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 m²; elevation is in m above sea-level; both Nature Conservancy (TNC) and Massachusetts (NHESP) eco-regional classifications are given; concentrations of phosphate (PO₄-P), ammonium (NH₃-N) and calcium (Ca) are in mg/L; pitcher-plant density (Sarracenia) is per m².

					Ecor	Ecoregion					
Site	Code	Bog type	Area	Elevation	TNC	NHESP	$^{\mathrm{pH}}$	$\mathrm{PO}_{4}\text{-}\mathrm{P}$	NH_4-N	Ca^{2+}	Sarracenia
Mainland sites											
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	28d	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	95.9	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	08.9	8.0
Halls Brook Cedar Swamp	HBC	Stream headwaters	11760	∞	221Ac	59e	4.11	0.07	0.20	13.00	5.44
Cape Cod site											
Shankpainter Ponds	SKP	Valley bottom	55152	-	221Ab	365	3.57	90.0	0.28	11.7	4.64
Island sites											
Arethusa Bog	AB	Streamside	2598	S	221Ab	59f	4.21	0.03	0.21	4.01	+0
Cranberry Bog	VOLF	Kettlehole	88427	29	221Ab	39f	4.47	0.27	0.85	7.92	+0
Schmitt Bog	SCH	Streamside	533	17	221Ab	59f	4.69	0.39	0.39	10.22	2.72‡
Taupshwa Bog	TAB	Kettlehole	16689	9	221Ab	59f	3.92	90.0	0.18	3.68	+0
Donut Pond Bog	DON	Kettlehole	8740	7	221Ab	59f	3.88	90.0	0.41	4.51	8.48

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

^{*} No Sarracenia

scanned and digitized USGS-EROS³ 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 m²). 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

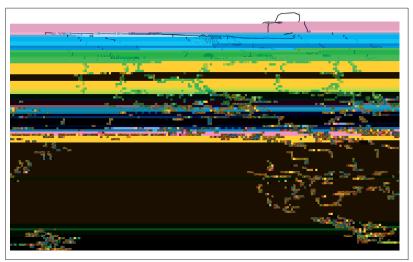


Figure 1. Map of Massachusetts illustrating locations of the 18 bogs sampled during the summers of 1999 and 2000. Abbreviations for site names are given in Table 1. Size and shading of symbols are proportional to species richness at each site. Total species richness at each site is given in Figure 2.

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

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 $\rm m^2$ 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 ($\rm NH_4$ -N) and phosphate ($\rm PO_4$

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 (log₁₀-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, log₁₀(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 Efroymson'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 andL. curvispinosis, 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).

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.

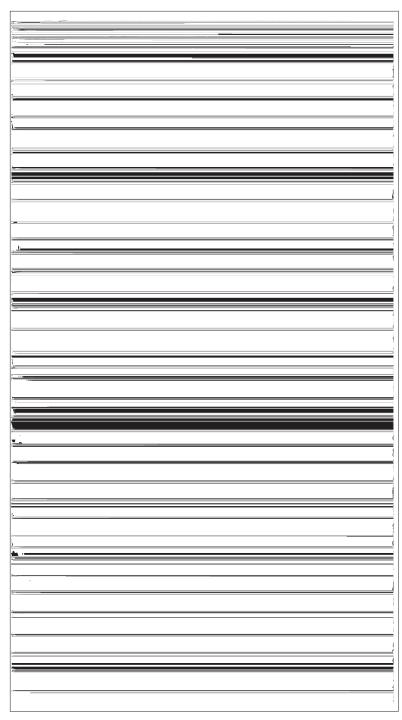


Figure 2. Legend on previous page.

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 SA.B 0.09l0bCr smegu467 1pj0.32t0w(ssl4Tj-26.7627Tsee tified 66 7

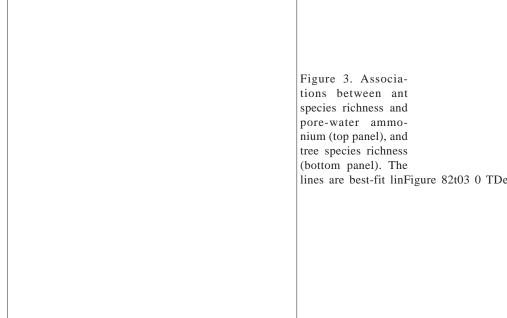
predictive equation was:

$$log_{10}(antS) = 0.72 + 0.47 \times log_{10}(treeS) + 0.31 \times log_{10}[NH4]$$

where antS is the number of ant species in each bog, treeS is the number of tree species in each bog, and $[NH_4]$ 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



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 NH₄, 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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