius nearcticus</i> Wheeler, 1906						1
<i>Polyergus lucidus</i> Mayr, 1870						2
<i>Temnothorax longispinosus</i> (Roger, 1863)						1
<i>Temnothorax schaumii</i> (Roger, 1863)						4
<b>Totals:</b>	<b>576</b>	<b>576</b>	<b>434</b>	<b>NA</b>	<b>1586</b>	<b>255</b>

Table 2.2: Results of the indicator species analyses for trail and interior transects

<b>All Incidence Data:</b>			
Species	Cluster	Indicator value	Probability
<i>Brachymyrmex depilis</i>	Interior	0.83	0.011
<i>Lasius neoniger</i>	Trail	0.74	0.035
<b>Colony Data Alone:</b>			
<i>Aphaenogaster picea</i>	Interior	0.78	0.019
<i>Lasius neoniger</i>	Trail	0.76	0.031
<i>Solenopsis molesta</i>	Trail	0.71	0.032

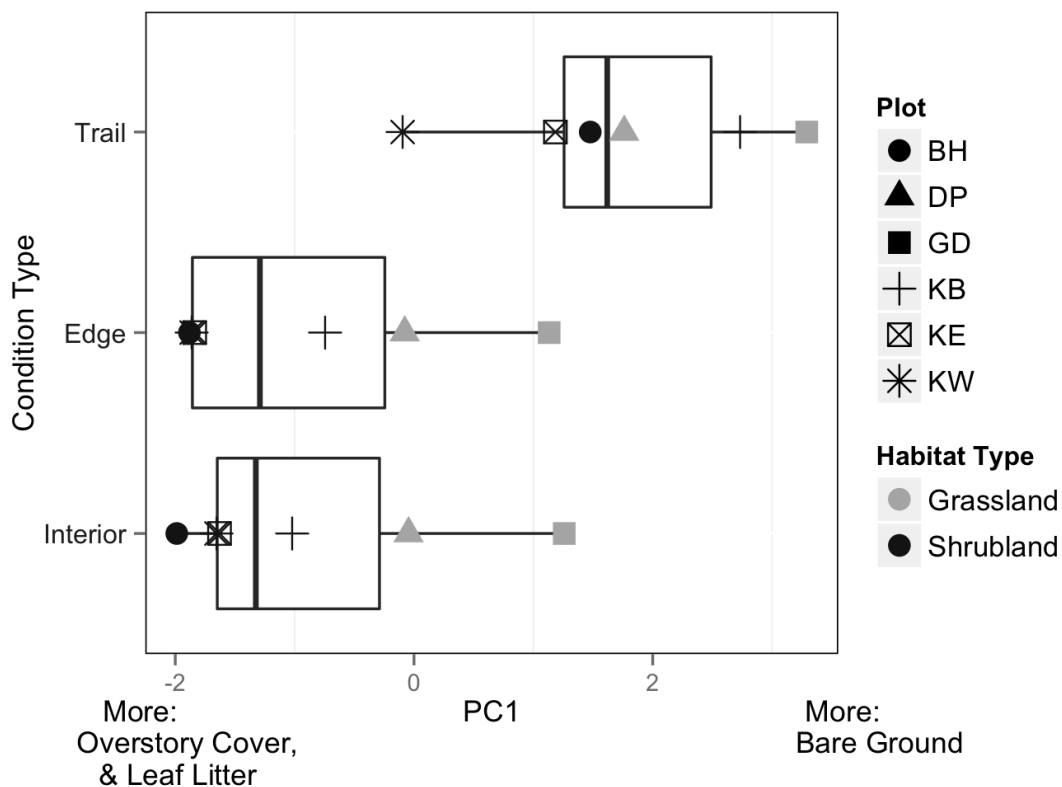


**Figure 2.1:** Map of the study plots at the Albany Pine Bush Preserve.

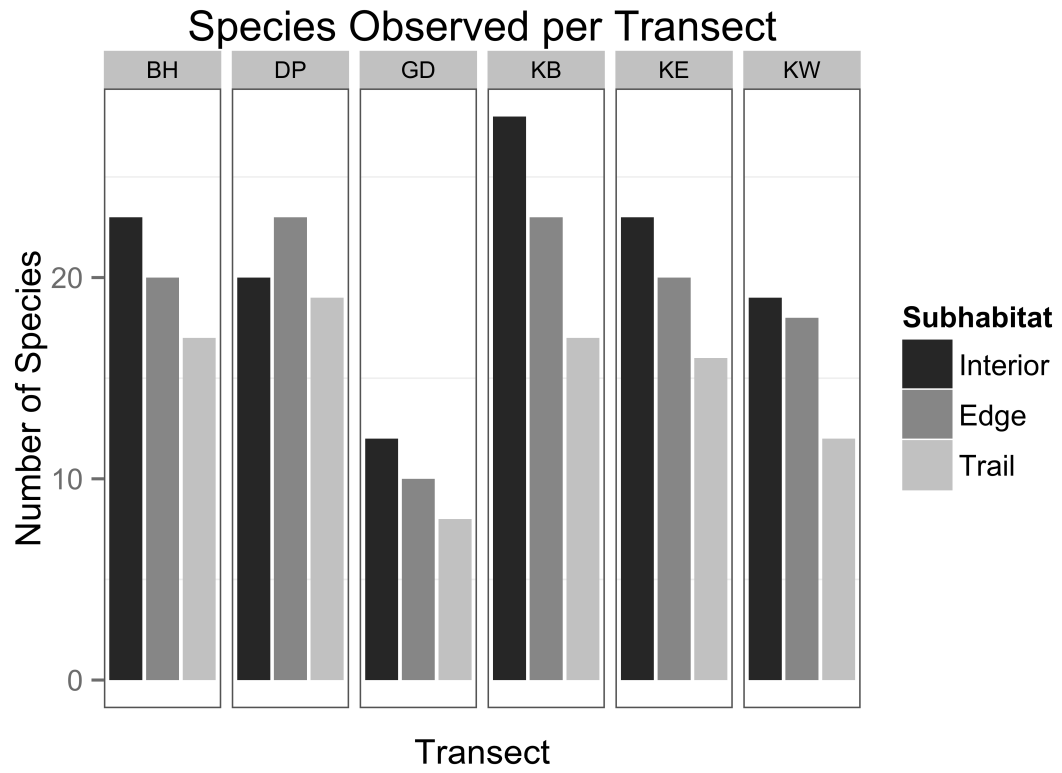


**Figure 2.2:** An example of a trail-transect quadrat and typical trail-edge boundary in the Albany Pine Bush Preserve. The edge of the trail quadrats were lined up with where vegetation height increased abruptly. Most trails had some amount of bare soil, but this varied greatly.

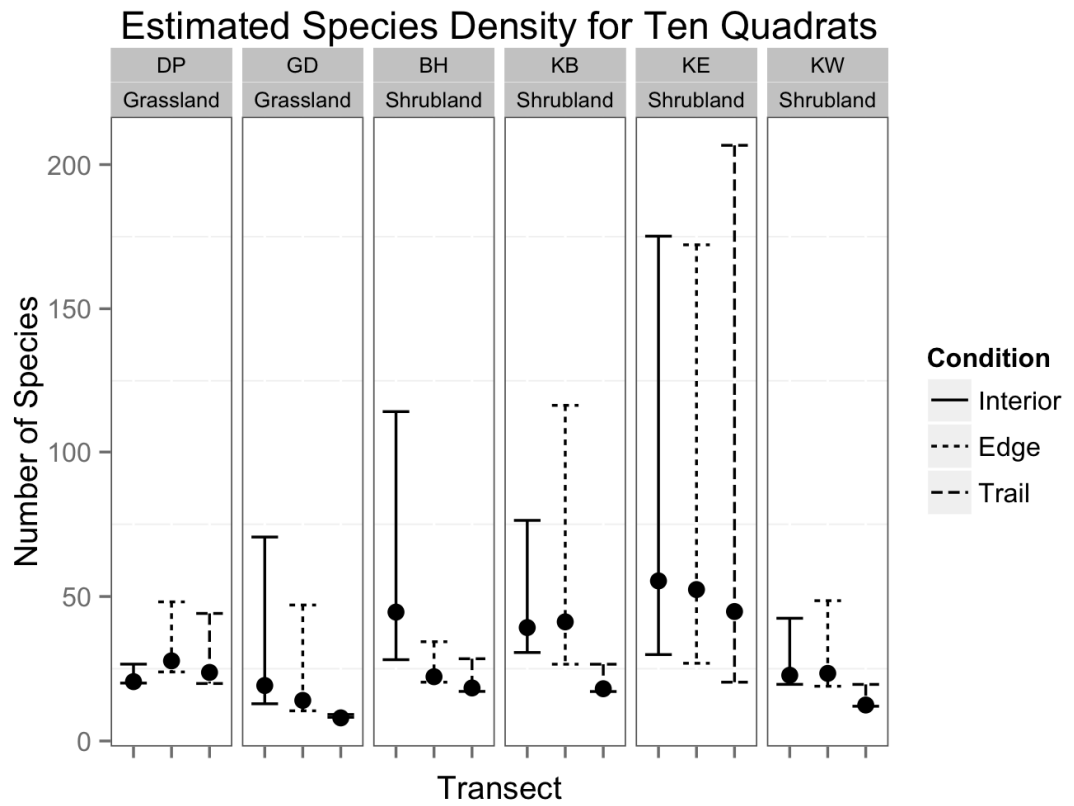
### Position of Transects along the First Principal Component of the Environmental Data PCA



**Figure 2.3:** Graph of the position of transects along the first principle component of the principal component analysis of environmental data. The data represented were generated through PCA of the environmental data collected at the quadrats and aggregated to the transect level. The points represent the position of the transects along the first principal component, and are separated by transect condition on the y axis. The x axis is labeled with the variables having loadings  $< -3$  on the left and  $> 3$  on the right.

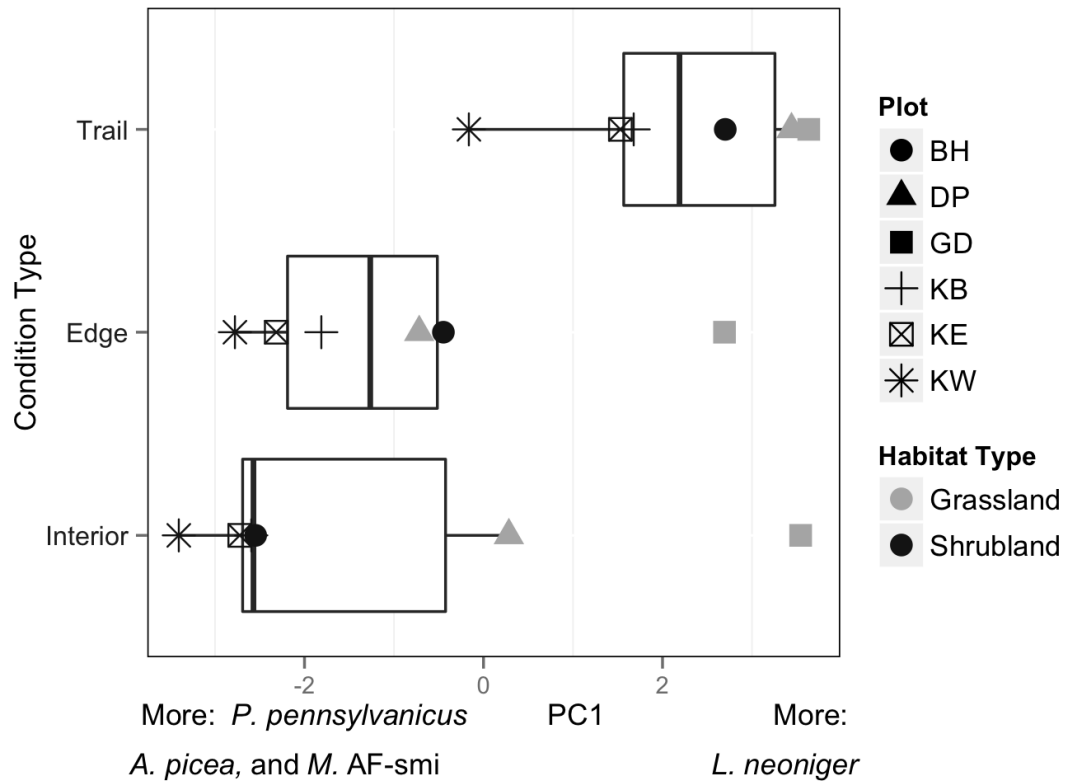


**Figure 2.4:** Bar graph of the number of species directly observed on each transect.



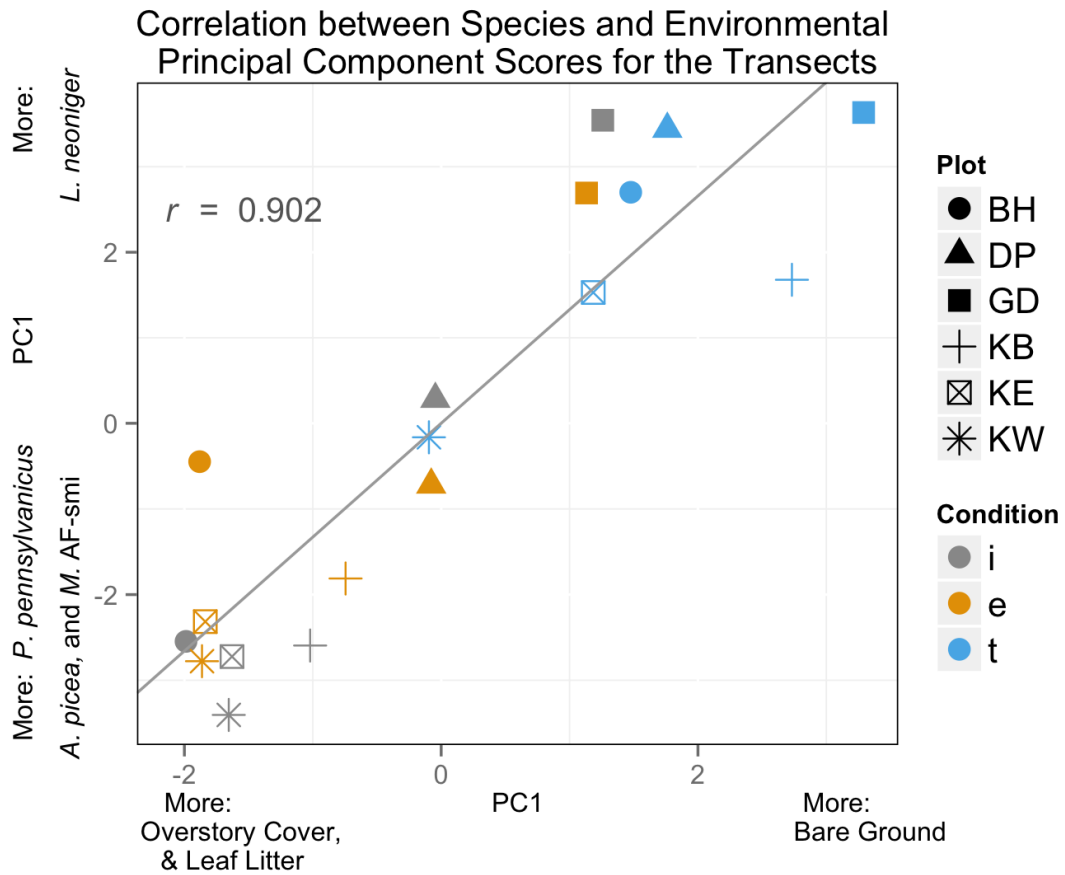
**Figure 2.5:** Graph of the point estimates and 95% confidence intervals for species richness of the transects based on the Chao2 formula. Very large confidence intervals result for large numbers of singletons and doubletons, and suggest that the transects were not sufficiently sampled.

### Position of Transects along the First Principal Component of the Species Data PCA



**Figure 2.6:** Graph of the position of transects along the first principle component of the principal component analysis of ant species data. The data above were generated through PCA of Hellinger-transformed ant species data (based on colonies alone) aggregated to the transect level. The points represent the locations of the transects along the first principal component, and are separated by transect condition on the y axis. The x axis label lists the species having loadings < -3 on the left and > 3 on the right.





**Figure 2.7:** Graph of the correlation between species and environmental principal component scores for the transects. The tight correlation between the positions of transects along the first principal component axis from the PCA of ant species data and the first PC axis from the PCA of environmental data demonstrates the close relationship between the measured environmental variables and the ant assemblage data. The axis labels show which variables were most important in defining the axes in the PCA and the direction of their weighting on the axis.

## BIBLIOGRAPHY

- Agosti, D., J.D. Majer, L.E. Alonso, and T.R. Schultz, editors. 2000. *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press.
- Albany Pine Bush Preserve Commission (APBPC), 2010. *Management Plan/Final Environmental Impact Statement for The Albany Pine Bush Preserve*. Albany Pine Bush Preserve Commission Technical report.
- Andersen, A.N., and J.D. Majer. 2004. Ants show the way down under: Invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* 2:291–298.
- AntWeb. Available online at <http://www.antweb.org>. Accessed 19 September 2014.
- AntWiki. Available online at <http://www.antwiki.org>. Accessed 29 August 2014.
- Banschbach, V.S., and E. Ogilvy. 2014. Long-term impacts of controlled burns on the ant community (Hymenoptera: Formicidae) of a sandplain forest in Vermont. *Northeastern Naturalist* 21:NENHC-1–NENHC-12.
- Barnes, J. K. 2003. *Natural history of the Albany Pine Bush*. New York State Museum, Albany, NY.
- Barrow, L., and C.L. Parr. 2008. A preliminary investigation of temporal patterns in semiarid ant communities: Variation with habitat type. *Austral Ecology* 33:654–662.
- Bestelmeyer, B.T. 2005. Does desertification diminish biodiversity? Enhancement of ant diversity by shrub invasion in south-western USA. *Diversity and Distributions* 11:45–55.
- Bestelmeyer, B.T., and J.A. Wiens. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecological Applications* 6:1225–1240.
- Bried, J.T., and N.A. Gifford. 2010. Mowing and herbicide of scrub oaks in pine barrens: baseline data (New York). *Ecological Restoration* 28:245–248.
- Bright, J.A. 1986. Hiker impact on herbaceous vegetation along trails in an evergreen woodland of Central Texas. *Biological Conservation* 36:53–69.
- CantyMedia. 2014. Weatherbase. Available online at <http://www.weatherbase.com>. Accessed 19 April 2014.
- Catling, P.M., and B. Kostiuk. 2011. Some wild Canadian orchids benefit from woodland hiking trails - and the implications. *The Canadian Field-Naturalist* 125:105–115.
- Chao, A., N.J. Gotelli, T.C. Hsieh, E.L. Sander, K.H. Ma, R.K. Colwell, and A.M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45–67.
- Choate, B., and F.A. Drummond. 2012. Ant diversity and distribution (Hymenoptera: Formicidae) throughout Main lowbush blueberry fields in Hancock and Washington Counties. *Community and Ecosystem Ecology* 41:222–232.
- Chow, M.H., S.I. Mancina, B. McMillan, and M. Jacobs. 2014. Effects of hiking trails on soil invertebrate abundance, taxonomic richness, and biodiversity. Poster session presented at: the Annual Meeting of the Society for Integrative and Comparative Biology; 2014 Jan 3-7; Austin, TX.

- Christian, C.E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* 413:635–639.
- Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9 and earlier. User's Guide and application. Available online at <http://purl.oclc.org/estimates>. Accessed 29 August 2014.
- Cornelisse, T.M., and T.P. Duane. 2013. Effects of knowledge of an endangered species on recreationists' attitudes and stated behaviors and the significance of management compliance for Ohlone tiger beetle conservation. *Conservation Biology* 27:1449–1457.
- Dangerfield, J.M., A.J. Pik, D. Britton, A. Holmes, M. Gillings, I. Oliver, D. Briscoe, and A. J. Beattie. 2003. Patterns of invertebrate biodiversity across a natural edge. *Austral Ecology* 28:227–236.
- Dauber J. and V. Wolters. 2004 Edge effects on ant community structure and species richness in an agricultural landscape. *Biodiversity and Conservation* 13:901–915.
- Del Toro, I., R.R. Ribbons, and S.L. Pelini. 2012. The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News* 17:133–146.
- Del Toro, I., K. Towle, D.N. Morrison, and S.L. Pelini. 2013. Community structure and ecological and behavioral traits of ants (Hymenoptera: Formicidae) in Massachusetts open and forested habitats. *Northeastern Naturalist* 20:103–114.
- Deluca, W.V., and D.I. King. 2014. Influence of hiking trails on montane birds. *The Journal of Wildlife Management* 78:494–502.
- Dindal, D.L., 1979. Pine Barrens: Ecosystem and Landscape, Chapter 30, pages 527– 539 . Academic Press, New York, NY.
- Eldridge D.J., M.A. Bowker, T.M. Fernando, E. Roger, J.F. Reynolds, and W.G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* 14: 709-722.
- Ellison, A.M. 2012a. The ants of Nantucket: unexpectedly high biodiversity in an anthropogenic landscape. *Northeastern Naturalist* 19:43–66.
- Ellison, A.M. 2012b. Out of Oz: opportunities and challenges for using ants (Hymenoptera: Formicidae) as biological indicators in north-temperate cold biomes. *Myrmecological News* 17:105–119.
- Ellison, A.M. and N.J. Gotelli. 2009. Ant distribution and abundance in New England since 1990. Harvard Forest Data Archive: HF147. doi:10.6073/pasta/5461edc9a2f3708f4ae60b6cf9c9ff45
- Ellison, A. M., N. J. Gotelli, E. J. Farnsworth, and G. D. Alpert. 2012. *A Field Guide to the Ants of New England*. 1st edition. Yale University Press, New Haven, CT.
- Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* 7:1221–1244.
- Fox J. and S. Weisberg. 2011. An {R} companion to applied regression, second edition. Thousand Oaks CA: Sage. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- Frouz, J., and V. Jilková. 2008. The effect of ants on soil properties and processes (Hymenoptera: Formicidae). *Myrmecological News* 11:191–199.

- Gotelli, N.J., and A.E. Arnett. 2000. Biogeographic effects of red fire ant invasion. *Ecology Letters* 3:257–261.
- Gotelli, N.J., and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- Gotelli, N.J., and A.M. Ellison. 2002. Biogeography at a regional scale: Determinants of ant species density in New England bogs and forests. *Ecology* 83:1604–1609.
- Gotelli, N.J., and A.M. Ellison. 2012. *A Primer of Ecological Statistics, Second Edition*. Sinauer Associates, Inc., Sunderland, MA.
- Gotelli, N.J., A.M. Ellison, R.R. Dunn, and N.J. Sanders. 2011. Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. *Myrmecological News* 15:13–19.
- Graham, J.H., A.J. Krzysik, D.A. Kovacic, J.J. Duda, D.C. Freeman, J.M. Emlen, J.C. Zak, W.R. Long, M.P. Wallace, C. Chamberlin-Graham, J.P. Nutter, and H.E. Balbach. 2009. Species richness, equitability, and abundance of ants in disturbed landscapes. *Ecological Indicators* 9:866–877.
- Greenslade, P.J.M. 1973. Sampling ants with pitfall traps: Diggin-in effects. *Insectes Sociaux* 20:343–353.
- Handel, S.N., S.B. Fisch, and G.E. Schatz. 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bulletin of the Torrey Botanical Club* 108:430–437.
- Herbers, J.M. 2011. Nineteen years of field data on ant communities (Hymenoptera: Formicidae): What can we learn? *Myrmecological News* 15:43–52.
- Immitzer, M., U. Nopp-Mayr, and M. Zohmann. 2014. Effects of habitat quality and hiking trails on the occurrence of Black Grouse (*Tetrao tetrix* L.) at the northern fringe of alpine distribution in Austria. *Journal of Ornithology* 155:173–181.
- Jeanne, R. L. 1979. A latitudinal gradient in rates of ant predation. *Ecology* 60:1211–1224.
- Jongman, R.H.G, C.J.F. ter Braak, and O.F.R. Van Tongeren, editors. 1995. *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, New York, NY.
- Kumschick, S., M.H. Schmidt-Entling, S. Bacher, T. Hickler, X. Espadaler, and W. Nentwig. 2009. Determinants of local ant (Hymenoptera: Formicidae) species richness and activity density across Europe. *Ecological Entomology* 34:748–754.
- Legendre, P., and E.D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280.
- Lyford, W.H. 1963. Importance of ants to brown podzolic soil genesis in New England. *Harvard Forest Paper* 7:1–18.
- MacGown, J., 2003. Ants (Formicidae) of the southeastern United States. Available online at <http://www.mississippiantomologicalmuseum.org.msstate.edu>. Accessed 19 April 2014.
- McCune, B., and J.B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Glenden Beach, OR.
- McGarigal, K., S. Kushman, and S. Stafford. 2000. *Multivariate Statistics for Wildlife and Ecology Research*. Springer-Verlag New York, Inc., New York, NY.

- Motzkin, G., W.A. Patterson III, and D.R. Foster. 1999. A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. *Ecosystems* 2:255–273.
- NatureServe. 2014. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.0. NatureServe, Arlington, VA. Available online at [www.natureserve.org/explorer](http://www.natureserve.org/explorer). Accessed 29 August 2014.
- New York State Department of Environmental Conservation (NYSDEC). 2014. Saratoga Sand Plains Wildlife Management Area. Available online at <http://www.dec.ny.gov/outdoor/62872.html>. Accessed 13 March 2014.
- Ouellette, G.D., F.A. Drummond, B. Choate, and E. Groden. 2010. Ant diversity and distribution in Acadia National Park, Maine. *Environmental Entomology* 39:1447–1456.
- Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, and H. Wagner. 2013. vegan: community ecology package. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Quero, J.L., F.T. Maestre, V. Ochoa, M. García-Gómez, and M. Delgado-Baquerizo. 2013. On the importance of shrub encroachment by sprouters, climate, species richness and anthropic factors for ecosystem multifunctionality in semi-arid Mediterranean ecosystems. *Ecosystems* 16:1248-1261.
- R Core Team. 2014. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <http://www.R-project.org/>.
- Rodriguez-Cabal, M.A., K.L. Stuble, B. Guénard, R.R. Dunn, and N.J. Sanders. 2012. Disruption of ant-seed dispersal mutualisms by the invasive Asian needle ant (*Pachycondyla chinensis*). *Biological Invasions* 14:557–565.
- Rome Sand Plains Resource Management Team (RSPRMT), 2006. Rome Sand Plains consolidated management plan. Available online at <http://www.dec.ny.gov/lands/22572.html>. Accessed 29 August 2014.
- Schloss, C.A., T.A. Nuñez, and J.J. Lawler. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *PNAS* 109:8606–8611.
- Ślipiński, P., M. Żmihorski, and W. Czechowski. 2012. Species diversity and nestedness of ant assemblages in an urban environment. *European Journal of Entomology* 109:197–206.
- Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture (NRCS). 2013. Web Soil Survey. Available online at <http://websoilsurvey.nrcs.usda.gov/>. Accessed 10 April 2014.
- Stewart, M.M., and J. Rossi. 1981. The Albany Pine Bush: a northern outpost for southern species of amphibians and reptiles in New York. *American Midland Naturalist* 106:282–292.
- Törn, A., A. Tolvanen, Y. Norokorpi, R. Tervo, and P. Siikamäki. 2009. Comparing the impacts of hiking, skiing and horse riding on trails and vegetation in different types of forest. *Journal of Environmental Management* 90:1427–1434.
- Tysler, R.W., and C.A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). *Conservation Biology* 6:253–262.
- Vasconcelos, H.L., E.H.M. Vieira-Neto, and F. M. Mudim. 2006. Roads alter the colonization dynamics of a keystone herbivore in neotropical savannas. *Biotropica* 38:661–665.

- Vasconcelos, H.L., J.M.S. Vilhena, and G.J.A. Caliri. 2000. Responses of ants to selective logging of a central Amazonian forest. *Journal of Applied Ecology* 37:508–514.
- Wagner, D.L., M.W. Nelson, and D.F. Schweitzer. 2003. Shrubland Lepidoptera of southern New England and southeastern New York: ecology, conservation, and management. *Forest Ecology and Management* 185:95–112.
- Wheeler, Jr., A.G. 1991. Plant bugs of *Quercus ilicifolia*: myriads of mirids (Heteroptera) in pitch pine-scrub oak barrens. *New York Entomological Society* 99:405–440.
- Wickham, H. 2007. Reshaping Data with the reshape Package. *Journal of Statistical Software*, 21(12), 1-20. <http://www.jstatsoft.org/v21/i12/>.
- Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer New York. <http://had.co.nz/ggplot2/book>.
- Wiezik, M., M. Svitok, A. Qieziková, and M. Dovčiak. 2013. Shrub encroachment alters composition and diversity of ant communities in abandoned grassland of western Carpathians. *Biodiversity Conservation* 22:2305–2320.
- Wolf, I.D., G. Hagenloh, and D.B. Croft. 2013. Vegetation moderates impacts of tourism usage on bird communities along roads and hiking trails. *Journal of Environmental Management* 129:224–234.
- Xie, Y. 2014. knitter: A general-purpose package for dynamic report generation in R. R package version 1.7. <http://yihui.name/knitr/>.