

## ANT DIVERSITY IN PITCHER-PLANT BOGS OF MASSACHUSETTS

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**ABSTRACT** – We conducted the first systematic inventory of ant species richness in pitcher-plant bogs of Massachusetts. Twenty-six species were collected in 18 bogs during 1999 and 2000. We collected the bog-specialist *Myrmica lobifrons* for the first time in Massachusetts and found that it occurred in bogs from the Berkshire Mountains to Nantucket. Ant species composition in bogs displayed a nested subsets pattern, in which the species composition of a bog with few species was generally a subset of the species composition of bogs with more species. This pattern appears to result from different colonization histories of the different bogs. We tested whether ant species richness differed among bog types, ecological subregions, or geographic regions of the state (mainland, Cape Cod, Islands), and whether ant species richness was correlated with variables measured at each bog including: latitude, longitude, elevation, bog mat area; vegetation composition and the density of the carnivorous plant *Sarracenia purpurea*; and nutrient availability. Among Massachusetts bogs, species richness of ants was predicted best by tree species richness within bogs and by the concentration of ammonium in bog pore-water. Ant species richness was highest in bogs of the Connecticut River Valley and the Massachusetts-Rhode Island border. These are also areas identified by the Massachusetts BioMap project as core areas for biodiversity in the state.

### INTRODUCTION

In biomass and ecological dominance, ants are one of the most important invertebrate taxa in terrestrial ecosystems (Alonso and Agosti 2000, and Hölldobler and Wilson 1990). Ants can be sampled rapidly, and the diversity of ants in a community is a good indicator for the diversity of other invertebrate species (Alonso 2000, Lawton et al. 1998, Majer 1983). Although ants of upland forests and deserts have been well studied by naturalists and entomologists (recent reviews in Bestelmeyer and Wiens 2001, Folgarait 1998, Johnson 2001, and Kaspari 2001), the same cannot be said of ants of wetlands (Francoeur 1986; Francoeur and Pepin 1975, 1978; Gotelli and Ellison 2002b; Lesica and Kannowski 1998; Vepsäläinen et al. 2000). We sought to address this deficiency for ant assemblages in wetlands of Massachusetts.

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Acidic peatlands, or bogs, are one of the most common wetland types in New England, but their ants are virtually unknown (Gotelli and Ellison 2002b). For example, ants were not systematically inventoried in the recently completed inventory of biological diversity in Massachusetts (BioMap: NHESP 2001). During a study of prey capture by the northern pitcher plant *Sarracenia purpurea* L. (Ellison and Gotelli unpublished data) at Hawley Bog in northwestern Massachusetts, we found that the dominant prey of this carnivorous plant were ants (see also Creswell 1991, Newell and Nastase 1998). The most common ant species was *Myrmica lobifrons* Pergande, a boreal bog specialist (Francoeur 1997) previously unrecorded from Massachusetts. To determine the extent of this species in Massachusetts, and to document ant species diversity in pitcher-plant bogs of the state, we conducted a state-wide inventory of the ant fauna of Massachusetts pitcher-plant bogs in 1999 and 2000.

This inventory also gave us the opportunity to test hypotheses regarding causes of ant species richness among Massachusetts bogs. In a parallel study, we had hypothesized that ants of bogs would be a subset of generalist ants that occurred more commonly in surrounding forests (Gotelli and Ellison 2002b). Instead, we found that bog ant communities are not a subset of forest ant communities but are composed of an identifiable, and often distinct, set of species. Across New England, species richness of ants in both bogs and surrounding forests is significantly associated with latitude (more species in the south) and vegetation composition (Gotelli and Ellison 2002b). However, in our previous study we did not examine patterns of species composition or richness at smaller spatial scales, such as within a single state (i.e., a narrow band of latitude). In the course of this study we looked at determinants of species richness among ants of Massachusetts bogs in more detail.

We examined two broad hypotheses concerning species richness of ants in Massachusetts bogs. First, we tested the hypothesis that the overall pattern of diversity of ant species among these bogs has a "nested subset structure." A nested subset structure of occurrences is one in which the taxa present in species-poor assemblages are also found in increasingly species-rich assemblages (Patterson and Atmar 1986). Such a pattern can reflect either the differential dispersal ability of taxa (Lomolino 1996) or their extinction in an orderly sequence (Wright et al. 1998). Conservation biologists often make use of nested structures in determining how to prioritize areas for conservation (Honnay et al. 1999). Areas of high diversity or unique (non-nested) assemblages are often the first ones targeted for protection.

Second, we tested the hypotheses that ant species richness in any given bog can be predicted from: 1) regional-scale variables (mainland vs. Cape Cod vs. Islands; bog type, eco-region); 2) geographic variables

(latitude, longitude, elevation, area); 3) community-level variables including vegetation composition (species diversity, diversity of specific functional groups, and the presence of the ant predator *Sarracenia purpurea*); or 4) the micro-habitat variable of nutrient availability (one measure of site productivity). In general, species richness of any taxon is lower on peninsulas and islands than it is on the mainland (e.g., Rosensweig 1995; Taylor 1987a, 1987b). Thus, we hypothesized that species richness of ants would be higher in mainland bogs than in bogs on Cape Cod, Martha's Vineyard, or Nantucket. At regional and community-wide scales, ant species richness has been associated with: geographic variables including latitude and elevation (Gotelli and Ellison 2002b); vegetation composition (Gotelli and Ellison 2002b, Morrison 1998) or productivity (Kaspari et al. 2000, Majer 1983); soil type (Peck et al. 1998); disturbance regime (Feener and Schupp 1998, Kaspari 1996, King et al. 1998); and the presence of non-native ant species (Gotelli and Arnett 2000, Holway 1998, and Porter and Savignano 1990). Because soil type and disturbance frequency are similar among bogs, and because non-native ants are unknown from these bogs and uncommon in New England<sup>1</sup>, we only tested the hypotheses that ant species richness is dependent on geography, vegetation, and nutrients.

## METHODS

### Site Selection

We sampled 18 bogs in Massachusetts during the summers of 1999 and 2000 (Table 1, Fig. 1). Sites were selected in consultation with the staff of the Massachusetts Natural Heritage and Endangered Species Program and the Massachusetts chapter of The Nature Conservancy. Primary criteria for selection were high quality, relatively undisturbed bogs (Kearsley 1999), with populations of the northern pitcher plant *Sarracenia purpurea*. We sampled bogs in a majority (9 of the 13) of ecological sub-regions of the state. We also sampled all five bog types (kettle hole, pond margin, stream headwaters, stream side, or valley bottom) that are present in Massachusetts (Kearsley 1999).

### Site Characteristics

At each site, latitude, longitude, and elevation (meters above sea level) in the center of the bog were determined using a Trimble Global Positioning System unit (Trimble Instruments, Sunnyvale, CA). Subsequently, digital aerial photographs were obtained from MassGIS<sup>2</sup> for each bog. When digital photographs were unavailable (3 sites), we

<sup>1</sup><http://www.sandiego.edu/ants>

<sup>2</sup><http://www.state.ma.us/mgis/massgis.htm>

<sup>3</sup><http://edc.usgs.gov/>

Table 1. Physical and geographic characteristics of bogs sampled for ant diversity. Code is used elsewhere to abbreviate bog names; bog type follows Kearsley (1999); area of the bog mat is in m<sup>2</sup>; elevation is in above sea-level; both Nature Conservancy (TNC) and Massachusetts (NHESP) eco-regional classifications are given; concentrations of phosphate (PO<sub>4</sub>-P), ammonium (NH<sub>4</sub>-N) and calcium (Ca) are in mg/L; pitcher-plant density (*Sarracenia*) is per m<sup>2</sup>.

Site	Code	Bog type	Area	Elevation	Ecoregion						<i>Sarracenia</i>
					TNC	NHESP	pH	PO <sub>4</sub> -P	NH <sub>4</sub> -N	Ca <sup>2+</sup>	
<b>Mainland sites</b>											
Clayton Bog	CB	Kettlehole	73120	210	221Ae	58b	3.90	1.03	0.71	8.36	0.64
Otis Bog	OB	Pond margin	89208	491	M212Cc	58d	3.61	0.03	0.36	13.30	14.08
Hawley Bog	HAW	Stream headwaters	36813	543	M212Cc	58c	5.32	0.38	0.19	22.50	7.52
Round Pond Bog	RP	Pond margin	10511	78	221Af	59a	4.25	0.05	1.47	11.20	0.48
Arcadia Bog	ARC	Kettlehole	1190	95	221Af	59b	3.80	0.04	0.17	1.43	1.28
Swift River Bog	SWR	Kettlehole	19699	121	221Af	59b	3.76	0.05	0.24	1.90	4.16
Bourne/Hadley Bog	BH	Valley bottom	105369	274	M212Bd	58g	6.56	0.26	0.74	14.40	8.96
Lake Jones Bog	WIN	Stream headwaters	84235	323	M212Bd	58g	4.49	0.40	0.19	4.24	8.16
Quag Pond Bog	QP	Pond margin	40447	335	M212Bd	58g	3.75	1.76	0.16	9.85	3.52
Chockalog Pond Bog	CKB	Pond margin	7422	152	221Ag	59c	3.39	0.05	0.85	23.00	0*
Ponkapoag Bog	PK	Pond margin	491189	47	221Aj	59c	3.57	0.07	0.21	6.80	0.8
Halls Brook Cedar Swamp	HBC	Stream headwaters	11760	8	221Ac	59e	4.11	0.07	0.20	13.00	5.44
<b>Cape Cod site</b>											
Shankpainter Ponds	SKP	Valley bottom	55152	1	221Ab	59f	3.57	0.06	0.28	11.7	4.64
<b>Island sites</b>											
Arethusa Bog	AB	Streamside	2598	5	221Ab	59f	4.21	0.03	0.21	4.01	0†
Cranberry Bog	VOLF	Kettlehole	88427	29	221Ab	59f	4.47	0.27	0.85	7.92	0†
Schmitt Bog	SCB	Streamside	533	17	221Ab	59f	4.69	0.39	0.39	10.22	2.72‡
Taupshwa Bog	TAB	Kettlehole	16689	6	221Ab	59f	3.92	0.06	0.18	3.68	0†
Donut Pond Bog	DON	Kettlehole	8740	7	221Ab	59f	3.88	0.06	0.41	4.51	8.48

\* *Sarracenia* only grew on the margins of Chockalog Pond Bog, not in the ant collection area.

† No *Sarracenia* were present on Martha's Vineyard at Arethusa Bog, Cranberry Bog, or on Nantucket at Taupshwa Bog. The Donut Pond population on Nantucket is one of two known populations on the island (pers. comm Karen Combs-Beattie, Nantucket Conservation Foundation).

‡ The *Sarracenia* population at Schmitt Bog may have been artificially established, although there are no historical records of such plantings. It is the only known population of *Sarracenia* on Martha's Vineyard (pers. comm. T. Simmons, Massachusetts Natural Heritage and Endangered Species Program).

scanned and digitized USGS-EROS<sup>3</sup> photographic prints. Aerial photographs were used to construct a set of shape files in a geographic information system (using Arc-View GIS 3.2, ESRI, Redlands, CA), from which we calculated bog area. The geographic distribution of our samples is shown in Figure 1, and additional site characteristics are given in Table 1.

### Ant Collection

We used standard methods for collection of ants: pitfall traps, tuna fish baits, and vegetation inspection sampling (Anderson 1997, Bestelmeyer et al. 2000, Gotelli and Arnett 2000, Wang et al. 2001). In the center of the bog mat at each bog, we established a 5 x 5 grid of 25 pitfall traps spaced 2 m apart (total sample area = 64 m<sup>2</sup>). Each pitfall trap consisted of a flagged 95 mm diameter plastic cup, filled with 20 mm of dilute soapy water, and buried so that the upper lip of each trap was flush with the surface of the *Sphagnum*. Traps were set during dry weather and left in place for 48 hours. At the end of this sampling period, the trap contents were collected and fixed in the field in 95% EtOH.

At each mainland site, two complete ant surveys of each grid at each bog were conducted, separated by approximately 42 days. The replicate survey was conducted to determine if there were any temporal differences in ant composition at the sites. These surveys were carried out between 2 June 1999 and 29 August 1999. Because we

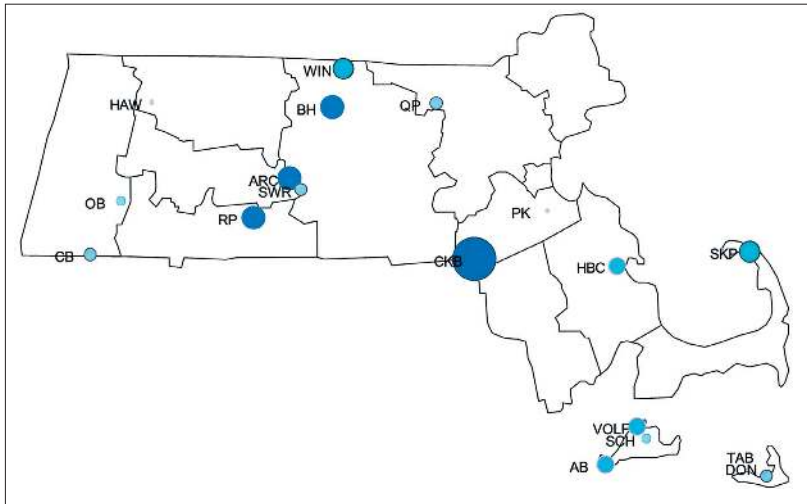


Figure 1. Map of Massachusetts illustrating locations of the 18 bogs sampled during the summers of 1999 and 2000. Abbreviations for site names are given in Table 1. Size and shading of symbols are proportional to species richness at each site. Total species richness at each site is given in Figure 2.

observed no systematic differences in ant faunas sampled on different dates at a given mainland site, we sampled the island sites only once (27–31 July 2000).

After each pitfall trap survey was completed, we removed the traps, refilled the holes with peat, and set out a tuna fish bait station consisting of 50 g of tuna placed on a 12.5 x 7 cm index card. Baits were allowed to attract and accumulate ants for 1 hour in the middle of the day and representative individuals were sampled with a suction aspirator. Approximately 3 minutes were spent sampling each tuna bait. After tuna-baiting, we actively searched each grid for 1 hour and hand-collected any ants that were found on the substrate, on the *Sphagnum* surface, or on low-growing vegetation. No attempt was made to locate ant colonies so we discuss only presence or absence of ant species, not their abundances (cf., Bestelmeyer et al. 2000). Rarefaction analysis (Gotelli and Graves 1996) showed that our estimates of species richness were not biased by abundance of the different species in our pitfall traps (Gotelli and Ellison 2002b).

This sampling method has the advantage that samples were standardized across sites and were focused on sections of the bogs with similar vegetation (bog centers, open *Sphagnum* mats). Thus we can directly compare species density (species per unit area) across sites. On the other hand, for larger bogs, the relative proportion of the bog area that was sampled was less than that sampled in small bogs. As a result, we may have missed rare species in large bogs with more heterogeneous habitats. However, by simultaneously sampling vegetation, we were able to account for the relatively small effects of variation in vegetation composition on ant species richness in these bogs (see RESULTS, Predictors of Species Richness, *Vegetation*, below).

All ants were counted and identified to species. Stefan Cover (Harvard University, Museum of Comparative Zoology [MCZ]) and André Francoeur (Université du Québec à Chicoutimi) confirmed our species identifications. Nomenclature for the genus *Myrmica* follows the unpublished classification of André Francoeur. Voucher specimens were deposited at the MCZ and with A. Francoeur.

### **Vegetation Sampling**

We recorded the plant species that occurred in 50 x 50 cm square quadrats centered on each pitfall trap ( $N = 25$  samples per site). Plant identification and nomenclature follows Gleason and Cronquist (1991). For purposes of analysis, we also classified each plant species into one of five functional groups: trees, shrubs, forbs, graminoids (grasses, rushes, sedges), or mosses. We did not distinguish among species of mosses (*Sphagnum* or others). Vegetation was sampled in July, the peak of the growing season. We are confident that we recorded the vast majority of

both early and late emerging plants. We also counted the number of pitcher plants, in order to test the hypothesis that pitcher-plant density affects ant species composition through selective predation.

### **Nutrient Availability**

After sampling vegetation we collected five pore-water samples at randomly chosen locations within each 64 m<sup>2</sup> sampling area. Fifty-ml plastic centrifuge tubes were pushed into the *Sphagnum* surface and they filled with water within 15 seconds. Samples were kept on ice in a cooler and returned to the lab within 48 hours for analysis. Concentrations of ammonium (NH<sub>4</sub>-N) and phosphate (PO<sub>4</sub>-P) were measured spectrophotometrically (APHA 1985) using EPA standard reagents (Hach Chemicals, Loveland, CO). Calcium was measured with an ion-sensitive electrode (Orion, Beverly, MA), and pH was measured with a pH electrode (Orion, Beverly, MA).

### **Data Analysis**

Distribution of ants was summarized in a presence-absence matrix (Fig. 2). This matrix allows for an initial visual and quantitative assessment of common and rare species. Occurrence data were compared with information on regional distribution of these species available in published (e.g., Creighton 1950, Gotelli and Ellison 2002b, and MacKay 2000) and unpublished sources (pers. comms. S. Cover and A. Francouer).

We tested the presence-absence matrix for a nested subset structure using the method of Atmar and Patterson (1993). We used their  $T$  (matrix “temperature”) statistic, which provides a standardized measure of matrix disorder (Wright et al. 1998). In a perfectly nested matrix,  $T = 0$ , whereas in a system where all species occur at random (in a completely disordered state),  $T = 100$ . The statistical significance of the observed  $T$  value was determined by Monte Carlo simulation using the Nestedness Temperature Calculator (Atmar and Patterson 1995). Five thousand simulations were done for each test. Atmar and Patterson’s  $T$  statistic is well-correlated with other measures of nestedness that have been proposed in recent years (see review by Wright et al. 1998).

Associations between ant species richness and regional-level variables (mainland vs. Cape Cod vs. Islands, bog type, ecoregion) were tested using the Kruskal-Wallis rank-sum test (a non-parametric test analogous to ANOVA). Relationships between ant species richness and geography, vegetation, and nutrients were first explored using simple pair-wise correlations. Data were transformed when necessary to meet the assumptions (normally distributed residuals, equal variances) of this parametric test.

An overall predictive model of the relationships between these variables and ant species richness was developed using stepwise multiple

regression (S-Plus version 6.0, Insightful Corp., Seattle, WA). We used this method to determine which independent variable or variables explained a significant component of the variation in total species richness of ants ( $\log_{10}$ -transformed). Prior to entering variables into the stepwise regression procedure, the independent variables were screened for multicollinearity, the linear correlations among the predictor variables (Montgomery and Peck 1982). Only seven uncorrelated variables (latitude, longitude,  $\log_{10}$ (bog area),  $\log$ -transformed concentrations of ammonium and phosphorus, and species richness of trees, shrubs, and graminoids) were entered into the stepwise regression model. Model selection was done using Efron's method (Montgomery and Peck 1982), and the best-fit model was determined by minimizing residual sums of squares and Akaike's Information Criterion (AIC) (Burnham and Anderson 1998).

## RESULTS

### Species Distribution Patterns

*Distribution.* We identified 26 species among the 7,864 individual ants collected in 1999 and 2000 (Fig. 2). The most common species encountered, at 17 of the 18 bogs, was the bog specialist *Myrmica lobifrons*. This species ranges throughout northern North America, where it nests in *Sphagnum* (Francouer 1997), but our records of *M. lobifrons* are the first for Massachusetts (pers. comm. A. Francouer).

Two of the three species of *Leptothorax* that we collected, *L. ambiguus* and *L. curvispinosus*, are not listed in modern records from Massachusetts in MacKay (2000), although older papers report their occurrence there (Alloway 1980; Sturtevant 1925, 1931). *Leptothorax ambiguus* nests predominantly in wetlands (MacKay 2000). *Leptothorax curvispinosus* reaches the northern limit of its range in Massachusetts (MacKay 2000). We also encountered two boreal species, *Camponotus herculeanus* and *Formica neorufibarbis*, near the southern limit of their ranges. Three of the species collected on Nantucket, *Myrmica lobifrons*, *M. sculptilis*, and *Aphenogaster rudis*, are new records for that island (cf. Johnson 1930).

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Figure 2. Maximally-packed (sensu Atmar and Patterson 1995) ant presence-absence matrix illustrating nested subset structure. Shading indicates the species is present. Orientation of this figure is 90° different from a normal nestedness diagram, which has species entered in columns and sites entered in rows. Abbreviations for sites as in Table 1. The Cape Cod site is indicated by a single-lined box, and the Islands sites are indicated by double-lined boxes. Nomenclature for *Myrmica* follows André Francoeur's unpublished revision of the genus (pers. comm. A. Francoeur). An asterisk (\*) indicates a forest-ant species.



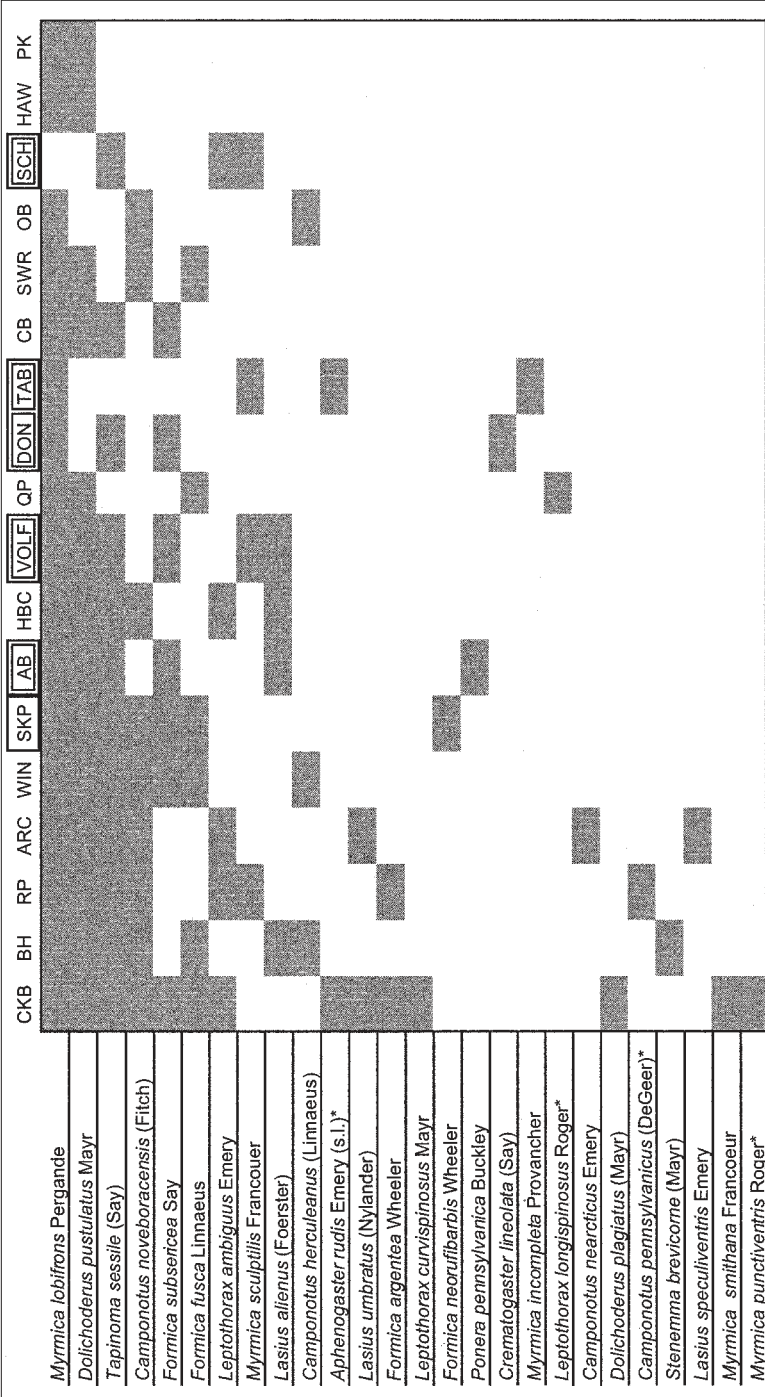


Figure 2. Legend on previous page.

We also collected a few individuals of four species that are much more common in the forests surrounding the bogs (Gotelli and Ellison 2002b). Three of these species—*Camponotus pennsylvanicus*, *Leptothorax longispinosus*, and *Myrmica punctiventris*—were represented by single specimens, each from a single bog, and another—*Aphenogaster rudis*—was represented by two specimens, one each from two bogs (Fig. 2). Their occurrence in our bog collections most likely reflects long-distance foraging by workers.

The remaining 19 species we collected in the bogs are generalists that tend to favor open habitats over heavily wooded ones. Two of these species, *Dolichoderus pustulatus* and *Tapinoma sessile*, are widespread in North America, tend to occur in open habitats, and occurred in most of the bogs sampled. The remaining species were represented in between one and nine bogs (Fig. 2).

*Nestedness.* Species distribution patterns were significantly nested ( $T = 15.1$ ,  $P = 1.6 \times 10^{-7}$ ; Fig. 2). This pattern is apparent by the high proportion of zeros in the lower right-hand diagonal of the presence-absence matrix (Fig. 2). This pattern is consistent for all the sites combined and for the mainland sites considered separately ( $T = 10.3$ ;  $P = 8.25 \times 10^{-7}$ ). The nested pattern also persists when the four forest ant species are removed from the analysis ( $T = 14.3$ ;  $P = 1.29 \times 10^{-7}$ ). Considered alone, the species distribution pattern of the Cape Cod and island sites is not nested ( $T = 44.3$ ;  $P = 0.69$ ).

The ordering of species (rows) and sites (columns) in Figure 2 best illustrates the nested pattern of species distribution because the matrix is “maximally packed” (Atmar and Patterson 1995). In this maximally packed matrix, the species ordering reflects increasing rarity (top to bottom). For bogs of Massachusetts, the ordering of sites reflects “longitudinal spread,” with sites in central Massachusetts occurring first, followed predominantly by the sites of Cape Cod and the Islands, and then the sites in the Berkshires Mountains. Overall, species richness was highest in bogs of the Connecticut River Valley and on the border between Massachusetts and Rhode Island.

### Predictors of Species Richness

*Regional variables.* Ant species richness did not differ significantly among locations (mainland, Cape Cod, Islands;  $P = 0.58$ , Kruskal-Wallis rank-sum test), bog types ( $P = 0.83$ , ANOVA), or ecological subregions ( $P = 0.58$ , ANOVA). The lack of associations between ecological subregion and ant species richness, and between bog type and ant species richness, persists when only the mainland data are considered ( $P = 0.88$ , and  $P = 0.89$ , respectively).

*Geography.* At the state level, ant species richness was not correlated with any of the geographic variables (latitude, longitude, eleva-

tion, or bog mat area;  $P > 0.15$ , all variables). This result also rules out one possible cause of the nested subset pattern described above: differential extinction of species caused by available area. Differential extinction through other causes (e.g., habitat fragmentation) could still have occurred. The lack of correlation of ant species richness with geographic variables is also consistent with the hypothesis that observed patterns of ant distribution in these bogs followed from different colonization histories of the bogs by the different taxa.

*Vegetation.* Across all the bogs, we identified 78 plant species distributed among trees (7 species), shrubs (15 species), forbs (41 species), and graminoids (15 species). Ant species richness was not associated ( $P > 0.30$ ) with total plant species richness or with species richness of any of the functional groups except for species richness of trees. Ant species richness was positively correlated with number of tree species in the plot ( $r = 0.53$ ,  $P = 0.02$ ; Fig. 3). Red maple (*Acer rubrum* L.) seedlings or saplings were present in 14 of the 18 bogs. Other tree species included: white pine (*Pinus strobus* L.), pitch pine (*Pinus rigida* Miller), black spruce (*Picea mariana* [Miller] BSP), Atlantic white cedar (*Chamaecyparis thyoides* [L.] BSP), tamarack (*Larix laricina* [Duroi] K. Koch), and gray birch (*Betula populifolia* Marsh). All of these species were present only as seedlings or small saplings except at Halls Brook Cedar Swamp (HBC), which had mature black spruce, Atlantic white cedar and gray birch, and Lake Jones Bog (WIN), which had mature black spruce. Relationships between ant species richness and plant species richness also were not influenced by differences in plant species richness among mainland, Cape Cod, and island habitats.

Density of pitcher plants at our sites ranged from 0 to 15 plants/m<sup>2</sup> (Table 1). However, there was no correlation between pitcher-plant density and ant species richness ( $P = 0.35$ ).

*Nutrients.* Ant species richness also was correlated positively with the concentration of ammonium (NH<sub>4</sub>) in the pore water of the bogs ( $r = 0.47$ ,  $P = 0.05$ ; Fig. 3). Ant species richness was not correlated with pore water pH or with the measured concentrations of calcium or phosphate ( $P > 0.4$ , all variables). Concentrations of these nutrients were correlated neither with each other ( $P > 0.3$ , all possible comparisons) nor with pH ( $P > 0.25$ , all comparisons). Similarly, nutrient concentrations and pH values were not correlated with species richness of any of the plant functional groups. These relationships also were not influenced by differences in pore-water chemistry among mainland, Cape Cod, and island habitats.

*Step-wise multiple regression.* In agreement with the exploratory correlation analyses, the stepwise regression procedure identified only tree species richness and pore-water concentration of NH<sub>4</sub> as significant predictors of ant species richness among the 18 bogs sampled. The

predictive equation was:

$$\log_{10}(\text{antS}) = 0.72 + 0.47 \times \log_{10}(\text{treeS}) + 0.31 \times \log_{10}[\text{NH}_4]$$

where antS is the number of ant species in each bog, treeS is the number of tree species in each bog, and  $[\text{NH}_4]$  is the concentration of ammonium in the pore water. This model explained 46% of the variation among bogs in ant species richness, and was significant at  $P = 0.01$ .

## DISCUSSION

This study, the first comprehensive survey of the ants of Massachusetts bogs, is notable for several reasons. First, we have expanded the state list of ants by one species, and added three additional species to the list of those documented on Nantucket. Areas identified in BioMap

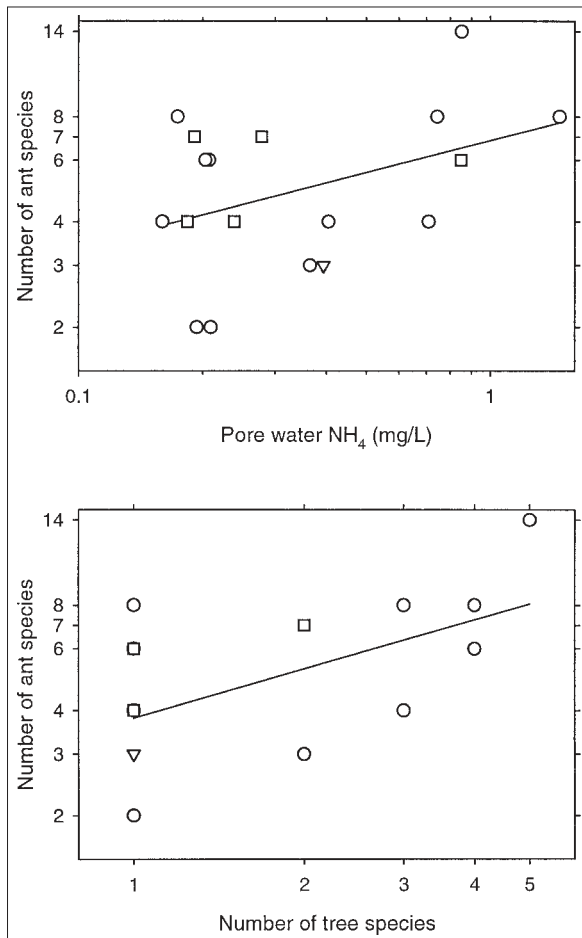


Figure 3. Associations between ant species richness and pore-water ammonium (top panel), and tree species richness (bottom panel). The lines are best-fit linear regressions on log-transformed data (note double logarithmic scales on both panels). Different symbols indicate different locations in the state: mainland sites (circles), Cape Cod site (inverted triangle), island sites (squares).

(NHESP 2001) as core areas of unique biological diversity in the state, notably the Connecticut River Valley and the Massachusetts-Rhode Island border, are also areas where we found the highest species diversity of ants in bogs. However, ants have not been ranked for rarity or population viability<sup>4</sup>, and acidic *Sphagnum* bogs were not inventoried in BioMap (NHESP 2001).

Second, we collected three boreal species (*Camponotus herculeanus*, *Formica neorufibarbis*, *Myrmica lobifrons*) that are near their southern range limits (Francouer 1997) and one (*Leptothorax curvispinosus*) at its northern limit. Careful monitoring of the distribution of these species would be valuable as northward shifts in their distributions could be good indicators of regional climatic warming (cf. Parmesan 1996). Regional warming (New England Regional Assessment Group 2001) could also result in new species colonizing these bogs, shifts in the distributions of existing species, or differential extinction engendered by novel interspecific interactions among ants in these bogs (cf. Gotelli and Ellison 2002a). Such changes could be manifested in significant changes in the observed nested structure of species among these bogs.

Third, the pattern of nested subsets observed in the species presence-absence matrix suggests some conservation priorities. Two of the highest diversity sites, Chockalog Pond Bog (14 species) and Round Pond Bog (8 species) are in areas with substantial development pressure, and are currently unprotected. Because ants are good indicators for the presence of other invertebrates (Alonso 2000, Lawton et al. 1998, Majer 1983), our results also suggest that these sites, along with the two other high-diversity sites (Bourne-Hadley Ponds and Arcadia Bog) should be carefully surveyed for other unique arthropods. Ant faunas of the bogs of Cape Cod and the Islands did not show a clear pattern of nested subsets. This result highlights the relative uniqueness of their ant assemblages, and points to these already protected sites, and other island bogs, as high priorities for continued monitoring.

The ant fauna of Massachusetts bogs is dominated by a small number of specialists of bogs and open areas. In this way, it resembles the species distribution pattern of ants in Finnish bogs (Vepsäläinen et al. 2000), the only other bogs for which the ant faunas are documented. Until the ant faunas of other bogs are studied in similar detail, however, there is no way to know if this pattern applies to bogs in general. Nevertheless, there are similarities between correlates of species richness in bogs and causes of species richness of ants in habitats where ants have been studied more extensively. For example, ant species richness in forests and grasslands increases with increasing heterogeneity of

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<sup>4</sup><http://www.natureserve.org>

vegetation (Bestelmeyer and Wiens 2001, Gotelli and Ellison 2002b, Morrison 1998) and density of trees (Weseloh 1995). In Massachusetts bogs, ant species richness increased with increasing diversity of tree seedlings and saplings, which provides a new layer of vegetational structure in these otherwise non-forested bogs. In upland habitats, ant species richness increases with several measures of productivity (e.g., Kaspari et al. 2000, Majer 1983). In Massachusetts bogs, ant species richness is associated with availability of  $\text{NH}_4$ , and nitrogen is the primary nutrient limiting vegetation productivity in bogs (Bedford et al. 1999). This is one of the first indications that ant species richness responds to nutrient availability per se, rather than to indirect measures of nutrients such as productivity or composition of vegetation that are associated with increased nutrients.

Pitcher-plant bogs are unique habitats scattered across the New England landscape, and unlike their counterparts in Canada and Scandinavia, they have not yet been heavily mined for peat or drained for forestry. While they are well-known for their unique assemblages of carnivorous plants, this study shows that bogs also should be protected for their distinctive ant communities. Ants are also known to be good indicators for the diversity of other invertebrate species (Alonso 2000, Lawton et al. 1998). Further inventories of ants in other habitats in Massachusetts and throughout New England could suggest additional focal areas for conservation and protection.

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