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RESEARCH ARTICLE

Communities in context: the influences of multiscale environmental variation on local ant community structure

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Abstract We explored the ways in which environmental variation at multiple spatial scales influences the organization of ant species into local communities. Ground-dwelling ants were sampled in sandhill habitat at 33 locations throughout northern Florida, USA. Variance partitioning of local, landscape, and regional datasets using partial redundancy analysis indicates that ant community composition is significantly influenced by environmental variability across all scales of analysis. Habitat generalists appear to replace habitat specialists at sites with high proportions of matrix habitat in the surrounding landscape. Conversely, habitat specialists appear to replace habitat generalists at sites with more sandhill habitat in the surrounding landscape and greater amounts of bare ground locally. Local niche differentiation leading to species-sorting, combined with the effects of spatially structured dispersal dynamics at landscape scales, may explain this pattern of community structure. Regional influences on local ant communities were correlated with geographical and environmental gradients at distinct regional scales. Therefore, local ant communities appear to be simultaneously structured by different processes that occur at separate spatial scales: local, landscape, and regional scales defined by spatial extent. Our results illustrate the importance of considering multiscale influences on patterns of organization in ecological communities.

Keywords Spatial scale · Community · Metacommunity · Local · Landscape · Regional · Generalist · Specialist · Ants · Sandhill

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Introduction

A focus of community ecology centers on the question of how environmental variation contributes to the identity of local communities. Community ecologists have traditionally emphasized the importance of local influences or broader scale regional patterns as structuring forces on local communities (MacArthur 1958; Whittaker 1960; Tilman 1982; Ricklefs 1987). The local scale can be defined as the spatial and temporal extent of, for example, foraging activities and interspecific interactions, whereas regional scales encompass the overall species pool and regional dispersal that is slow in ecological time (Srivastava 1999). In recent years it has become well established that processes at intermediate or landscape scales provide important structuring forces on local communities (Holt 1993; Brotons et al. 2003; Leibold et al. 2004). This is the scale at which the spatial dynamics of metapopulations or metacommunities play out (Holt 1993). Within landscapes, interpatch movement combined with allochthonous flows of resources between neighboring habitats can have tremendous influences on local competitive interactions, predator-prey dynamics, and system productivity (Polis et al. 1997; Henschel et al. 2001; Holt and Barfield 2003). The magnitude and direction of such cross-habitat flows are influenced by the composition and arrangement of the landscape mosaic in which they occur (Cadenasso et al. 2004). Consequently, the composition and arrangement of environmental features at landscape scales are fundamental determinants of local community structure.

Local species coexistence is influenced through a variety of mechanisms related to the partitioning of available resources or evading predation in a heterogeneous local environment (Amarasekare 2003). Coexistence at landscape scales might be achieved through trade-offs in performance within particular habitats (Kneitel and Chase 2004). If the competitive hierarchy changes with habitat type, a spatially heterogeneous landscape can be important for maintaining coexistence at landscape and regional scales. However, this broader-scale mechanism of coexistence can also facilitate local coexistence through spatial dynamics such as source-sink movement or mass effects (Shmida and Wilson 1985; Chesson 2000). Therefore the structure of the surrounding landscape can have strong influences on local community structure, which may not be predicted based on an assessment of local conditions alone. Local and landscape processes can each be influenced by regional processes, such as the spatial position of communities along regional environmental gradients, or variation in the regional source pool that determines which species are available for local colonization (Gotelli and Ellison 2002; Graves and Rahbek 2005). Considering structuring forces at each of these scales should provide the spatial context necessary for a more thorough understanding of community organization (Holt 1993).

Ants are ideal case study species because they interact with their environment at multiple spatial scales. Worker castes generally interact with the local environment through foraging and defense activities, while alates (winged adults) can interact with the environment at broader scales while dispersing. The diversity of ants in Florida and worldwide is due, in part, to a spectacular array of social behaviors that allow for coexistence through local niche partitioning (Hölldobler and Wilson 1990). However, the effects of heterogeneity in the surrounding landscape on ant communities have not been thoroughly investigated (But see Schoereder et al. 2004; Debuse et al. 2007).

In this paper, we use three datasets to analyze the contribution of variation at local, landscape, and regional scales to the structure of local ant communities in Florida sandhill habitat. The three scales are differentiated by spatial extent. Many studies have examined the influences of factors at each of these scales in isolation or in pairs, but few have examined their effects simultaneously. We use a variance partitioning approach (Borcard et al. 1992) to determine how variation in local ant communities is explained by factors that arise from these three spatial scales and how explained variation is correlated across scales. Our aims are to describe the ways in which local ant communities are structured by a multiscale environment and to suggest hypotheses for the mechanisms behind the patterns that we observe.

Study area and methods

Study area

The study took place on the sandy ridges of northern Florida (See Appendix S1 for site descriptions and map). Sandhill habitat, a rolling savanna-like ecosystem, is characterized by an open canopy of longleaf pine (*Pinus palustris*) and scattered oak species. The understory is a sparse yet diverse mix of wiregrass (*Aristida stricta*) and other perennial herbs with few shrubs (Myers and Ewel 1990). Bare patches of the well-drained sandy soil are not uncommon in this fire maintained habitat.

Sandhills were once more common throughout the southeastern United States. Much of the habitat, however, has been severely degraded or destroyed in recent decades under anthropogenic pressures (Noss et al. 1995). Adjoining habitats include a blend of natural and human modified land cover. Natural land cover includes mixed hardwood-pine forests, pine flatwoods, freshwater marsh, and forested swamp habitats (Myers and Ewel 1990). These forest types are structurally denser than sandhill habitat and contain poorly drained mesic to hydric soils. Modified land cover includes urban areas, pasture, agriculture, extractive sand mining, commercial pine plantation, and disturbed natural land cover types. A land cover classification conducted by the Florida Fish and Wildlife Conservation Commission (FWC) was used to measure attributes of these land cover types. The FWC map was derived from Landsat ETM imagery acquired in 2003 and contains 43 land cover classes with a resolution of 30 m (Stys et al. 2004). Natural pine flatwoods and commercial pine plantations are confused in this classification and were therefore combined into one class (pineland) by Stys et al. (2004). These two habitats are structurally similar, with relatively dense understories and poorly drained acidic soil (Myers and Ewel 1990).

Site selection

We selected thirty-three 30 × 30 m sample sites across a region of northern Florida to span a range of variation in landscape context while standardizing for sandhill habitat locally. Sites were chosen from a selection pool of 2000 locations randomly generated as points in sandhill habitat as classified by the FWC map. All points were located at least 20 m from the habitat boundary to minimize direct edge effects. This was only relevant for sites within very small sandhill patches. We centered circles of radii 100, 300, 500, and 1000 m on each point and measured landscape metrics in a GIS environment at each spatial extent (i.e., focal patch area, focal patch perimeter–area ratio, number sandhill patches, number of land cover classes, and area of each land cover class). We used ArcView 3.3 (ESRI 1999) for all GIS applications. Hierarchical clustering was used to assemble the selection pool into relatively homogeneous groups that represent the full range of heterogeneity in landscapes containing sandhill across the study region. A preliminary list of sites was chosen from each of these groups. Each site was validated in the field prior to sampling in order to sample within a range of local habitat quality. This precluded the sampling of some landscape types. For example, sites in highly degraded landscapes, containing very high proportions of urban land cover, had very poor local habitat quality (e.g., fire suppressed and overgrown) and consequently were not selected for sampling. The 33 sites selected for this study span most of the gradient in surrounding landscape heterogeneity within the study region (see Appendix S2 for further explanation). The sample sites are each separated by at least 1 km, occur within separate patches, and span a range of over 250 km, covering most of the north–south extent of sandhill habitat on the Florida peninsula.

Field sampling and identification

Ground-dwelling ants were sampled by pitfall trapping and litter extraction using Winkler sacks. At each site, 16 pitfalls were arranged in a square grid of 4 rows and 4 columns with rows and columns separated by 10 m. Pitfalls were deployed for 72 h during periods without precipitation. After pitfalls were retrieved, five litter samples were collected in 1 m quadrates at the four corners and the center of each site for Winkler extraction following Agosti et al. (2000). Each site was sampled twice between May and October 2005.

All ant specimens, excluding males and queens, were identified to species. Since ant species have different foraging strategies, raw abundance data can misrepresent the relative abundance of a given species. Therefore, the number of occurrences of each ant species (number of traps in which a species occurred) was used as a measure of relative abundance at each site (King and Porter 2005). Occurrence data were Hellinger-transformed, following Legendre and Gallagher (2001), for all analyses to account for the many zeros in the community data table that result with species turnover between sites. Rarefaction curves were drawn for each site to determine the adequacy of sampling.

Quantifying local, landscape, and regional variables

To assess local habitat characteristics, the percent cover of vegetation and bare ground was estimated within a 1 m quadrat centered on each pitfall trap location. Cover estimates for grass, litter, other herbaceous plants, shrubs, trees, dead wood, and bare ground were recorded before ant sampling and rounded to the nearest 5%. Site level mean values were used in all analyses.

We measured landscape metrics (See Appendix S3 for a complete list) for the 33 sample sites within circular areas of radii 100, 250, 500, 750, and 1000 m centered on each site. Landscape composition variables (e.g., the area of each land cover class) and landscape arrangement variables (e.g., mean nearest neighbor) were measured within each circular area. The normalized difference vegetation index (NDVI) was used as a measure of landscape productivity and heterogeneity. NDVI data were derived from the MODIS satellite platform at a resolution of 250 m (Carroll et al. 2005).

Principal Coordinates of Neighbor Matrices (PCNM) is a method used to obtain an uncorrelated set of explanatory variables that can be used in regression or ordination analyses to describe spatial relationships in community data (Borcard and Legendre 2002). Each PCNM variable can be used to model spatial dependence at specific spatial scales. PCNM analysis has proven superior to its predecessor, trend-surface analysis, in that it more fully explains spatial dependence across a continuous range of scales instead of a single broad scale (Borcard et al. 2004). The method has been used to explain spatial dependencies among sample locations within a site (Borcard et al. 2004) and spatial relationships concerning dispersal among sites within a landscape (Urban et al. 2006). However, since our sites span a range of over 250 km and are separated by distances greater than the scale dispersal processes in landscapes would be expected to occur (i.e., metacommunity dynamics), we obtained a set of PCNM variables to describe the multiscale regional influences on ant communities.

PCNM variables were derived following Borcard and Legendre (2002) and Borcard et al. (2004). The general procedure to obtain the set of explanatory spatial variables involves three steps: (1) calculation of a Euclidian distance matrix comprised of the geographic distances between sites, (2) modification of the geographic distance matrix by replacing distances greater than the minimum needed for all sites to remain connected within a network with an arbitrarily large number, and (3) principal coordinates analysis on the modified distance matrix. The principal coordinate axes that correspond to positive eigenvalues are retained as the set of explanatory PCNM variables. Borcard et al. (2004) provide a more thorough explanation of this analysis along with a set of ecologically relevant examples.

Principal coordinates analysis on the modified distance matrix returned 11 PCNM variables, which explain the spatial dependence of communities across a range of regional scales. Specific distances corresponding to the spatial scale of each PCNM variable can be calculated if sample sites are arranged regularly along a linear transect or grid. Since the sample sites in this study were arranged irregularly throughout the region, the exact spatial scale of each PCNM variable could not be quantified. Qualitatively, though, the first PCNM variable corresponds to very broad scale spatial structure and successive variables correspond in turn to increasingly finer scale spatial structure. The broadest scale roughly corresponds to the spatial extent of the entire study region ($\sim$250 km) and finest scale roughly corresponds to the distance between neighboring sites, allowing us to define and examine regional influences across a continuous range of scales.

Statistical analysis

Redundancy analysis (RDA) is the canonical version of principal components analysis and is a method used to examine how much of the variation in one dataset can be explained by the variation in another. We used partial RDA to determine how sets of local, landscape, and regional scale variables simultaneously explain the variation in the structure of local ant communities (Borcard et al. 1992). The analyses yield eight fractions of the total variation that allowed us to separate pure and shared fractions among the three explanatory datasets. The varpart function, a component of the vegan package (v1.8-2; Oksanen et al. 2006), in R (v2.4.0; R Development Core Team 2006) was used to perform this set of analyses. We reduced the long list of potential explanatory variables (Appendix S3) to only those that significantly explain variation in the ant community data, by using regression with forward selection ($P < .05$) on each variable class separately. To investigate species level effects, a set of generalized linear models were used to investigate how the number of occurrences of ant species at each site varies in response to the first significant axis of a RDA combining local and landscape variables as descriptors.

Analyses were separately run using the landscape metrics measured at each of the five spatial extents (100, 250, 500, 750 and 1000 m) to determine the spatial scale to which ant communities best respond to the larger landscape (Thies et al. 2003). Results observed using the 500 m data explained the greatest amount of variation in the ant community data, therefore the landscape data at this spatial extent were used in all subsequent analyses. A circle of radius 500 m is biologically relevant to the arena in which ants can interact with the landscape through winged dispersal (Hölldobler and Wilson 1990).

Since PCNM variables represent spatial structure at specific scales, six of the seven significant PCNM variables were grouped to form three regional scale classes: broad (PCNM 1 and 2), medium (4 and 5), and fine (7 and 9). PCNM 3 was excluded from this analysis to provide separation between the broad and medium regional scales. The PCNM groupings were arbitrary and limited by the significant variables returned in the selection process. Groupings were not preconceived to analyze communities at particular scales that would reflect particular structuring processes. A set of three redundancy analyses, each constrained by the PCNM variables of the corresponding scale class, were performed to examine the how factors emergent at each of the three regional scales influence local communities. Tests of significance on all RDA axes combined as well as individual axes were performed with 999 permutations under the full model. To determine how environmental variation at each of these regional scales influences ant communities, we used linear regression of the first significant RDA axis for each spatial model (broad, medium, and fine) with stepwise selection of the pool of local and landscape variables.

Results

Ant sampling and identification

Excluding males and queens, pitfall trapping and Winkler extraction yielded 25,761 individuals from 64 species in 23 genera (Appendix S4). The observed number of species ranged from 17–33 with a mean of 25.2 ± 3.9 (1 SD) species per site. Rarefaction analysis indicated that sites were well sampled, as curves for all sites appeared to approach an asymptote. Though Florida is home to the largest number of exotic ant species in the United States (Deyrup et al. 2000), non-native species occurred infrequently and in low abundances, ranging from 0 to 3 species with a mean of 1.3 species per site, which provides evidence that all sites are reasonably undisturbed. For example, *Solenopsis invicta*, the red imported fire ant, was present at three sites but occurred in low densities, not dominating any species assemblage. King and Porter (2007) found a similar low occurrence of exotic invasion in undisturbed upland habitats in Florida.

Variable selection and multi-scale variance partitioning

The significant environmental variables identified by the forward selection process represent a range of landscape composition and site level habitat data (Table 1). Of the eleven derived PCNM variables, variables 1, 2, 3, 4, 5, 7, and 9 significantly explained regional influences on ant communities (Table 1). This represents structuring forces across a range of regional scales: from very broad (i.e., across the entire study area) to finer scales (i.e., groups of neighboring sites).

Results of the partial redundancy analysis indicate that variation among ant communities is significantly explained by local, landscape, and regional influences (Fig. 1; see Appendix S5 for full results). In the following results, the variation explained in each RDA model is reported as the adjusted R^2 (R^2_{adj}). Though R^2 values are often reported as the variation explained in ordination analyses, this value presents a biased estimate of the population R^2. Reporting values of R^2_{adj} accounts for the inflation of R^2 values associated with the number of predictor variables and sample size (Peres-Neto et al. 2006). The variation explained by total local, landscape, and regional factors (7.8, 14.5, and 26.9% respectively), are represented in Fig. 1. The combined model explains 35.5% of the variation, leaving 65.5% of the variation in the ant data attributed to unidentified factors. There

Table 1 Local, landscape, and regional variables selected for use in partial RDA. The spatial scales of variables are distinguished between local (site level characteristics), landscape (land cover variation within a 500 m radius), and regional (PCNM variables)

Variable code	Description	Scale	*P*
Elev	Elevation	Local	0.016
BG	Mean bare ground	Local	0.002
Pine	Area pineland	Landscape	<0.001
Mar	Area freshwater marsh	Landscape	0.007
H_Urb	Area high impact urban	Landscape	0.035
PCNM1	PCNM Axis 1 (Broader spatial scale)	Regional	<0.001
PCNM2	PCNM Axis 2	Regional	<0.001
PCNM3	PCNM Axis 3	Regional	0.026
PCNM4	PCNM Axis 4	Regional	0.003
PCNM5	PCNM Axis 5	Regional	0.022
PCNM7	PCNM Axis 7	Regional	0.003
PCNM9	PCNM Axis 9 (Finer spatial scale)	Regional	0.006

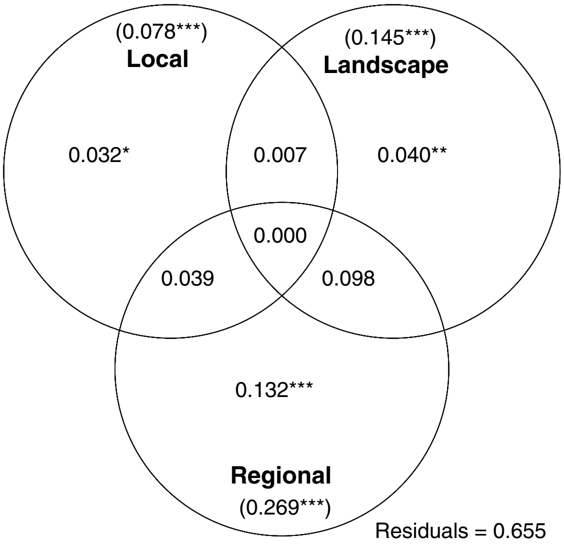

Fig. 1 Diagram illustrating the proportions of variation (R^2_{adj}) in ant community structure that is explained by the pure and shared fractions of local, landscape, and regional variation. Total variation explained by each spatial scale is given in parentheses. *P*-values showing the significance of each fraction of variation were estimated with 999 permutations under the full model. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

is substantial overlap between the variation explained by local and regional factors and the variation explained by landscape and regional factors. Of the total local and landscape influence on ant communities, over 63% is mixed with regional effects, indicating that ant communities are structured by environmental variables that are themselves spatially autocorrelated at broader scales. However, there was very little overlap in the variation explained by local and landscape scale environmental variables, suggesting that these factors provide independent structuring forces on the ant communities observed in this study.

Local and landscape influences

Local and landscape environmental variation together significantly explained 21.6% of the variation in the ant data (Fig. 2). The first RDA axis is largely dominated by the effects of the amount of pineland in the landscape and the amount of bare ground locally. The amount of high impact urban cover, the amount of bare ground, and elevation vary strongly with both axes 1 and 2, whereas the influence of freshwater marsh cover is seen along axis 2. Though community composition is influenced by landscape and local variables, stepwise multiple regression suggests that species richness is not affected by local or landscape environmental variation.

The amount of pineland within 500 m of study sites is strongly correlated with the first axis and accounts for much of the variation in the ant community. The total area of this land cover type can be viewed as a surrogate for sandhill habitat loss and fragmentation since it is correlated with a reduction in sandhill habitat as well as the arrangement of sandhill patches within each landscape. As the amount of pineland in the landscape increases, the total amount of sandhill decreases, and sandhill patches become smaller, more numerous, isolated, and irregular in shape. Pineland is negatively

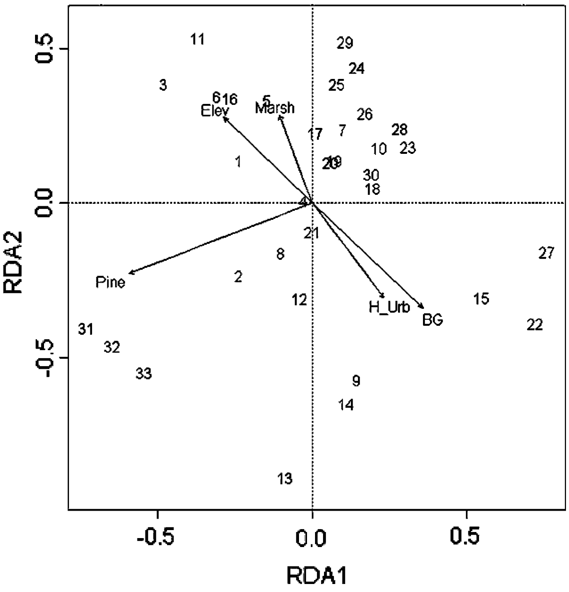

Fig. 2 Redundancy analysis biplot for the first and second significant axes ($P < .005$) for the model combining local and landscape descriptive factors. The length of the arrows along each axis increases with the strength of correlation with the respective axis scores. The angle between arrows indicates the degree of correlation with other environmental variables. Positions of site numbers represent the site scores relative to the first two axes

correlated with the total amount of sandhill ($R^2 = .479$, $P < .0001$, $N = 33$), focal patch area ($R^2 = .308$, $P < .001$, $N = 33$), mean sandhill patch area ($R^2 = .301$, $P < .001$, $N = 33$), and mean patch perimeter ($R^2 = .344$, $P < .001$, $N = 33$) in each 500 m radius circle. Moreover, pineland area has a significant positive correlation with the perimeter to area ratio ($R^2 = .200$, $P = .009$, $N = 33$) and the number of sandhill patches ($R^2 = .167$, $P = .018$, $N = 33$), and mean nearest neighbor of sandhill patches ($R^2 = .221$, $P = .006$, $N = 33$) in each landscape.

In order to characterize ant communities by the species that comprise these assemblages, species response curves were generated from the generalized linear models for axis 1 of the RDA (Fig. 3). Results reveal that sites with little pineland in the surrounding landscape (therefore high proportions of intact sandhill) and greater proportions of bare ground locally support a greater number of open habitat specialists. These open habitat specialists are replaced by habitat generalists at the opposite end of the community axis, where local sandhill sites are embedded within greater amounts of pineland habitat. We define open habitat specialists, a priori, as species that require open structured habitats with a sparse understory and well drained sandy soil. Habitat generalists are defined as species that can exist in either open habitats or more densely vegetated habitats with thicker leaf litter layers and more mesic soil conditions. These classifications are based upon published abundance and habitat association data (Van Pelt 1958; Lubertazzi and Tschinkel 2003; King 2007).

Regional influences

Total regional scale influence explained 26.9% of the variation in the ant community data. Redundancy analysis at each regional spatial scale indicates that spatial dependence on environmental variation at broad, medium, and fine scales significantly explains 46.8%, 25.3%, and 24.2% of the total regional component respectively (Table 2A). Linear regression with stepwise selection on the first (orthogonal) significant axis of the broad scale RDA model indicates that regional gradients in the amount of pineland surrounding sites and local elevation are most important in spatially structuring ant communities across the broad regional scale. Spatial structure at the fine regional scale is most influenced by shorter environmental gradients in the mean area of bare ground within sites, followed by the area of high impact urban cover surrounding sites. The amount of high impact urban cover followed by the mean area of bare ground have the largest influence on the spatial structure at the medium regional scale (Table 2B).

Discussion

Variation in local sandhill ant communities is dependent on environmental variation at local, landscape, and regional spatial scales (Fig. 1). Locally, elevation and the amount of bare ground contribute to the structure of local ant communities. This suggests that species-sorting mechanisms provide important structuring forces through local niche partitioning (Chase and Leibold 2003; Leibold et al. 2004). For example, elevation can be associated with the depth of the water table, which might influence the

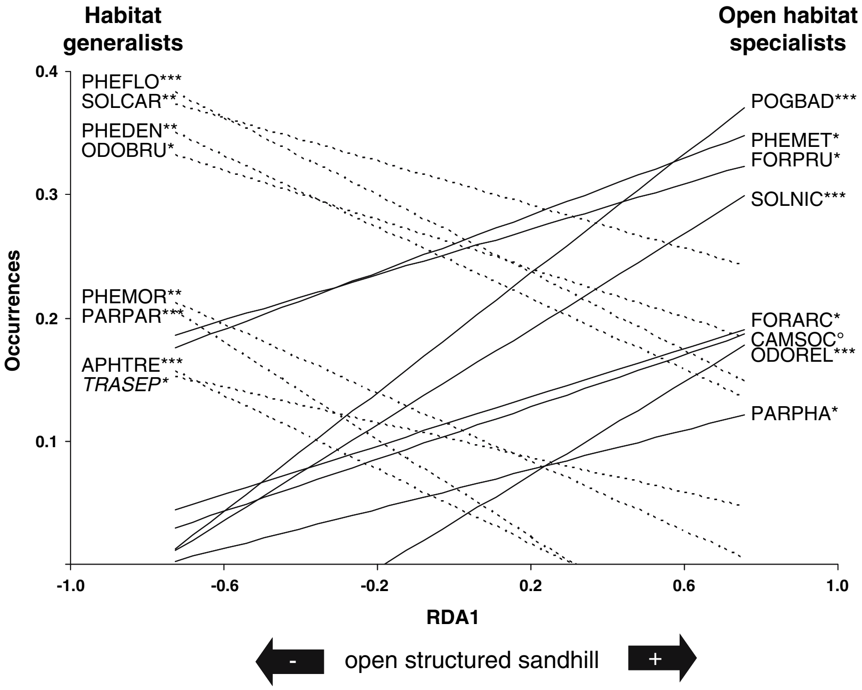

Fig. 3 Species response to the first axis of the RDA model combining local and landscape variables (occurrence data are Hellinger transformed). Species significantly responding to the first RDA axis were identified using generalized linear models. Solid and dotted lines separate the trajectory of species that increase and decrease with axis 1. Increasing axis 1 scores reflect an increase in the amount of local bare ground cover and the amount of sandhill habitat in the landscape, and a decrease in the amount of pineland and other matrix habitats in the surrounding landscape. Results illustrate the separation of open habitat specialists from habitat generalists. The only exception (noted in italics) being *Trachymyrmex septentrionalis* (TRASEP), which is rarely found outside of open structured habitats within Florida. $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$, $^{o}P = 0.054$

Table 2 (A) Proportion of the total spatial dependence explained by each regional spatial scale; (B) Correlation of the spatial dependence of ant communities with environmental variation at each regional spatial scale

		Regional spatial scale		
		Broad (PCNM 1&2)	Medium (PCNM 4&5)	Fine (PCNM 7&9)
A	P	<0.005	0.017	0.01
	R^2_{adj}	0.126	0.068	0.065
	Percent of total regional variation explained	46.80%	25.30%	24.20%
B	Significant variables	Pine, Elev	H_Urb, BG	BG, H_Urb
	P	<0.001	0.003	<0.001
	R^2_{adj}	0.486	0.285	0.396

suitability of local nest sites. This is especially true for deep nesting species such as *Pogonomyrmex badius* (Tschinkel 2004). Small changes in local conditions, like the amount of bare ground, may allow for the persistence of species that might otherwise be excluded, especially in combination with broader scale structuring forces. The amount of pineland, urban, and freshwater marsh habitat in the surrounding landscape significantly explained local community structure, providing evidence that spatially dependent spillover from neighboring habitats may have strong influences on local ant community composition (Holt 1993; Polis et al. 2004; Rand et al. 2006). Cook et al. (2002) recognized that the sources of variation in local community patterns can be masked without considering the importance of infiltration by matrix species. This may explain why ant species richness did not vary significantly with any of the variables measured in this study. Local communities may become saturated as matrix species quickly replace those extirpated from the area (Debinski and Holt 2000). Regional scale heterogeneity also significantly influences ant community structure. Communities are influenced by different environmental factors, such as ecological gradients, whose effects are realized at separate regional scales, indicating that the extent to which a region is defined can influence the results and interpretation of an analysis.

Local and landscape influences

Since local and landscape influences usually occur over relatively short ecological time scales (as opposed to the longer time scales over which regional influences occur) we discuss their effects together. The main axis in Fig. 2 is organized along an environmental gradient primarily defined by landscapes with high proportions of pineland and fragmented sandhill at one end, and landscapes with high proportions of intact and open structured sandhill at the other. Results of generalized linear models reveal that the occurrence of habitat generalists and open habitat specialists can also be arranged along this axis of community structure (Fig. 3). These two sets of species (i.e., habitat generalists and open habitat specialists) are important community players, accounting for over 66% of the occurrences and 76% of the raw abundance of ants in the study. Sandhill habitat is less productive than much of the intervening matrix habitat (e.g., pineland) and has greater variation in and extremes of microclimate. Higher tolerance of these conditions by open habitat specialists may be traded for habitat generalization in some species that are also encountered in more densely structured habitat (Kneitel and Chase 2004). However, since the local habitat type was standardized in our study, it is unclear why habitat generalists, normally the inferior competitor in the habitat preferred by specialists (MacArthur 1972), appear to be supplanting open habitat specialists at sandhill sites embedded in landscapes with high proportions of non-sandhill habitat. The landscape-dependent colonization rate of generalist ant species was empirically demonstrated by Schoereder et al. (2004), who described how small tropical forest remnants, which tended to be more isolated, were more often invaded by generalist ant species from the surrounding matrix. The apparent replacement of open habitat specialists with habitat generalists may occur through a number of possible mechanisms that occur at multiple spatial scales. At local scales, a generalist, whose diet overlaps with that of a specialist, might persist if alternate resources are available for utilization. Chase (1996) experimentally showed that a generalist can even reverse the competitive hierarchy if enough alternate resources are present for exclusive use, due to the larger numerical effect of the generalist. At landscape scales, spatial dynamics, such as source-sink dynamics or mass effects, may permit habitat generalists to avoid local exclusion through repeated invasion and replenishment from neighboring habitats (Brown and Kodric-Brown 1977; Shmida and Wilson 1985; Pulliam 1988). Holt (2004) developed a model that explains how continuous immigration by an inferior competitor allows it to persist in habitats where it otherwise would not. When the rate of immigration is sufficiently high, the inferior competitor can even exclude the superior competitor. Similarly, a model created by Marvier et al. (2004) reveals that habitat loss can promote the invasion of habitat generalist species despite being competitively inferior to the resident habitat specialists.

Alternatively, such spatial dynamics do not necessarily involve the deterministic extinction of habitat specialists. Stochastic extinction in areas surrounded by little sandhill may be followed by dispersal limitation and an inability of specialists to recolonize these isolated patches (Hanski and Gilpin 1991). Habitat generalists would then be free to colonize isolated sandhill patches from surrounding areas and persist unchallenged by competition.

If the local environment varies in such a way that alternate resources become available that would allow habitat generalist to coexist with habitat specialists, one would expect a corresponding increase in total species richness. This seems unlikely in this case since total species richness was not significantly related to any of the environmental variables or community axes measured. Likewise, spatial dynamics, such as mass effects, would predict an increase in local species richness (Shmida and Wilson 1985, but see Holt 2004), which was not observed here. We suggest at least two general mechanisms should be considered to describe observed patterns of community structure: (1) habitat generalists begin to supplant habitat specialists through competitive processes relating to spatial dynamics as the proportion of sandhill habitat in the surrounding landscape decreases (Holt 2004), or (2) stochastic extinction of habitat specialists (or deterministic extinction unrelated to interspecific ant interactions), coupled with landscape dependent dispersal limitation preventing specialist recolonization, allows habitat generalists to become established and persist in sandhill habitat. Work has begun on designing experimental studies to better understand these potential mechanisms.

Regional scale influences

Variation at regional scales has long been known to affect the structure of local communities (Curtis 1959; Whittaker 1960). The significant spatial dependence of communities on regional variation, as described by PCNM analysis, indicates that local ant communities are influenced by variation at broader scales than would be accounted for by metacommunity dynamics and interspecific interactions. This effect has been demonstrated in many studies that relate community structure to historical and biogeographical factors (Marquet and Cofre 1999; Bestelmeyer and Wiens 2001; Gotelli and Ellison 2002; Graves and Rahbek 2005). The distribution of the Florida biota is influenced by paleogeographic factors relating to the advance and retreat of the Atlantic Ocean, which left regionally isolated assemblages separated by biogeographical boundaries (Myers and Ewel 1990). For example, the presence of *Odontomachus relictus* is an endemic species native to a few sandy Florida ridges that date to the Pleistocene, is greatly influenced by such historical factors (Deyrup and Cover 2004). It is likely that the variation explained by the regional component (Fig. 1) is strongly dependent on such historic factors, which may also be correlated with present regional habitat distributions.

The position of local communities along large scale biotic or abiotic gradients can influence community structure in a variety of ways, but the explanation of observed differences among local communities is strongly dependent on the spatial extent at which the region is defined (Wiens 1989; Karlson and Cornell 1998). We show that regional influences can be subdivided into a range of spatial extents. The explained variation in local ant community structure was correlated with different types of environmental variation at each regional spatial scale (Table 2). This result indicates that ecological structures are likely influenced simultaneously by separate processes across a continuous range of spatial scales. When the region is defined at the broadest scale (i.e., the 250 km extent of the entire study region), the amount of pineland in the surrounding landscape and the local elevation forms an environmental gradient that significantly influences local ant community structure (Table 2). Regions defined at smaller spatial extents contain shorter environmental gradients that influence ant communities in different ways. When regions are defined at a finer spatial scale (approximately conforming to the average distances between neighboring sites) the amount of bare ground within sites and the area of urban land cover in the surrounding landscape forms a significant environmental gradient. Regions defined at intermediate extents play host to similar structuring forces as regions defined at finer scales, though the area of urban land cover gains in significance over the amount of bare ground.

The differences in structuring forces at these three regional scales reflect differences in the scales at which environmental variation is manifest, as well as the scale of more localized land use and management practices. For example, the amount of bare ground is likely influenced by fire management activities, which occur at the scale of individual reserves, that is, over scales similar to the fine regional scale we define here. Urban land use activities occur at slightly broader scales and may influence the ant communities observed here through alterations to fire regimes, (non-ant) exotic species introduction, or other types of disturbance (Hoffmann and Andersen 2003). The amount of pineland in the landscape increases with latitude as a result of land use practices and natural habitat distributions, which reflects the broad scale regional influence on ant community structure and the correlation with landscape processes. Elevation also forms a regional gradient, which reflects the regional correlation with local processes. However, as the significance of the pure local and landscape components of the variance partitioning analysis indicates (Fig. 1), this does not explain the effect these factors have on communities in individual landscapes, it merely illustrates how finer-scale variables can be spatially autocorrelated at broader scales. When sites are divided into northern, central, and southern groups, qualitatively similar effects of local and landscape variation are seen within each grouping.

Conclusions

Our results hint that the metacommunity concept (reviewed in Holyoak et al. 2005) might offer a mechanistic framework for the analysis of spatially structured ant communities. A meta-analysis by Cottenie (2005) illustrated how a variance partitioning approach, similar to the one conducted here, can reveal the ways in which metacommunities are structured. For example, the species sorting perspective assumes communities are structured by differences in local habitat through niche separation, and that interpatch dispersal maintains local diversity as environments change. The mass-effects perspective predicts that high rates of immigration can prevent the loss of competitively inferior species from local communities (Leibold et al. 2004). The significance of the pure local fraction of variation in our study suggests that the species sorting perspective might apply here. However, the significance of the pure landscape fraction coupled with the apparent replacement of habitat specialists with habitat generalists suggests that the mass-effect perspective might also apply (Cottenie 2005). However, as noted above, it is unclear whether a mass effect is present or stochastic processes are at work in this system. Either way, the significance of landscape scale factors on local communities suggests that a metacommunity approach might be useful as a framework for testing alternative hypotheses relating to the multiscale influences on local communities.

In sum, our results show that ant communities have complex relationships with a multiscale environment. Care should be taken when interpreting the results of single scale (or even two scale) analyses of relationships between the environment and the ant community. Failing to consider local communities in the context of the structuring forces simultaneously originating from multiple spatial scales risks confusing potential mechanisms behind observed differences in ecological patterns. The level of species turnover among sites would suggest that spatial and environmental heterogeneity at multiple scales is important for maintaining a diverse regional species pool. Therefore, continued anthropogenic pressure resulting in habitat loss or reduced habitat quality on sandhills is cause for concern. Alteration of the landscape to favor habitat generalists may reduce the viability of open habitat specialists across the range of remaining sandhill, thereby reducing the potential for regional coexistence and the maintenance of important ecological interactions. Given the importance of multi-scale environmental variation to sandhill ant communities, our study provides further evidence that multi-scale adaptive management strategies are a necessity since uncoordinated localized management may prove ineffective (Cumming and Spiesman 2006).

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