

The Ants of Nantucket: Unexpectedly High Biodiversity in an Anthropogenic Landscape

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Abstract - This first comprehensive assessment of the ant fauna of Nantucket Island, MA revealed that 43% of New England ant species and 70% of New England ant genera occur on an island occupying only 0.07% of New England's land area. Ants collected by four different research groups between 2000 and 2009 included 32,158 individual ants (2911 incidences) from 384 spatially and temporally distinct samples representing 14 different vegetation community types. The majority of the ant species were collected from anthropogenically derived and maintained sandplain grasslands, sandplain heathlands, and Scrub Oak shrublands. These three communities are state-ranked S1 community types; the lower state-ranked communities of beaches and sand dunes, bogs, salt marshes, and forest fragments had distinct ant assemblages with much lower species richness. The large number of samples described here, from a wide range of vegetation community types, expands the known list of Nantucket ant species more than three-fold and provides a baseline for future assessment of the effects of ongoing, long-term ecosystem management on Nantucket.

Introduction

Ants are one of the “little things that run the world” (Wilson 1987). They account for 10–15% of the animal biomass in most terrestrial habitats (Alonso and Agosti 2000) and they perform a myriad of ecosystem services (Folgarait 1998), including, at least in New England, turning over more soil than earthworms (Lyford 1963). The structure of ant assemblages—i.e., the number of ant species and their relative abundance—is associated with habitat size and type (e.g., Goldstein 1975, Gotelli and Ellison 2002). Ant species richness may be associated positively with human population density (Schlick-Steiner et al. 2008), but ant assemblage structure responds rapidly to changes in environmental conditions and usually reaches a new (quasi-)equilibrium on time-scales ranging from years to only a few decades (Wike et al. 2010, Zettler et al. 2004).

Grazing and logging are examples of anthropogenic drivers that can bring about rapid changes in the structure of ant assemblages. For example, on short time scales (<10 years), ant species richness declined when forests were converted to agriculture or pasture (Dunn 2004) and in intensively grazed grasslands relative to nearby forests in Argentina and Mexico (Bestelmeyer and Wiens 1996, Quiroz-Robledo and Valanzuela-Gonzalez 1995), but in dry climates in both Australia and North America, ant species diversity was unaffected by moderate to intensive grazing (Bestelmeyer and Wiens 2001, Read and Andersen 2000). In

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the southeastern US, ant species richness declined with increasing pesticide use and agricultural intensification (Peck et al. 1998).

On decadal time scales, logging per se has less of an impact on ant assemblage structure than conversion of forests to other uses (Dunn 2004). More ant genera have been found in clearcuts and mature (20–25 years old) forest stands than in 5- and 15-year-old stands (Wike et al. 2010). Ant species richness also increased within 2 years following *Tsuga canadensis* (L.) Carr. (Eastern Hemlock) removal (Sackett et al. 2011) and remained high throughout 15–20 years of succession from forest clearings to young hardwood stands (Ellison et al. 2005). However, little is known about the very long-term effects on ant species richness of grazing and conversion of forestlands to open habitats, as represented by the over 200 years of intensive land-use on Nantucket Island, off the southeast coast of Massachusetts (Fig. 1).

Most ecosystems in New England reflect centuries of human land use (Foster and Aber 2004). The sandplain grasslands, sandplain heathlands, and Scrub Oak shrublands of Nantucket are the result of centuries of overgrazing and other human land uses (Dunwiddie 1989, Macy 1880). These vegetation community types are now uncommon in New England; in Massachusetts, they are all state-ranked S1 (vegetation) community types (“typically five or fewer occurrences, very few remaining acres or miles of stream, or especially vulnerable to extirpation in Massachusetts for other reasons”; Swain and Kearsley 2001). These vegetation communities also host many species that were common in the mid-1800s at the height of agricultural activities, but now, following 150 years of reforestation, are rare (Motzkin and Foster 2002, Sorrie and Dunwiddie 1996). In short, Nantucket Island is a premier example of a 19th-century landscape (Dunwiddie 1989), and “the primary management strategy of the Nantucket Conservation Foundation is to maintain sandplain grassland, sandplain heathland, and Scrub Oak shrublands in accordance with documented Nantucket vegetation community types” (Andrew McKenna-Foster, Maria Mitchell Natural History Museum, Nantucket, MA, 23 December 2009 pers. comm.).

In this paper, I present new data on the ants of Nantucket Island, MA—the first comprehensive survey of the Island’s ants since the 1920s. I explore relationships between ant species diversity and vegetation community types, and test whether different vegetation community types host different ant faunas. This work is part of a broader effort to document patterns and drivers of the diversity of the ants of New England (Ellison et al., in press).

Methods

Nantucket Island: its history, vegetation, and historical ant collection

Nantucket is a small island ($\approx 125 \text{ km}^2$) off the southeast coast of Massachusetts (Fig. 1), located between $41^\circ 14'$ and $41^\circ 24'$ N latitude and between $69^\circ 57'$ and $70^\circ 14'$ W longitude. It has an average annual temperature of 10°C and receives an average of 1000 mm of rainfall each year.

Like Martha's Vineyard and Cape Cod to its north, Nantucket is part of the terminal moraine that was deposited $\approx 15,000$ years ago during the Wisconsin Glaciation by the Laurentide Ice Sheet (Oldale 2001). As sea level rose, Buzzards Bay formed to its north ≈ 5000 years ago, whereupon Nantucket was isolated from Cape Cod and the rest of the mainland (Oldale 2001). Prior to European settlement in the mid-1600s, Nantucket was home to Native Americans of the Wampanoag Tribe (Philbrick 1998). From the early 1700s to nearly 1850, it was the most prominent whaling port in the world (Macy 1880, Melville 1851), but it declined as a commercial port following the 1846 "Great Fire" that burned Nantucket Town, concurrent siltation of the harbor, and the development of railroad connections from the mainland whaling port of New

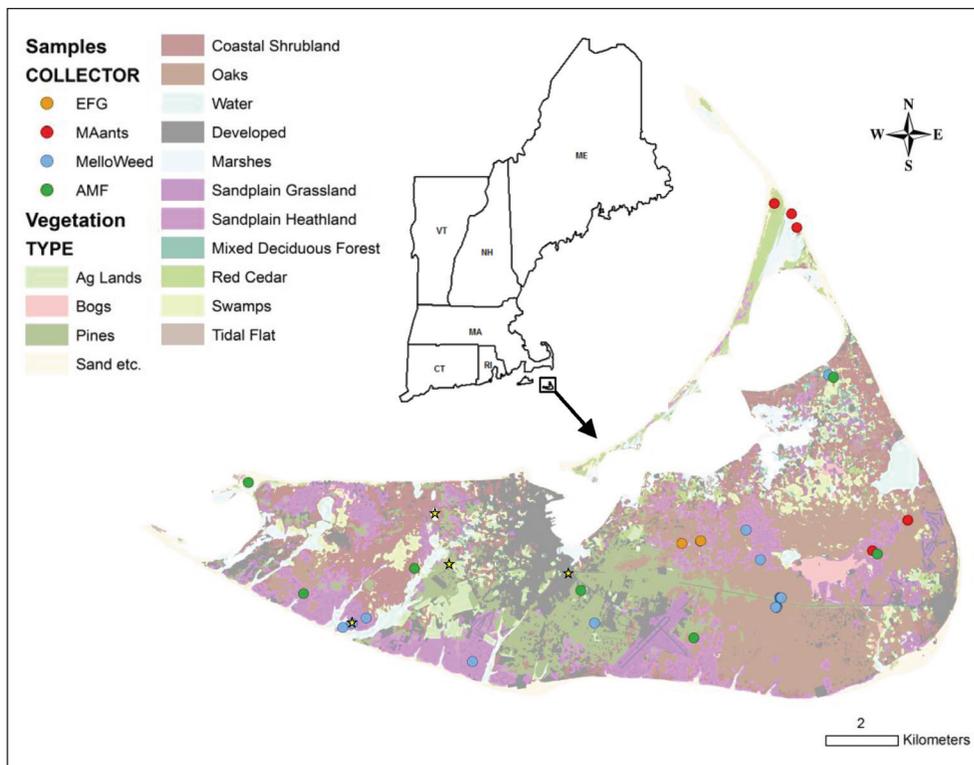


Figure 1. Nantucket Island, illustrating the natural communities of Nantucket and the locations where and when ants were sampled. Yellow stars indicate approximate locations of Charles Johnson's samples from the 1920s (historical information from Avery 2009, Gardner 1947, and Walling 2009); the northernmost site is Maxcy Pond. Circles identify locations of samples taken between 2000 and 2009. Orange circles indicate the bogs collected by Aaron Ellison and Elizabeth Farnsworth in 2000; blue circles indicate sites collected by Mark Mello and Aaron Weed from 2005–2009; green circles indicate sites collected by Andrew McKenna-Foster in 2006; and red circles indicate sites collected by Aaron Ellison, Mark Johnston, and Kelly McBride in 2007. Vegetation classification based on a 1993 inventory by The Nature Conservancy. Precise information on collection localities, including geographic coordinates and vegetation community type at each location, is in Ellison and Gotelli (2009).

Bedford to the rest of the United States. The colonial peak of its population was in 1840, when just over 9000 individuals were recorded in the decennial census. The population fell to <3000 by 1910, and did not reach 9000 again until 2000. The 2010 census listed 10,172 permanent residents on the island (US Census Bureau 2010).

Despite millennia of occupation by Native Americans, Nantucket was heavily forested before Europeans colonized the island (Dunwiddie 1990, Motzkin and Foster 2002). The colonists rapidly cleared and farmed the island, their sheep heavily grazed it, and by the end of the 19th century, there was virtually no forest cover on the island (Dunwiddie 1989, Macy 1880). Now, the remaining “natural” vegetation—forests and wetlands—is highly fragmented and occurs only in small patches restricted to Nantucket State Forest, the forested wetlands at Squam Swamp, remnant patches at Coskata-Coatue (see Field sampling, below), and a few kettle-hole bogs.

Currently, the predominant vegetation of Nantucket is a continuous mosaic of anthropogenically derived and maintained sandplain grasslands, sandplain heathlands, and Scrub Oak thickets (Dunwiddie 1989, Motzkin and Foster 2002, Sorrie and Dunwiddie 1996). Sandplain grasslands are dominated by *Schizachyrium scoparium* (Michx.) Nash (Little Bluestem), *Carex pensylvanica* Lam., and other graminoids; in these grasslands there is <50% cover of *Arctostaphylos uva-ursi* (L.) Spreng. (Bearberry), *Gaylussacia baccata* (Wangenh.) K. Koch (Black Huckleberry), or other shrubs. Sandplain heathlands are dwarf shrublands dominated by Bearberry, Huckleberry, *Hudsonia tomentosa* Nutt. (Woolly Beachheather), and/or *Corema conradii* (Torr.) Torr. ex Louden (Broom Crowberry). Scrub Oak thickets are dominated by *Quercus ilicifolia* Wangenh. (Scrub Oak) and *Quercus muehlenbergii* Engelm. (Chinquapin Oak), with understories of various Ericaceae, notably Black Huckleberry, Bearberry, or *Vaccinium angustifolium* Aiton (Lowbush Blueberry).

Despite intensive collecting of ants in Massachusetts throughout the 20th century (Ellison et al., in press), only one small ant survey was conducted on Nantucket prior to those described here. Charles Williston Johnson, of the now-defunct Boston Society of Natural History (Johnson 2004), collected insects throughout the island in the late 1920s. The ants were sent to William Morton Wheeler at Harvard, who identified them and published a list of the 17 species that he identified (Wheeler 1928). Johnson (1930) reprinted the list of species, along with some locality information. Most of his collecting was done at Maxcys [sic] Pond, with a few additional species collected from the town Common (i.e., the public grazing area), the Fairgrounds, and the Coleman Bird Sanctuary. The specimens were returned to Johnson by Wheeler, and are now in the collection of the Maria Mitchell Association (Anonymous 1933; Andrew McKenna-Foster, 21 June 2011 pers. comm.). In September 2011, I examined these specimens, checking species identifications and updating the nomenclature to reflect current taxonomy (Bolton and Alpert 2011); this re-examination added one species to Wheeler’s list (Appendix 1).

Field sampling

The data presented here are from collections made on Nantucket between 2000 and 2009 by four different research groups (Fig. 1); detailed geographic information on collection dates and localities are permanently stored in, and publicly available from, the online Harvard Forest Data Archive, dataset HF-147 (Ellison and Gotelli 2009).

In July of 2000, ants were collected from Taupawshas Bog and Donut Pond Bog by Aaron Ellison and Elizabeth Farnsworth using an array of 25 pitfall traps and 25 bait stations, litter sampling, and hand-collecting (the ALL protocol of Agosti and Alonso 2000); additional details on sampling methods are given in Ellison et al. (2002). Samples were collected from both bog mats and from the Scrub Oak thickets that surrounded the bogs.

From 2004–2008, Mark Mello and Aaron Weed set out arrays of barrier pitfall traps across the island (Weed and Mello 2007). Each barrier pitfall trap consisted of plastic 473-ml cups containing 20 ml of propylene glycol as a preservative, four 1- × 0.15-m plastic barrier strips, and five 0.12-m² plywood squares for rain covers. Barriers were embedded in the soil at right angles to a central cup, and four additional cups were set at the end of each barrier. Traps were left in place for 12–22 days (mean = 14.5 days) from May through October each year. In 2004, Mello and Weed sampled sandplain grasslands at Ram Pasture (the former Lot Palmer Farm [Gardner 1947], which became the Coleman Bird Sanctuary [Albertson 1926] sampled by Johnson in the 1920s); coastal heathlands at the Smooth Hummocks north of Bartlett Farm Road; annually burned Scrub Oak thickets; a *Pinus rigida* Mill. (Pitch Pine) woodland in Nantucket State Forest; and an *Acer rubrum* L. (Red Maple) / *Nyssa sylvatica* Marsh. (Tupelo) forest at Squam Swamp. From 2005–2008, their sampling was focused on the sandplain grassland at Ram Pasture, and a Scrub Oak thicket that had been burned in 2003. Also in 2005, Mello and Weed sampled dense networks of barrier pitfall traps in the Milestone Harrier Restoration area, a sandplain heathland mixed with Scrub Oak that has been mown annually since 1996, and in taller Scrub Oak thickets with dense understories of Black Huckleberry south of the Milestone Harrier Restoration area. Although Mello and Weed were focused on collecting beetles (Weed and Mello 2007), numerous ants also accumulated in their pitfall traps; the ants were extracted from the rest of the pitfall “by-catch” and sent to me for identification.

In 2006, Andrew McKenna-Foster collected spiders in pitfall traps and Berlese funnels from: the coastal dunes at Eel Point dominated by *Myrica pensylvanica* (Mirb.) Kartesz (Bayberry), *Toxicodendron radicans* (L.) Kuntze (Poison Ivy), and *Vaccinium oxycoccus* L. (Small Cranberry); a Scrub Oak/Pitch Pine stand with a dense understory of Black Huckleberry, *Viburnum dentatum* L. (Viburnum), Bayberry, and Lowbush Blueberry at Madequecham; a sandplain grassland owned by the Massachusetts Audubon Society; a Scrub Oak/Pitch Pine/Black Huckleberry plot at Sheep Pond; and in the Red Maple/Tupelo swamp forest at Squam Swamp (McKenna-Foster and Beaton n.d.). Five pitfall traps (240-ml

jars with propylene glycol + ethanol as preservative) were placed at each location throughout the summer. Traps were 10 m apart and were left open to collect arthropods on four occasions for three days at all sites except for the sandplain grassland, where traps were set only twice: once for four days and once for seven days. At each site, 1 m² of leaf litter was collected and distributed among eight 15-cm diameter Berlese funnels and placed under four 60-watt light bulbs. Arthropods were extracted from the litter for four days directly into 70% ethanol. Ants from both the pitfall traps and the litter samples were extracted from these samples and sent to me for identification.

In July of 2007, ants were collected at Sesachacha Heathlands and Coskata-Coatue by Aaron Ellison, Mark Johnston, and Kelly McBride. Habitats sampled at Sesachacha included sandplain grasslands, sandplain heathlands, and Scrub Oak thickets. Habitats sampled at Coskata-Coatue included a coastal oak/Pitch Pine/*Ilex opaca* Aiton (Holly) forest, a maritime beach/dune covered with *Amophila breviligulata* Fernald (American Beachgrass), a salt marsh berm, and a maritime *Juniperus virginiana* L. (Juniper) woodland. Sampling at Sesachacha and Coskata-Coatue consisted of one person-hour of careful searching and hand-collecting within a 75- × 75-m (5625 m²) plot in each habitat.

Finally, in 2009, Mark Mello set out 11 barrier pitfall traps (as described above) for beetles in restored sandplain grassland habitats at Norwood Farm, operated by the Norwood Farm Trust. Ants were extracted from the samples and sent to me for identification.

Sampling methods and sampling effort differed among the different collectors and at the different sample sizes, but all used pitfall traps or hand collecting. Ellison et al. (2007) found that for northeastern US sites, these two methods of collection yielded the most species and had substantial overlap with each other and with collections made with baiting or litter collections. We accounted for differences in sample sizes from different sites using regression analysis (see Statistical analyses, below).

Species identification, vouchers, and data availability

Ants were identified to species using current keys (Creighton 1950; Ellison et al., in press; Fisher and Cover 2007); nomenclature follows Bolton and Alpert (2011). Voucher specimens are deposited at Harvard's Museum of Comparative Zoology (MCZ) and at the Maria Mitchell Association on Nantucket. All other specimens are stored in the Harvard Forest sample archives either in 95% ethanol or dry-mounted and pinned. Raw data are publicly available from the online Harvard Forest Data Archive, dataset HF-147 (Ellison and Gotelli 2009).

Statistical analyses

For analysis purposes, an isolated pitfall trap or bait station, a single barrier trap (which included multiple pitfall cups), a single litter sample (spread across multiple Berlese funnels), or a temporally bounded (1-hr) hand-collection was considered a single "sample". From the 384 samples of pitfall traps, bait stations,

litter samples, and hand-collections, I identified 32,158 individual specimens. Because a single colony represents a genetic “individual” and some colonies have large numbers of workers that accumulate in pitfall traps, whereas others have few workers, using counts of individual specimens instead of counts of colonies can bias estimation of species richness (Gotelli et al. 2011). When nest locations are unknown (as is the case here), the number of species occurrences, or “incidences”, in a single sample (e.g., five individuals of a single species from a single sample equals one incidence) is considered a better measure of abundance than counts of individual workers (Gotelli et al. 2011). Thus, I use the number of incidences (2911), not the number of workers, in all analyses. Note, however, that the rank abundance of individual specimens was highly correlated with the rank abundance of the number of incidences (Fig. 2), which suggests little differences among collections in relative abundance of individual species. Additional assessment of the effects of sampling effort and sample size in each vegetation

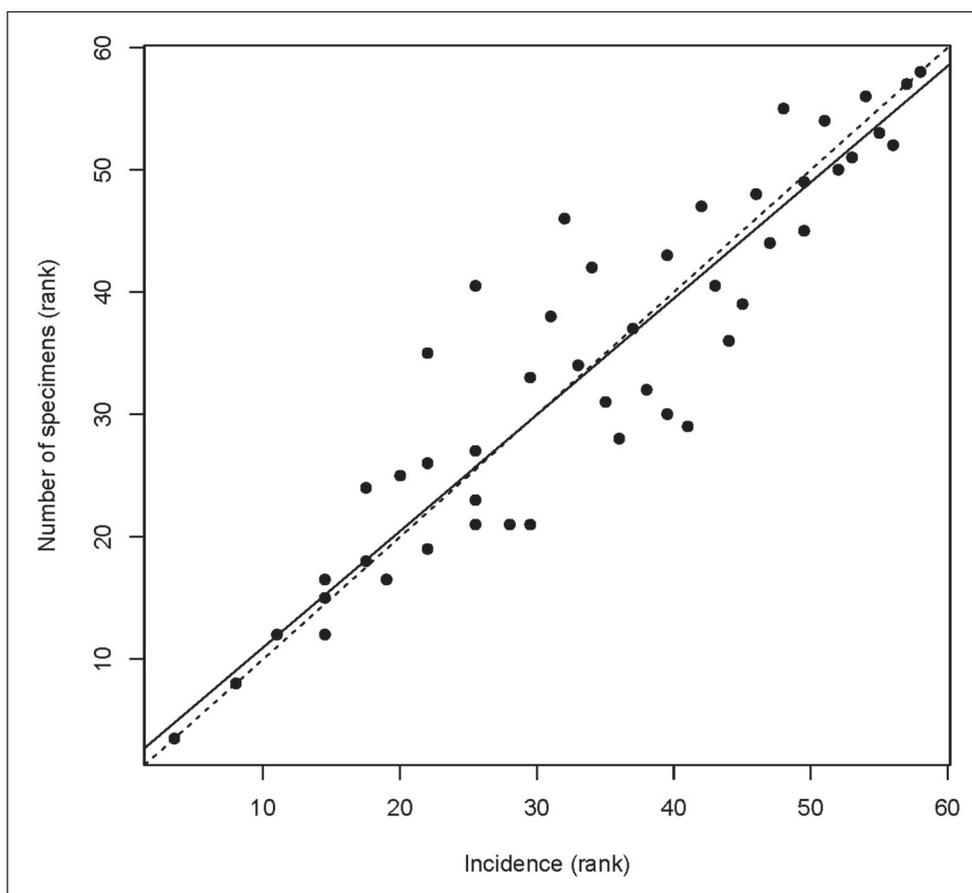


Figure 2. The relationship between the rank order of the number of specimens and the rank order of the number of incidences of all ants collected on Nantucket Island between 2000 and 2009. The dotted line is the 1:1 line, and the solid line is the actual relationship between incidences and specimens (slope = 0.95, $r^2 = 0.90$, $P < 0.001$); there is no difference in the rank-order of incidences and specimens ($X^2 = 24.8$, d.f. = 57, $P = 1.0$).

community was done by regressing ant species richness in each community on the (\log_{10} -transformed) number of incidences. Provided the data met the assumptions of linear regression, a linear increase in richness with incidences would reflect a sampling effect.

All analyses except for species accumulation curves and estimation of the total number of species on Nantucket were done using the R statistical software, version 2.12.2 (R Development Core Team 2011). Relevant functions and libraries used included: cor and lm in the stats library for correlation and linear regression, respectively; chisq.test in the stats library for chi-square tests; d in the vegetarian library for computing beta diversity across natural community types (method of Jost 2007; 100 bootstrap iterations); and metaMDS in the vegan library for non-metric multidimensional scaling (NMDS; Minchin 1987) and ordination. For the NMDS, data were first standardized using the Wisconsin transformation (based on the maximum number of species and the total number of species per site: Oksanen 1983); the Bray-Curtis dissimilarity metric (Faith et al. 1987) was used for the ordination. Species accumulation curves (i.e., sample-based rarefaction curves; Gotelli and Colwell 2001) and 95% confidence intervals (Colwell et al. 2004) were computed using the EstimateS software, version 8.2.0 (Colwell 2011). The expected number of species on Nantucket was estimated (extrapolated) from the data using the Chao-1 estimator (Chao 1987) as programmed in EstimateS.

Results and Discussion

Species richness of Nantucket ants

These seven years of intensive collecting on Nantucket yielded 58 species in 22 genera (Appendix 1, Fig. 3). This effort increases the ant species previously known from Nantucket more than three-fold (Appendix 1), and only one of the 18 species that were collected in the 1920s, *Formica obscuriventris*, was not collected again between 2000 and 2009 (Appendix 1). Despite having only 0.07% of the land area of New England, Nantucket hosts 43% of the 136 species, 70% of the 32 genera, and five of the six subfamilies known from, or suspected to occur in, New England (Ellison et al., in press). Although such a rich ant fauna might be expected in relatively undisturbed New England habitats (Ellison et al., in press), hundreds of years of intensive land use have transformed Nantucket's original ecosystems, and these anthropogenically derived habitats are maintained by active management (Dunwiddie 1989).

Elsewhere in the world, deforested and heavily grazed ecosystems generally support fewer ant species than forested and ungrazed habitats (e.g., Bestelmeyer and Wiens 1996, Dunn 2004, Wike et al. 2010). However, Schlick-Steiner et al. (2008) have shown that ant species richness increases with human population density in some anthropogenic landscapes, but their relationship between population density, island area, and ant species richness predicts <12 ant species for Nantucket. Even using Schlick-Steiner et al.'s

(2008) equations that include plant diversity, which is particularly high on the island (>1200 plant species; Sorrie and Dunwiddie 2006), the expected number of ant species increases to only 14 species, and only a few more species would be expected to be added for the island's 10 °C annual temperature (Sanders et al. 2007, Schlick-Steiner et al. 2008). A more detailed analysis of ant assemblages in each habitat suggests some reasons for the unexpectedly high diversity of ants observed on Nantucket.

Structure of Nantucket ant assemblages

As is characteristic of most samples of species abundance, the overall ant species-abundance curve was pronouncedly log-normal (Fig. 4). There were a handful of common species—*Tapinoma sessile*, *Formica incerta*, *Lasius alienus*, *Nylanderia parvula*, *Aphaenogaster rudis*, *A. treatae*, *Crematogaster lineolata*, and a widespread, but as yet undescribed, species of *Myrmica* (species code AF-scu; Ellison et al., in press)—and a very long tail of rare species. Of particular interest among the rare species, for which only one or two individuals were collected, were *Myrmica semiparasitica* and *Anergates atratulus*. *Myrmica semiparasitica* is a social parasite of the woodland species *M. punctiventris*; it was described only in 2009 (Francoeur 2009), and the two Nantucket records are only

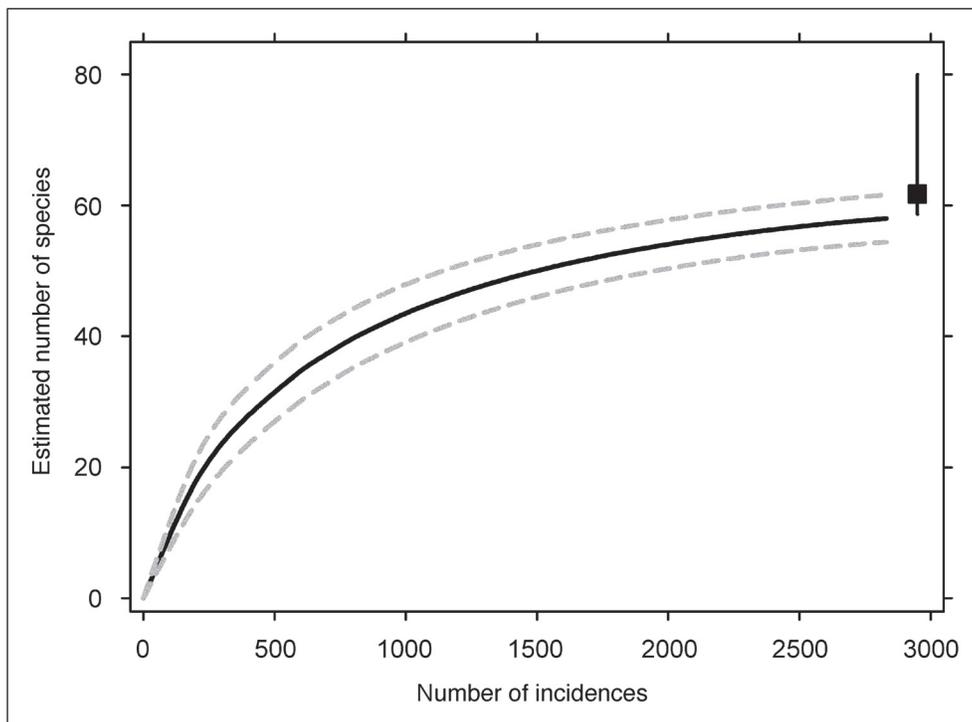


Figure 3. Species accumulation curve for ants collected on Nantucket Island between 2000 and 2009. The solid line is the observed data, and the grey dotted lines are 95% confidence intervals based on 1000 bootstrap samples. The Chao-1 estimate (and 95% confidence intervals) of the estimated total number of ant species on Nantucket is indicated by the solid square (and vertical line).

the fourth and fifth time this species has been collected anywhere in the world (Ellison et al., in press). *Anergates atratulus* is a non-native social parasite of its non-native host, the pavement ant *Tetramorium caespitum* (Bruder and Gupta 1972); the Nantucket record is only the second time that this species has been collected in New England (Ellison et al., in press). These two rare species were collected in rare vegetation community types: sandplain grasslands, Scrub Oak shrublands, and Pitch Pine heathlands.

Certain species were associated with particular natural community types (Appendix 1, Fig. 5). *Myrmica lobifrons* is a bog specialist, and, along with the wetland species *Myrmica incompleta*, was associated strongly with the two

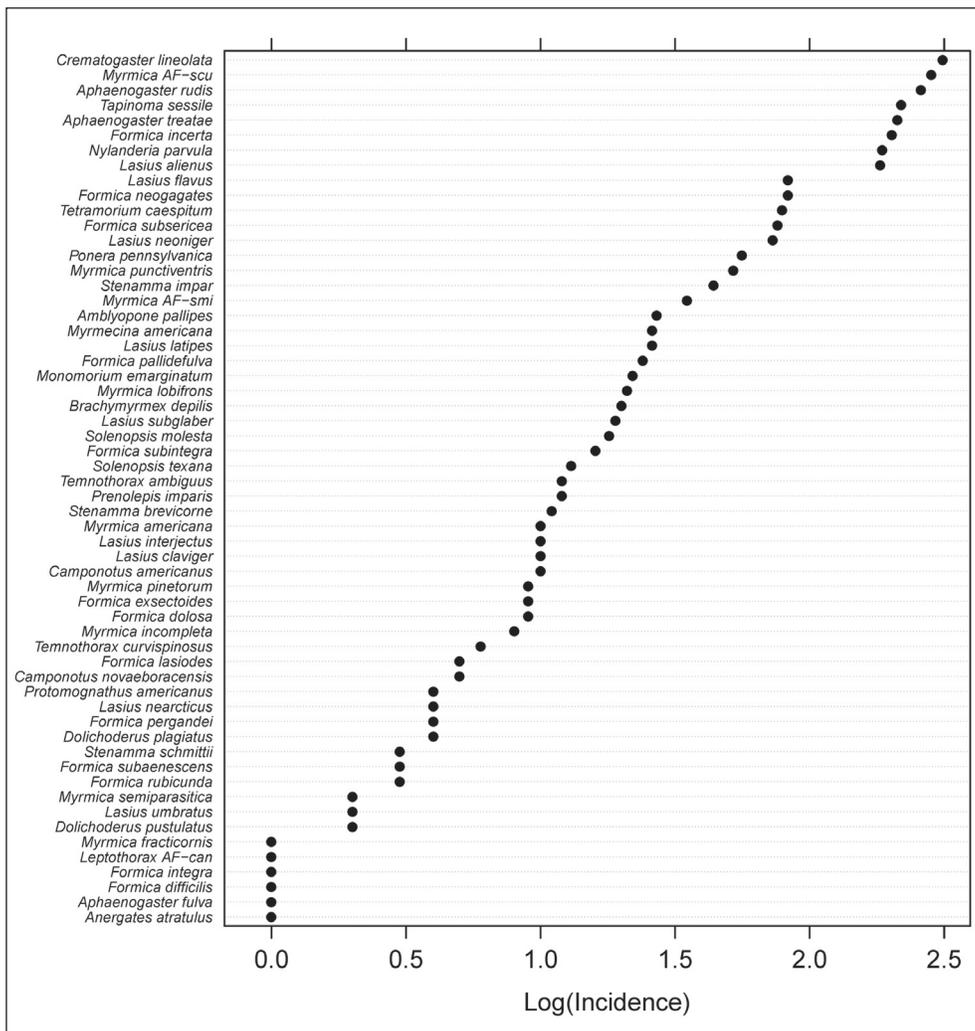


Figure 4. Rank-abundance plot of the 58 ant species collected on Nantucket Island between 2000 and 2009. The abundance shown is the log₁₀ of the number of incidences in the total sample for each species. Like virtually all species-abundance curves that have been published, this plot illustrates that there are a few common species and many rare species in the Nantucket ant assemblage.

sampled kettle bogs. *Dolichoderus plagiatus* and *Lasius neoniger* were most abundant along the landward edges of salt marshes. The pavement ant, *Tetramorium caespitum*, has expanded its range into maritime juniper woodlands and sand dunes, where it nests at the base of American Beachgrass, displacing *L. neoniger*. Ants in the wide-ranging *Aphaenogaster rudis* species complex were the only ants found in the one collection made in a residential area, but this habitat is the most under-sampled of any on the island; further collections in town centers and residential areas undoubtedly would yield more species such as *Tetramorium caespitum* and carpenter ants (*Camponotus* spp.).

The remaining ant assemblages separated out the woodland communities (deciduous forest, Red Maple/Tupelo swamp, Pitch Pine barrens, White Pine stands, and Scrub Oak shrublands) from the more open heathland and grassland communities (sandplain grasslands, sandplain heathlands, and Scrub Oak heathlands) (Figs. 5 and 6). The most common ants in the shrubby woodlands included *Crematogaster lineolata*, *Formica rubicunda*, *Myrmica punctiventris*,

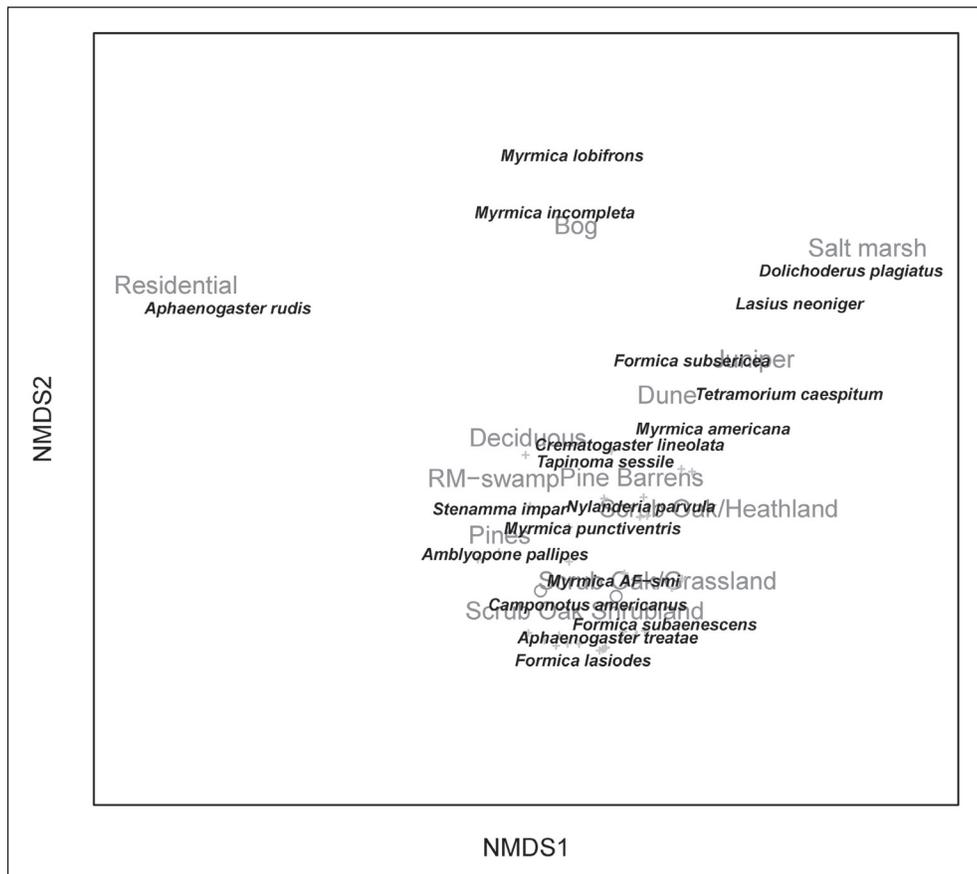


Figure 5. Ordination plot of the non-metric multidimensional scaling of the ant assemblages of the different vegetation communities sampled on Nantucket Island between 2000 and 2009. The community types are written in grey, and the ant species most commonly associated with each community are written in black.

and *Tapinoma sessile*, whereas the more common ants in the open heathlands and grasslands included *Aphaenogaster treatae*, *Formica pallidefulva*, *F. pergandei*, and *Lasius umbratus*. True forest specialists, including carpenter ants (*Camponotus americanus* and *C. novaeboracensis*) and *Lasius nearcticus*, were uncommon anywhere on the island (Fig. 4).

Similarity analysis (Fig. 6) provided additional statistical support for inferences drawn from the ordination plot (Fig. 5); 3–4 distinct assemblages (sensu Jost 2007) were identified in these data. The bog and residential areas were species-poor, clearly different from each other, and clearly different from all of the other sampled communities (Fig. 6). The ant assemblages of the woodland and open communities formed a continuum from maritime to uplands, and from woodland to open (Fig. 6). The maritime communities (salt marsh edges, beaches and dunes, juniper woodlands) had far fewer species than the grasslands, heathlands, Scrub Oak woodlands, and forests, but the species in the maritime communities were simple subsets of the species in the upland communities. The vegetation communities with the most ant species also were those of highest conservation concern (Fig. 6).

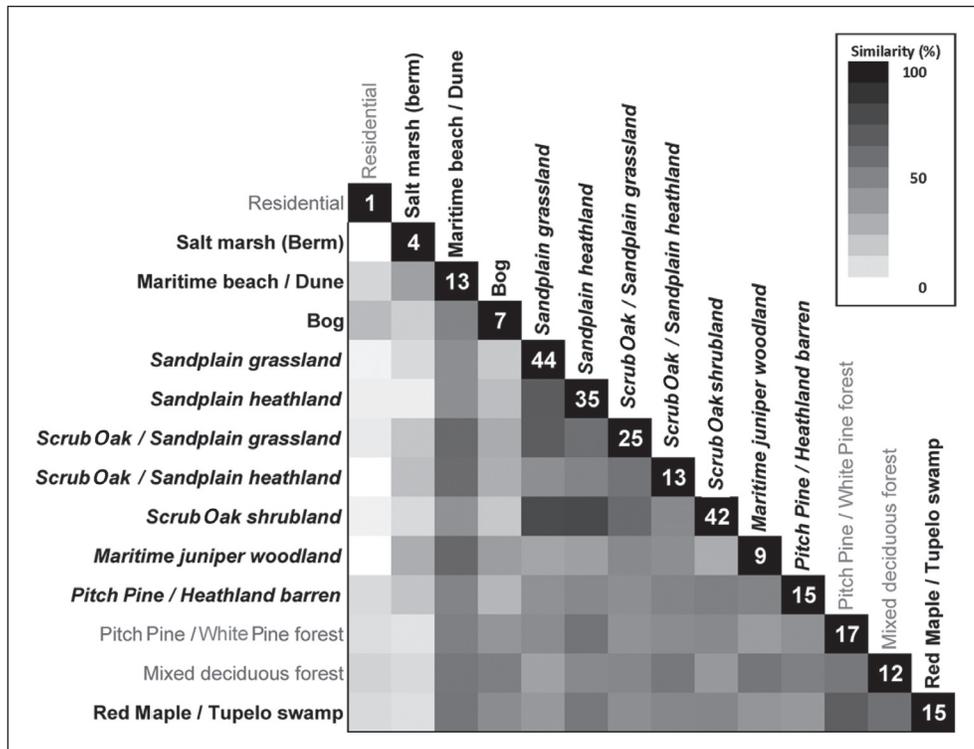


Figure 6. Similarity (beta diversity) in ant assemblages of the different natural communities sampled on Nantucket Island between 2000 and 2009. Shading (from white to black) indicates increasing similarity (from 0–100%). The numbers on the diagonal are the total number of ant species collected in each natural community. The font of the community indicates the state ranking of that habitat (community type): S1 in ***bold-italic***, S2 or S3 in **bold**, and S5 in grey.

It was not possible to determine how contemporary land management, the goal of which is to maintain vegetation community types and landscapes created by land use occurring from the 17th to the 19th centuries, has altered the structure of ant assemblages. Johnson's 1927 ant collection (Wheeler 1928, Johnson 1930) was too small and restricted in habitats to compare with the data presented here, but it is noteworthy that 17 of the 18 species he collected in 1927 were collected again in the last decade, and most of the species that he collected are also species of open habitats (Appendix 1). This result suggests that the ant assemblages on Nantucket likely have stabilized and that the species identified above could serve as useful indicators of successful management of the anthropogenically derived sandplain grasslands, sandplain heathlands, and Scrub Oak shrublands. In contrast, the ant assemblages of "natural" communities—bogs, other wetlands, and forests likely are relicts of more widespread assemblages, and these assemblages may lose more species over time (Schoereder et al. 2004). Future standardized collections focused on all of Nantucket's vegetation community types would allow for a more rigorous test of this hypothesis.

Were the samples biased by collection effort?

Although there was a strong and significant positive relationship between the number of incidences and the number of species across the 14 sampled vegetation community types (i.e., a sampling effect: $r^2 = 0.89$, $P = 9.2 \times 10^{-7}$; Fig. 7), further examination of the residuals (deviations of observed data from the regression line) revealed that they were not normally distributed. This result suggested that the relationship between the number of incidences and species richness in the natural communities was not random. In particular, Figure 7 shows that several of the most species-rich communities of conservation concern (Scrub Oak shrublands, sandplain heathlands, and Scrub Oak/sandplain grasslands) had more ant species than expected for the number of incidences, whereas the most species-poor communities (the bogs and maritime beach/dunes) had fewer ant species than expected for the number of incidences. The Pitch Pine/heathland barren also had many more species than expected for the number of incidences in the overall sample.

This overall result appears to be driven by the species-rich communities that are "pulling" the regression line towards the left of Figure 7. The bogs were sampled intensively using many methods (Ellison and Gotelli 2009, Ellison et al. 2002), and the number of ant species collected from Nantucket bogs and on its beaches and dunes was not unusual (Ellison et al., in press). The sampling intensity of pitfall trapping in the sandplain grasslands, sandplain heathlands, and Scrub Oak shrublands was indeed high, but not disproportionately high relative to the other habitats when scaled to the number of samples (Ellison and Gotelli 2009, Weed and Mello 2007). Nevertheless, these habitats still had many more species than would have been expected.

How does the Nantucket ant fauna compare with the ants of mainland New England?

Compared with other counties in New England, Nantucket has a relatively small area (Fig. 8A). Note that Nantucket County includes not only Nantucket Island ($\approx 125 \text{ km}^2$) but also the islands of Tuckernuck ($\approx 3.6 \text{ km}^2$) and Muskeget ($\approx 3.1 \text{ km}^2$), neither of which have been systematically surveyed for ants. Both for counties of its size, and for all counties in New England, the observed ant species richness of Nantucket is in the upper 20%; more ant species have been recorded in only ten other counties (out of 67 total) in all of New England (Fig. 8A). The high species richness of Nantucket Island could reflect the intensive sampling of ants on the island (Fig. 8B); the intensive sampling described here provides more specimen records from Nantucket Island than from any other county in New England, except for York County, ME (Ellison et al., in press). However, many other counties, including half of those on mainland

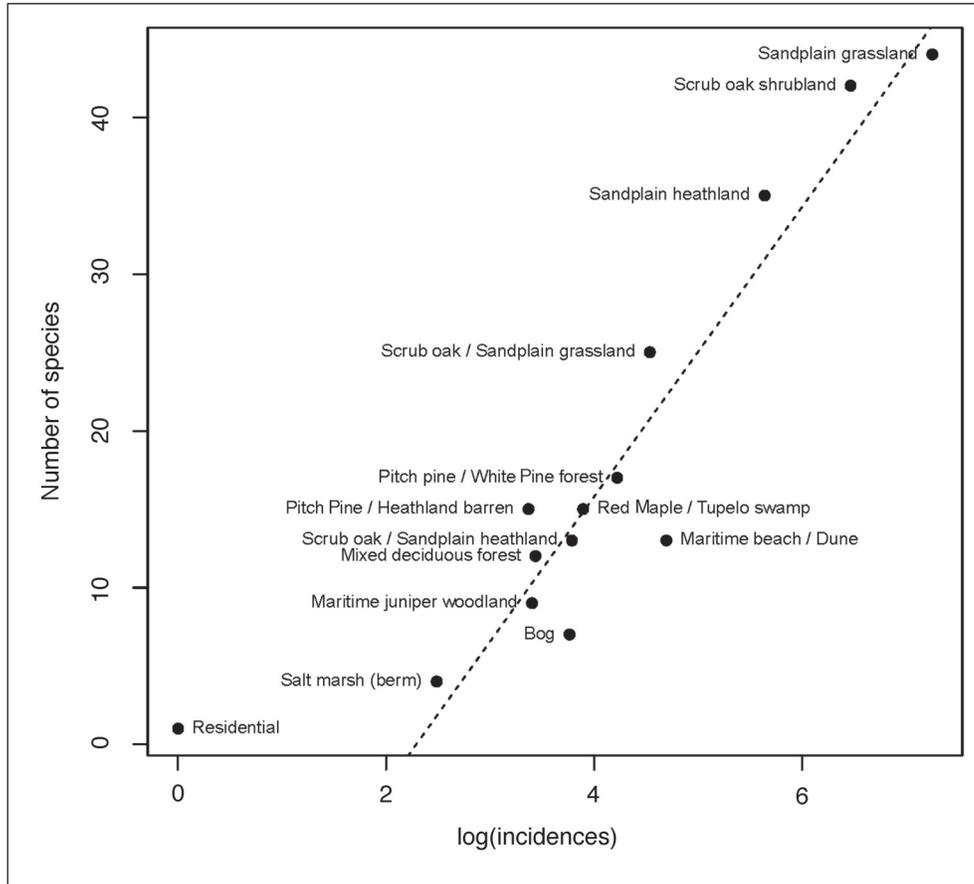


Figure 7. Relationship between species richness and the \log_{10} (number of incidences) in the overall sample. The dotted line is the best-fit linear regression of the observations. As the residential site was an outlier—it was represented in the dataset by only a single incidence, which by definition can only have 1 species—it was excluded from the regression analysis.

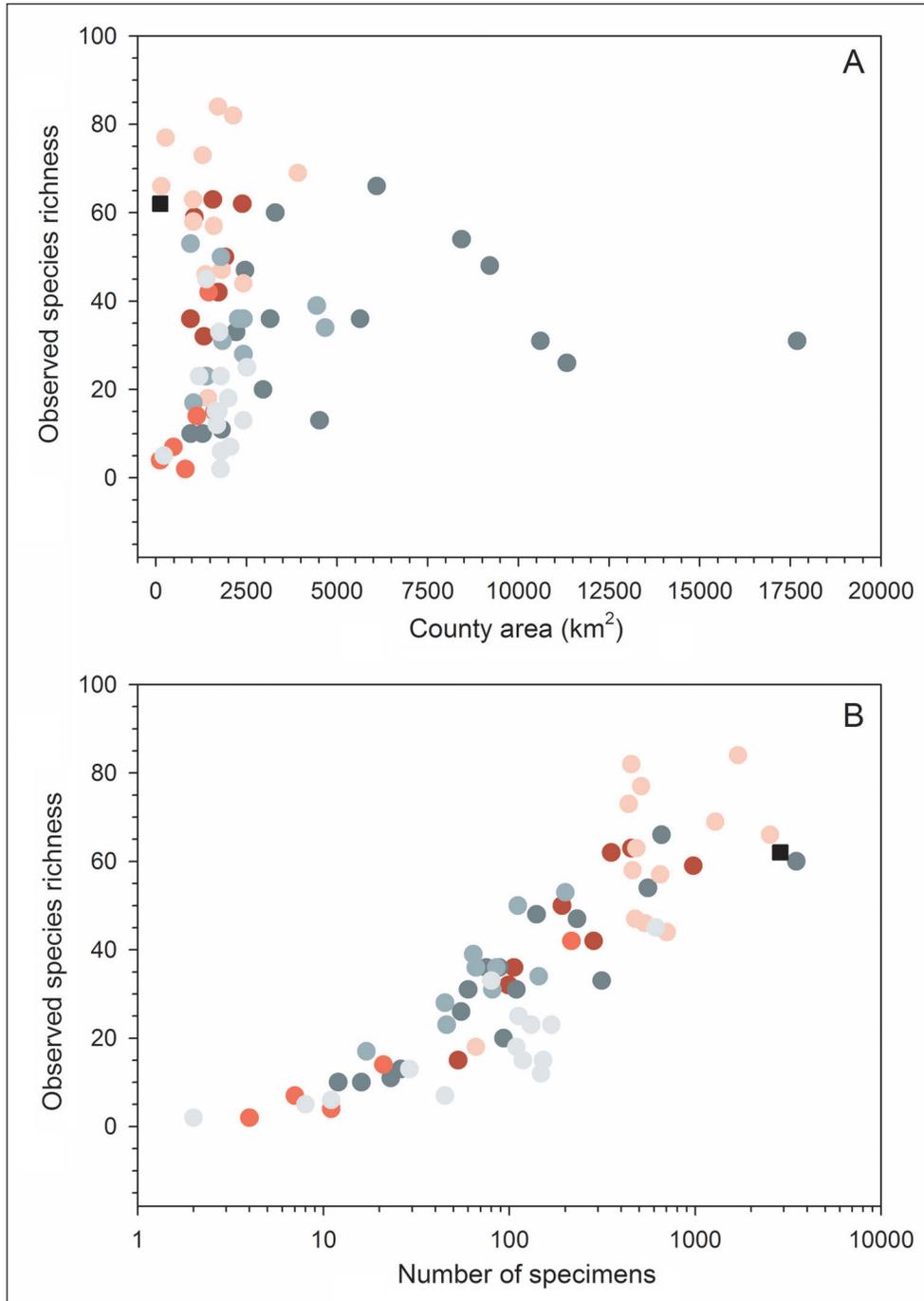


Figure 8. Relationship between species richness and county area (A) and sampling intensity (B) throughout New England. Individual county areas from US Census Bureau data; sampling intensity data from Ellison et al. (2012). Different colors indicate different states (dark blue = Maine; blue = New Hampshire; light blue = Vermont; light red = Massachusetts; red = Rhode Island; dark red = Connecticut); the black square is Nantucket (data from this paper).

Massachusetts, have more recorded species despite having fewer specimen records (Ellison et al., in press; Fig. 8B). I conclude, therefore, that the high species richness observed on Nantucket Island more likely reflects the diversity of habitats on Nantucket than it does a sampling effect.

Could there be still more ant species on Nantucket?

Not only was the observed species richness much higher than would be expected on a small island with a relatively high population density (80 people/km²), historically extensive land use, and ongoing active ecosystem management, the estimated species richness (Chao-1 estimator) for Nantucket was 62 species (95% confidence interval = [59–80]; Fig. 3). This result suggests that there are still a few more species to be found on the island. Where would it be best to look?

Six subfamilies of ants are represented in New England; five were collected on Nantucket (Appendix 1). The missing subfamily, the Proceratiinae, includes three species in the single genus *Proceratium*, all of which nest in rotten logs in forests and woodlands. These species, along with the three New England species in the genus *Pyramica* (Myrmicinae), might yet be found in the woodland fragments on Nantucket. However, the small size and fragmented distribution of forests on the island makes it unlikely that their populations would persist over the long term (Schoereder et al. 2004).

Other missing genera include the New England native genera *Formicoxenus*, *Harpagoxenus*, and *Pheidole* (all Myrmicinae) and *Polyergus* (Formicinae), and the non-native genus *Pachycondyla* (Ponerinae). All of the native genera except *Harpagoxenus* are warm-climate species that could occur on Nantucket given suitable habitat. *Formicoxenus provancheri* (Emery) is a social parasite of bog-dwelling *Myrmica* species, and could be found in the kettle bogs with its host. *Polyergus lucidus* Mayr is a slave-making species of *Formica incerta*. As this host is one of the most common species in the sandplain grasslands, there is no reason that *P. lucidus* couldn't survive there as well, but it is generally uncommon (Marlin 1971) and rare throughout New England (Ellison et al., in press). *Pheidole pilifera* (Roger) is a seed-harvesting species that is common in open areas, but it is rare in the pure-sandy soils of pine barrens and sandplain grasslands, and would be unexpected on Nantucket.

New England overall has only 13 non-native ant species, and most are (sub)tropical “tramp” species that nest only in heated structures (Ellison et al., in press). Only five can handle New England's winter climate, and two of those, *Tetramorium caespitum* and its specialist parasite *Anergates atratulus*, already are on Nantucket. Two more, *Nylanderia flavipes* (Smith) and *Pachycondyla chinensis* Emery are rare in New England (Ellison et al., in press) but are increasing in abundance in the urbanized Mid-Atlantic states (Pećarević et al. 2010). The last, *Myrmica rubra* (L.), is widespread in coastal New England and maritime Canada from eastern Rhode Island north to Nova Scotia (Grodén et al. 2005; Ellison et al., in press) in salt marshes, coastal woodlands, urban

areas, and along river margins. There is certainly suitable habitat for *M. rubra* on Nantucket, and it seems unlikely that it is too warm on Nantucket for *M. rubra* to persist. Perhaps the long period of sustained land use and management has allowed the ant communities to stabilize to an extent that it is difficult for *M. rubra* to establish.

Conclusion

There are distinctive, unusually species-rich assemblages of ants in the sandplain grasslands, sandplain heathlands, and Scrub Oak shrublands that were created by colonial-era land use and that are maintained by active management. Likewise, there are distinctive, species-poor assemblages of ants in bogs, forest remnants, and on sandy beaches and dunes. The large number of samples described here, from a wide range of vegetation community types, provide a useful baseline for future studies of Nantucket's biodiversity and suggest that some species of ants may be valuable indicators for evaluating ecosystem management and restoration on the island.

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Appendix 1. Ant species of Nantucket, their occurrence in the different vegetation community types sampled, the state rank of each vegetation community type (following Swain and Kearsley 2001), and the total species richness of each vegetation community type. A single asterisk (*) indicates a species in the 2000–2009 sample that was also collected by C. W. Johnson in the early 1900s (Wheeler 1928). A double asterisk (**) indicates a species that was collected by Johnson (Wheeler 1928) but not collected in 2000–2009. Nomenclature follows Bolton and Alpert (2011); subfamilies are in **bold-faced type**. The species codes for the one undescribed species of *Leptothorax* and the two undescribed species of *Myrmica* parallel those used by André Francoeur for his forthcoming revision of these two genera (see also Ellison et al., in press). Community types: R= residential, SM = salt marsh, B/D = beach/dune, B = bog, SG = sandplain grassland, SH = sandplain heathland, SO/SH = Scrub Oak/sandplain grassland, SO/SH = Scrub Oak/sandplain heathland, SOS = Scrub Oak shrubland, MJW = maritime juniper woodland, PP/HH = Pitch Pine/heath barren, PPF = Pitch Pine Forest, MDF = mixed deciduous forest, RM/TS = Red Maple/Tupelo swamp.

	Community type														
	R	SM	B/D	B	SG	SH	SO/SG	SO/SH	SOS	MJW	PP/HH	PPF	MDF	RM/TS	
State Rank	–	S3	S3	S2	S1	S1	S1	S1	S1	S1	S1	S5	S5	S3	
Species richness	1	4	13	7	44	35	25	13	42	9	15	17	12	15	
Amblyoponinae					✓	✓			✓			✓		✓	
<i>Amblyopone pallipes</i> (Haldeman)					✓	✓			✓			✓		✓	
Ponerinae					✓	✓		✓	✓			✓		✓	
<i>Ponera pennsylvanica</i> Buckley					✓	✓		✓	✓			✓		✓	
Dolichoderinae					✓	✓			✓		✓			✓	
<i>Dolichoderus plagiatus</i> (Mayr)		✓			✓	✓			✓		✓			✓	
<i>D. pustulatus</i> Mayr					✓	✓			✓					✓	
<i>Tapinoma sessile</i> (Say)			✓	✓	✓	✓			✓	✓		✓		✓	
Formicinae					✓	✓			✓			✓		✓	
<i>Brachymyrmex depilis</i> Emery					✓	✓			✓			✓		✓	
<i>Camponotus americanus</i> Mayr					✓	✓			✓			✓		✓	
<i>C. novaeboracensis</i> (Fitch)					✓	✓			✓			✓		✓	
<i>Formica difficilis</i> Emery					✓	✓			✓			✓		✓	
<i>F. dolosa</i> Buren					✓	✓			✓			✓		✓	
<i>F. exsectoides</i> Forel					✓	✓			✓			✓		✓	
<i>F. incerta</i> Buren			✓		✓	✓		✓	✓	✓		✓		✓	
<i>F. integra</i> Nylander					✓	✓			✓			✓		✓	
<i>F. lasioides</i> Emery					✓	✓			✓			✓		✓	

	Community type													
	R	SM	B/D	B	SG	SH	SO/SG	SO/SH	SOS	MJW	PP/HB	PPF	MDF	RM/TS
<i>F. neogagates</i> Viereck					✓	✓	✓	✓	✓	✓	✓		✓	
* <i>F. obscuriventris</i> Mayr					✓	✓	✓	✓	✓					
* <i>F. pallidiflava</i> Latreille					✓	✓	✓	✓	✓					
<i>F. pergandei</i> Emery					✓	✓			✓				✓	
<i>F. rubicunda</i> Emery					✓	✓	✓	✓	✓					
<i>F. subaenescens</i> Emery					✓	✓	✓	✓	✓					
<i>F. subintegra</i> Wheeler					✓	✓	✓	✓	✓				✓	✓
* <i>F. subsericea</i> Say		✓	✓	✓	✓	✓	✓	✓	✓			✓	✓	✓
* <i>Lasius alienus</i> (Foerster)			✓	✓	✓	✓	✓	✓	✓			✓	✓	✓
<i>L. claviger</i> (Roger)					✓	✓	✓	✓	✓					
* <i>L. flavus</i> (Fabricius)					✓	✓	✓	✓	✓					
<i>L. interjectus</i> Mayr					✓	✓	✓	✓	✓					
<i>L. latipes</i> (Walsh)					✓	✓	✓	✓	✓					
<i>L. nearcticus</i> Wheeler					✓	✓	✓	✓	✓					
<i>L. neoniger</i> Emery		✓	✓	✓	✓	✓	✓	✓	✓					✓
<i>L. subglaber</i> Emery			✓	✓	✓	✓	✓	✓	✓					
<i>L. umbratus</i> (Nylander)					✓	✓	✓	✓	✓					
<i>Nylanderia parvula</i> (Mayr)					✓	✓	✓	✓	✓			✓	✓	✓
<i>Prenolepis imparis</i> (Say)					✓	✓	✓	✓	✓			✓	✓	✓
Myrmicinae														
<i>Anergates atratulus</i> (Schenck)					✓	✓	✓	✓	✓					
<i>Aphaenogaster fulva</i> Roger					✓	✓	✓	✓	✓				✓	✓
<i>A. rudis</i> Enzmann (species complex)	✓		✓	✓	✓	✓	✓	✓	✓			✓	✓	✓
<i>Aphaenogaster treatae</i> Forel					✓	✓	✓	✓	✓				✓	✓
* <i>Crematogaster lineolata</i> (Say)			✓	✓	✓	✓	✓	✓	✓			✓	✓	✓
<i>Leptothorax</i> sp. nov. (<i>L.</i> sp. AF-can)					✓	✓	✓	✓	✓			✓	✓	✓
* <i>Monomorium emarginatum</i> DuBois					✓	✓	✓	✓	✓					✓
<i>Myrmecina americana</i> Emery					✓	✓	✓	✓	✓					✓
* <i>Myrmica americana</i> Weber					✓	✓	✓	✓	✓					✓
<i>M. fracticornis</i> Forel					✓	✓	✓	✓	✓					✓
* <i>M. incompleta</i> Provancher				✓	✓	✓	✓	✓	✓					✓

	Community type													
	R	SM	B/D	B	SG	SH	SO/SG	SO/SH	SOS	MJW	PP/HB	PPF	MDF	RM/TS
<i>M. lobifrons</i> Pergande				✓										
<i>M. pinetorum</i> Wheeler					✓	✓		✓	✓			✓	✓	✓
<i>M. punctiventris</i> Roger					✓				✓		✓	✓		
<i>M. semiparasitica</i> Francoeur						✓		✓	✓		✓	✓		
* <i>Myrmica</i> sp. nov. (<i>M.</i> sp. AF-scu)			✓		✓	✓		✓	✓		✓	✓		
<i>Myrmica</i> sp. nov. (<i>M.</i> sp. AF-smi)					✓	✓		✓	✓		✓	✓		
<i>Protomognathus americanus</i> (Emery)						✓			✓					
<i>Solenopsis molesta</i> (Say)					✓			✓	✓					
<i>Solenopsis</i> sp. nov. (<i>S.</i> cf. <i>texana</i> Emery)					✓			✓	✓					
<i>Stenamma brevicorne</i> (Mayr)					✓	✓			✓		✓	✓	✓	✓
<i>S. impar</i> Forel						✓			✓					
<i>S. schmitti</i> Wheeler						✓			✓					
<i>Tennothorax ambiguus</i> (Emery)					✓	✓			✓					
<i>T. curvispinosus</i> (Mayr)						✓			✓					
<i>Tetramorium caespitum</i> (L.)		✓	✓		✓	✓		✓	✓		✓	✓	✓	✓