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BIOGEOGRAPHY AT A REGIONAL SCALE: DETERMINANTS OF ANT SPECIES DENSITY IN NEW ENGLAND BOGS AND FORESTS

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Abstract. We examined species density gradients of ants of New England in 22 ombrotrophic bogs and their surrounding forests. We tested the hypothesis that species density was correlated with large-scale geographic variables (latitude, longitude, elevation) and small-scale site variables (habitat area, vegetation composition, light availability). Species density was consistently higher in forests than in bogs. Ant species density measured in three other New World studies yielded similar results, with steeper diversity slopes in closed canopy vs. open habitats. In New England bogs and forests, latitude was the single most important predictor of species density, even though the latitudinal span of the entire study region was less than three degrees. Diversity patterns documented in our study of mid-latitude ant communities are similar to those seen in studies spanning tropical and temperate habitats. Species density of forest ants was associated strongly with latitude, elevation, light availability, and vegetation composition. Species density of bog ants was less predictable and was correlated only with latitude and vegetation. Overall, our results suggest that species–energy relationships are important at regional spatial scales. Explanations for the latitudinal gradient in ant species density may not depend on unique differences between tropical and temperate communities, but could operate at all latitudes.

Key words: ant species richness; bog habitat; forest habitat; habitat complexity; latitudinal gradient; New England; New World ants; productivity gradients; species density; species–energy relationship; vegetation structure.

INTRODUCTION

Latitudinal gradients in species richness remain one of the most widely documented, but least understood, phenomena in biogeography (Rosenzweig 1995, Taylor and Gaines 1999, Colwell and Lees 2000). At the continental scale, latitudinal variation in species richness is associated with parallel gradients in net primary productivity (Currie and Paquin 1987, Kaspari et al. 2000) and habitat structure (Kerr and Packer 1997). However, understanding the causes of geographic gradients at large spatial scales is difficult because of the influence of historical and evolutionary processes (Ricklefs and Schluter 1993), the contribution of regional source pools (Cornell 1999), and, for animal taxa, the influence of taxonomic composition and habitat structure of terrestrial vegetation (Huston 1994, 1999, Gross et al. 2000, O'Brien et al. 2000). Because local and regional effects can mask or amplify larger scale latitudinal patterns of species richness, new insights may be gained by examining latitudinal gradient patterns at regional scales (e.g., Graves 1991), rather than across a temperate–tropical gradient. Within a small latitudinal span, vegetation structure is more likely to be homogenous, and the source pool of potentially colonizing species is more likely to be similar at the two ends of the sampled region.

Ants are an ideal taxon for examining the latitudinal gradient in species richness because they are important terrestrial omnivores (Hölldobler and Wilson 1990) and because ant species richness varies widely among regions (Andersen 1997*a*, Longino and Colwell 1997, Kaspari et al. 2000). The control of ant species diversity is also sensitive to spatial scale (Andersen 1997*b*). At the continental scale, ant species richness is correlated with latitude (Kusnezov 1957, Cushman et al. 1993), productivity (Andersen 1992, Kaspari et al. 2000), and the presence of non-native species (Gotelli and Arnett 2000). At the regional and local scale, ant species richness is sensitive to plant cover and diversity (Morrison 1998), soil type (Peck et al. 1998), disturbance regime (Kaspari 1996, Feener and Schupp 1998), and the presence of non-native species (Porter and Savignano 1990, Holway 1998).

In this study, we used a standardized sampling regime to estimate ant species density (number of species/64 m^2) in 22 ombrotrophic bogs and adjacent forests of New England. This area encompasses a region of relatively homogenous habitat and spans only three degrees of latitude. We asked three questions with these

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differences in regional species pools can be discounted. Second, does the latitudinal gradient persist after statistically controlling for differences among sites in the composition of vegetation? If so, then the latitudinal gradient in species density cannot be attributed solely to correlations with habitat structure and complexity. Finally, how do patterns in our data compare with those from three other studies of ant species diversity in the New World (Jeanne 1979, Kaspari et al. 2000, Gotelli and Arnett 2000)? Such comparisons reveal generalities that cannot be discerned from individual studies.

MATERIALS AND METHODS

Field sampling

We sampled 22 high-grade, undisturbed bogs and their surrounding forests in Vermont, Massachusetts, and Connecticut (Appendix A). At each site, we sampled ants in bogs and forests using a standardized protocol that included pitfall traps, tuna fish baits, leaf litter samples, and hand-collection from vegetation; all ants were counted and identified to species (Appendix B). For an ''ant's-eye'' view of vegetation and light, we used small-quadrat surveys to quantify vegetation composition, and hemispherical canopy photography to estimate light availability (global site factor [GSF]) and leaf area index (LAI; Appendix B).

Statistical analyses

The response variable in all of our analyses was species density, the total number of species collected in the sampling grid (64 m^2) at each site. Measures of species density reflect both the underlying species richness of the community and the number of individuals collected or sampled (Gotelli and Colwell 2001). This problem may be especially acute in ant surveys, because ant catches are affected by trap design, local temperature conditions, and activity patterns of ants (Andersen 1991). We used rarefaction (Gotelli and Entsminger 2000) and multiple regression of pitfall ant abundances to ensure that the differences we detected in species density were not due solely to differences in the number of individual ants collected at each site (Appendix C). Because our sample size was relatively small ($N = 22$ sites) and the number of predictor variables in our multiple regression analysis was large (seven for bogs, eight for forests), we examined them carefully for multicollinearity and report their partial regression coefficients and regression diagnostics. Predictor variables were largely uncorrelated with one another (Appendix F), which increases the reliability of the final regression models.

We used principal components analysis (PCA) to derive plant species loadings for forest and bog habitats at each site (Appendix D). Corresponding scores for each habitat (PC axis 1 and PC axis 2; Appendix A) were entered as independent variables in stepwise multiple regression analyses. Ant species density was regressed on latitude, longitude, elevation, and plant composition. Analyses of bog ant species density also included bog area as a possible predictor variable. Analyses of forest species density also included LAI and GSF as possible predictor variables.

In a separate analysis, we compiled raw data from three other studies of latitudinal gradients in ant species density: Jeanne (1979), Gotelli and Arnett (2000), and Kaspari et al. (2000). In each of these studies, ant species density was measured in the field using standardized pitfall and baiting methods (Bestelmeyer et al. 2000) at multiple sites in the New World. We used an analysis of covariance with latitude as the covariate to ask two questions (1) Do the slopes of the latitude diversity curves differ significantly among the four studies (study × latitude interaction term)? (2) Do the slopes of the latitude diversity curves differ consistently between open and closed canopy habitats (habitat × latitude interaction term)? After conducting the overall ANCOVA, we calculated individual slopes for each of the regressions.

RESULTS

Forest and bog species density

In total, just over 10 000 individual ants were collected, 6163 of which came from pitfall traps. We identified 24 species of ants in nine genera from the bogs, and 37 species in 14 genera from surrounding forests (Appendix E). Species density per bog site averaged 4.9 ± 0.63 species/64 m^2 (mean $\pm$ 1 SE) with a range of 2–14 species, whereas species density per forest site averaged 9.2 ± 0.92 species/64 m^2 with a range of 4–18 species (matched pairs $t = 5.98$, df = 21, $P < 0.0001$). The bog ant fauna was dominated by *Myrmica lobifrons* and *Dolichoderus pustulatus*, and the forest ant fauna was dominated by *Aphaenogaster rudis* (s.1.), *Camponotus pennsylvanicus*, and *Leptothorax longispinosus*. Whereas *D. pustulatus* is a generalist that occurs in a variety of open habitats, *M. lobifrons* is a specialist of boreal bogs and other humid microsites (A. Francoeur, *personal communication*). Twenty-two species were common to both habitats, with two species collected only from bogs and 15 species collected only from forests. Our species list for forest sites is typical for New England forests (Jeanne 1979, Herbers 1989, Weseloh 1995).

Geographic gradients in ant species density

Species density of bog ants declined significantly ($P = 0.041$) with increasing latitude, and was marginally associated ($P = 0.081$) with vegetation composition. Only these two predictor variables, latitude and the second PC score for vegetation, emerged from the stepwise regression model for species density of bogs. These two predictor variables were uncorrelated ($r = -0.20$), and together explained 30% of the variance in species density of bog ants (Fig. 1a). Full regression diagnostics are reported in Appendix F.

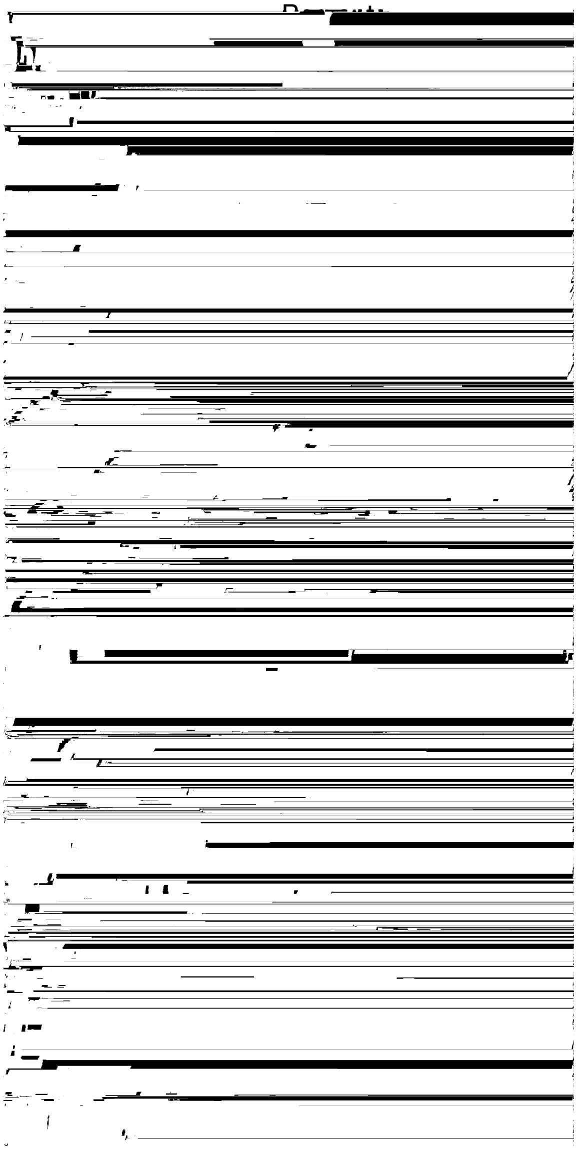

FIG. 1. Contour plots of ant species density (no. species/64 m^2) as a function of the two best predictor variables (identified by stepwise multiple regression) in bog and forest habitats. Elevation is measured as m a.s.l. (meters above sea level). For bog habitats, the final model was Bog Species Density = 62.652 − 1.343(latitude) − 0.742(Bog PC-2); r^2 = 0.302. For forest habitats, the final model was $\log_{10}$(Forest Species Density) = 7.40 − 0.132(latitude) − 0.007(elevation) + 0.031(Forest PC-1) + 0.037 (Forest PC-2) − 2.042(GSF) − 0.128(LAI); r^2 = 0.831 (LAI, leaf area index; GSF, global site factor). All regression coefficients were significant at P # 0.05 except Bog PC 2 (P = 0.081).

For forest ants, the stepwise multiple regression model identified six correlates of species density, two with positive coefficients (first and second PC scores for vegetation composition), and four with negative coefficients (latitude, elevation, GSF, and LAI). The two strongest predictors (largest F ratio to enter the model) were latitude and elevation. All of the regression coefficients were significant at $P < 0.05$ in the final model, which explained 83% of the variance in species density of forest ants (Fig. 1b). Full regression diagnostics are reported in Appendix F.

Comparisons with other studies

The analysis of covariance revealed significant heterogeneity in the slopes of the richness vs. latitude regressions (latitude

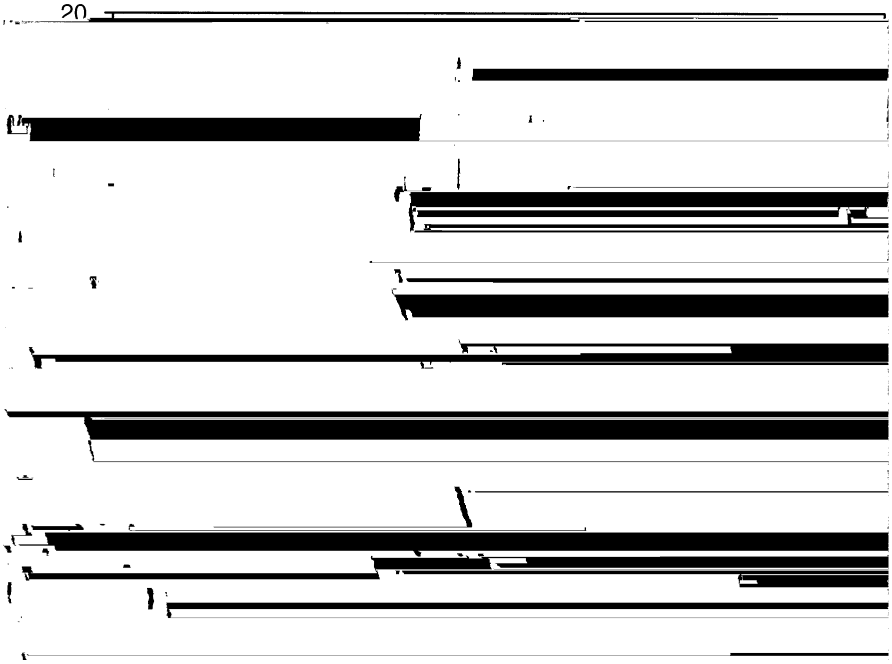

FIG. 2. Plot of ant species density vs. latitude in the current study (main plot), and in three other New World studies (Jeanne 1979, Gotelli and Arnett 2000, Kaspari et al. 2000) that span a much wider latitudinal range (inset plot). Best-fit regression lines are shown for ‘‘open’’ habitats (open symbols, dashed line) and ‘‘closed canopy’’ habitats (closed symbols, solid line).

though there was expected heterogeneity of regression slopes among studies, the latitudinal gradient of ant species density over a narrow span of mid-latitude sites is remarkably similar to the latitudinal gradient displayed from tropical to temperate regions. The abscissa of the graphs in Fig. 2 for our study (42–45°N) and

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LITERATURE CITED

Andersen, A. N. 1992. Regulation of ''momentary'' diversity by dominant species in exceptionally rich ant communities of the seasonal tropics. American Naturalist **140**:401–420.

Andersen, A. N. 1997*a*. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography **24**:433–460.

Andersen, A. N. 1997*b*. Using ants as bioindicators: multiscale issues in ant community ecology. Conservation Ecology **1**(1):8. [Online, URL: ⟨http://www.consecol.org/vol1/iss1/art8⟩.]

Bestelmeyer, B. T., D. Agosti, L. E. Alonso, C. R. F. Brandão, W. L. Brown Jr., J. H. C. Delabie, AND R. Silvestre. 2000. Field techniques for the study of ground-dwelling ants: an

Does solar energy control organic diversity? Butterflies, moths and the British climate. Oikos **48**:195–205.

Turner, J. R. G., J. J. Lennon, and J. A. Lawrenson. 1988. British bird species distributions and the energy theory. Nature **335**:539–541.

Weseloh, R. M. 1995. Forest characteristics associated with abundance of foraging ants (Hymenoptera: Formicidae) in Connecticut. Environmental Entomology **24**:1453–1457.

Wright, D. H. 1983. Species–energy theory: an extension of species–area theory. Oikos **41**:496–506.

APPENDIX A

A table presenting physical characteristics of the study sites is available in ESA's Electronic Data Archive: *Ecological Archives* E083-025-A1.

APPENDIX B

A description of sample methods is available in ESA's Electronic Data Archive: *Ecological Archives* E083-025-A2.

APPENDIX C

A description of statistical methods is available in ESA's Electronic Data Archive: *Ecological Archives* E083-025-A3.

APPENDIX D

A table presenting PCA loadings for vegetation data is available in ESA's Electronic Data Archive: *Ecological Archives* E083-025-A4.

APPENDIX E

A table of presence–absence matrices for bog and forest ants is available in ESA's Electronic Data Archive: *Ecological Archives* E083-025-A5.

APPENDIX F

Tables and descriptions of diagnostics for multiple regression analyses of geographic gradients in ant species diversity are available in ESA's Electronic Data Archive: *Ecological Archives* E083-025-A6.