

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 colo-

nizing 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 1997a, Longino and Colwell 1997, Kaspari et al. 2000). The control of ant species diversity is also sensitive to spatial scale (Andersen 1997b). 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 m²) 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 data. First, does species density correlate with latitude over such a narrow latitudinal span? If so, then explanations for the latitudinal gradient that depend on differential speciation rates in the tropics or historical

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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 m²) 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 re-

gressed 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 \times latitude interaction term)? (2) Do the slopes of the latitude diversity curves differ consistently between open and closed canopy habitats (habitat \times 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 m² (mean \pm 1 SE) with a range of 2–14 species, whereas species density per forest site averaged 9.2 ± 0.92 species/64 m² 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.l.), *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.

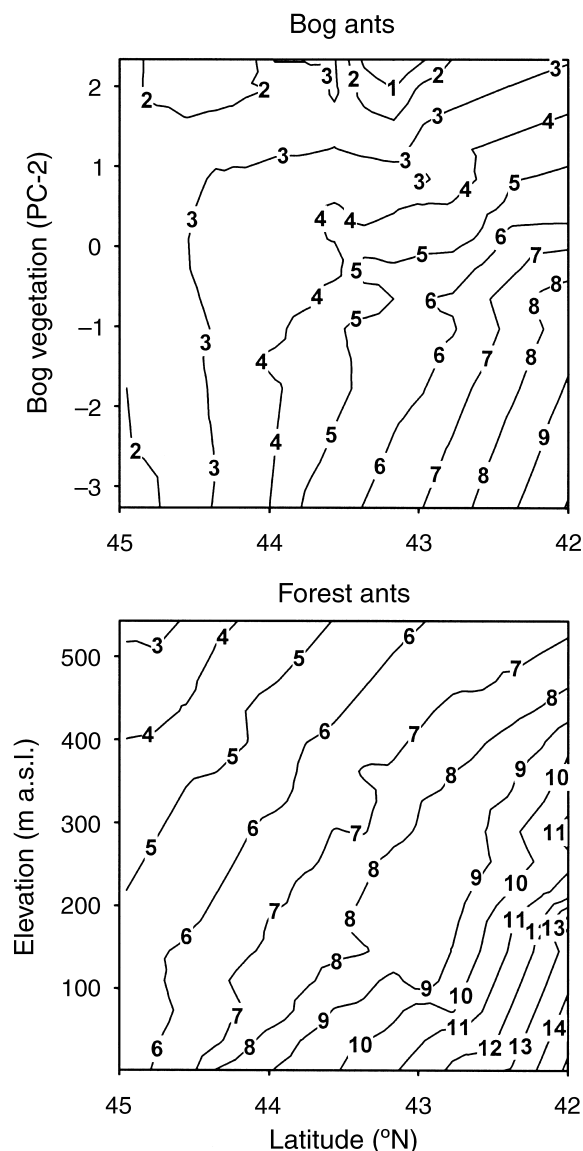


FIG. 1. Contour plots of ant species density (no. species/64 m²) as a function of the two best predictor variables (identified by stepwise multiple regression) in bog and forest habitats. Elevation is measured as m a.s.l. (meters above sea level). For bog habitats, the final model was Bog Species Density = 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 $P \leq 0.05$ 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 regres-

sion 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 \times study, $F = 4.7$, $df = 3$, 103, $P = 0.004$) for the current study compared to those of Jeanne (1979), Kaspari et al. (2000), and Gotelli and Arnett (2000). However, the analysis also revealed a consistent difference between the slopes calculated for open vs. closed-canopy habitats (latitude \times habitat, $F = 33.7$, $df = 1$, 103, $P < 0.0001$). In all studies, slopes were steeper for closed-canopy habitats (closed-canopy vs. open-habitat slopes: current study, -2.34 vs. -1.14; Jeanne [1979], -0.98 vs. -0.34; Kaspari et al. [2000], -1.79 vs. 0.78; Gotelli and Arnett [2000] -0.88 vs. -0.60; Fig. 2).

DISCUSSION

The correlation between latitude and species density that has been documented on a continent-wide scale for many taxa, including ants, also emerges in our small-scale study of forest and bog ants (Fig. 2). In both forests and bogs, latitude is the most significant predictor of species density (Fig. 1). The result is noteworthy, because we statistically accounted for the contribution of many variables potentially correlated with latitude, including vegetation composition and light availability. Multi-collinearity among the set of predictor variables was minimal (Appendix F), which strengthens the result that latitude was the most important predictor variable. Moreover, the latitudinal span of our study was only three degrees (Appendix A), whereas many previous studies of regional species diversity have used single blocks that are 1×1 degree in size (McCoy and Connor 1980, Lyons and Willig 1999). Finally, the results are surprising because our samples were taken at a small spatial scale (64 m²). In spite of these limitations, the final model for forest ants is highly predictive. The number of species expected in a small forest plot can be accurately forecast with measures of latitude, elevation, light availability, and vegetation composition ($r^2 = 0.83$). For ants in adjacent bogs, the correlations are weaker; the final model incorporates fewer variables and it does not provide especially accurate predictions ($r^2 = 0.30$).

Although latitude was a significant predictor of species density in both bogs and forests, there were consistent differences in the patterns of species density in these two habitats. Forest plots supported more species, both at the local and regional scales, and the slope of the latitudinal diversity gradient was steeper for forest than bog habitats. Our comparative analysis suggests that these habitat differences are not specific to bogs, but are characteristic of open habitats in general. Al-

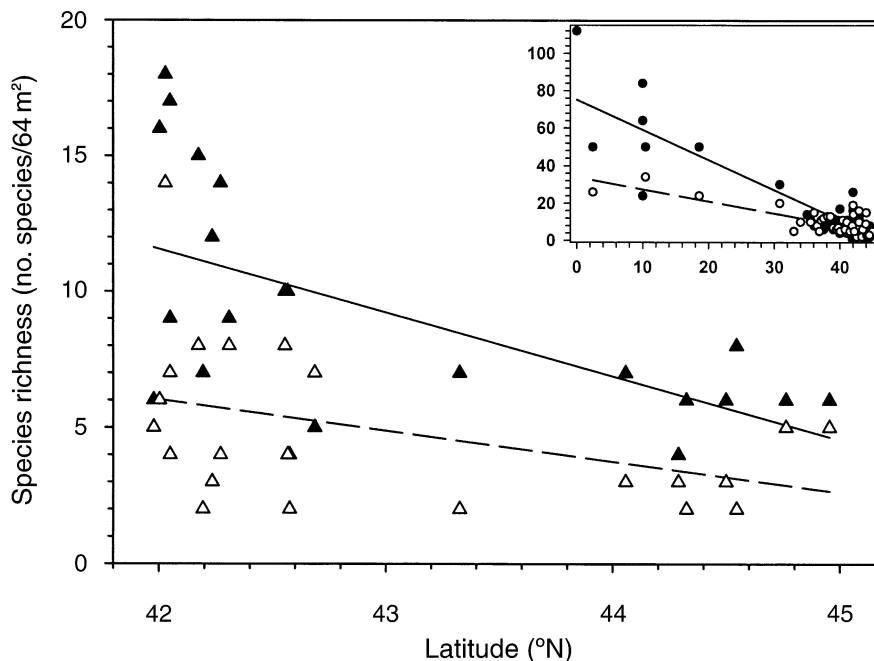


FIG. 2. Plot of ant species density vs. latitude in the current study (main plot), and in three other New World studies (Jeanne 1979, Gotelli and Arnett 2000, Kaspari et al. 2000) that span a much wider latitudinal range (inset plot). Best-fit regression lines are shown for "open" habitats (open symbols, 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 the set of four New World studies (0–45°N) could easily be interchanged. This apparent "self-similarity" in pattern suggests that the causes for the latitudinal gradient do not depend on idiosyncratic differences between temperate and tropical communities, but operate just as strongly within temperate communities (Scheiner et al. 2000).

Our results provide insight into the mechanisms that might be responsible for the latitudinal gradient in species diversity of ground-foraging ants. Explanations based on differential speciation rates in tropical vs. the temperate latitudes (Rohde 2001) are not supported, because the gradient in diversity persisted over a narrow latitudinal span (Fig. 2). Explanations based on the existence of different regional species pools (Cornell 1999) can be discounted because the species in our study were not segregated into distinct high- and low-latitude species pools (Appendix E). Similarly, our results do not support the idea that variation in habitat structure or complexity entirely accounts for the latitudinal gradient in species density. Ant species density is especially sensitive to small-scale structure and complexity of vegetation (Herbers 1989, Weseloh 1995, Morrison 1998); in our study, vegetation composition

and light availability were important correlates of species density, particularly for forest ants. Nevertheless, latitude was still the most important correlate of ant species diversity, even after accounting for variation among sites in light availability and vegetation composition (Fig. 1).

Our results are consistent with a growing body of literature suggesting that energy is directly or indirectly responsible for the latitudinal gradient in species richness (Wright 1983, Turner et al. 1988, Fraser and Currie 1996, Kaspari et al. 2000). Experiments and studies of resource use are necessary to distinguish among the different variants of the energy hypothesis (Srivastava and Lawton 1998). These scenarios include the "more individuals hypothesis," which invokes a sampling model of greater abundance (and hence taxon richness) with increasing productivity (Kaspari et al. 2000); and the "ambient energy hypothesis," which posits direct inputs of energy, rather than site productivity, as the causal mechanism (Turner et al. 1987, 1988). Regardless of the details, our study demonstrates that local species density of forest ants is highly predictable, and supports the contention of Kaspari et al. (2000) that associations between energy and species density are expressed at small spatial scales.

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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.