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Patterns of co-occurrence and body size overlap among ants in Florida's upland ecosystems

Joshua R. King

University of Florida, Entomology & Nematology Department, P.O. Box 110620, Gainesville, FL 32611, USA; current address: Department of Biological Science, Florida State University, Tallahassee, FL 32306-4370, USA (e-mail: jking@bio.fsu.edu)

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Within ant communities, competitive asymmetry is hypothesized to dictate, in part, the co-occurrence patterns of species. I intensively sampled ant communities from 5 upland ecosystem types in Florida, USA. I used null model analyses to test two general assembly rules and one specific to ant communities: (1) reduced co-occurrence of species among communities, (2) regular spacing of body sizes within communities, and (3) competition hierarchies. Species were segregated by habitat (species co-occurrence was reduced among ecosystems) but there was no evidence for competition hierarchies at local scales (species co-occurrence patterns were random within ecosystems). There was limited evidence that body size distributions are regularly spaced at both the regional and local scale. Thus, while competition between species may result in character displacement between similar species, it does not appear to form competition hierarchies at the local scale at which ants actually interact.

Introduction

An open question is to what degree interspecific competition dictates assembly rules, or patterns of species within communities, for a wide variety of taxa (Weiher & Keddy 1999, Gotelli & McCabe 2002, LeBrun 2005). Among ants, interspecific competition at local scales for resources, for example, fighting over baits, has been the most studied form of species interactions (Davidson 1977, Vepsäläinen & Pisarski 1982, Morrison 2000) and is widely assumed to be the most important factor in determining which ant species can coexist in communities (Hölldobler & Wilson 1990 and references therein). Behaviorally dominant species with large colonies, large worker body size, and aggressive, territorial behavior are believed to influence the composition and relative abundance of local ant faunae through competitive suppression or exclusion of some, but not other ant species (Savolainen & Vepsäläinen 1988, Hölldobler & Wilson 1990, Andersen & Patel 1994). In this manner, behaviorally dominant species are hypothesized to create spatial co-occurrence patterns and in the extreme, may create mosaic-like patterns of non-overlapping territories (Room 1971). These competition hierarchies (*sensu* Savolainen & Vepsäläinen 1988, LeBrun 2005) represent an extreme form of competitive asymmetry where some ant communities are hypothesized to be organized by behaviorally dominant species, at least in part, with effects on founding success, niche differentiation, and resource partitioning (Vepsäläinen & Pisarski 1982, Cole 1983, Savolainen & Vepsäläinen 1988, Hölldobler & Wilson 1990, Andersen & Patel 1994).

A well-defined example of an ant competition hierarchy was described by Savolainen and Vepsäläinen (1988, 1989) where communities of boreal ants on the Tvärminne archipelago were structured by competitive interactions. In this fauna, polycalic red wood ant species (*Formica*) were behaviorally dominant and shown to affect the foraging behavior and composition of other species at baits. Furthermore, the dominant *Formica* species were also shown to affect the foraging range and distribution of nests of subordinate species perhaps by excluding nests from their territories. These dominant species thus organize the distribution of subordinate species' foraging and nesting sites. A number of similar examples are described in Hölldobler and Wilson (1990) and cited as examples of how many ant communities are organized.

In contrast, recent community-level experimental work has shown that some behaviorally dominant species have no obvious impact on the vast majority of co-occurring species (Gibb & Hochuli 2004, King & Tschinkel 2006). Rather, these dominant species seem able to exclude or suppress only ecologically similar species (Gibb & Hochuli 2004), if any species at all (King & Tschinkel 2006). Similarly, null model analyses of co-occurrence and body size patterns within temperate and tropical ant communities have contrasted with the patterns expected if assembly rules were determined primarily by interspecific competition in the form of competition hierarchies (Gotelli & Ellison 2002, Ribas & Schoereder 2002). To date there have been few studies of social insect communities that utilized null models and hypothesis testing for evidence of competition-induced assembly rules across scales (Gotelli & Ellison 2002), despite the power of these approaches to help understand the role of competition in community assembly (Strong *et al*. 1979, Simberloff & Boecklen 1981, Dayan & Simberloff 2005). Here I use null model analyses of community-wide co-occurrence patterns and ecological character displacement (*sensu* Dayan & Simberloff 2005) to search for evidence of competition-induced ecological assortment and assembly rules for ant communities in Florida's upland ecosystems.

Using competition theory, two assembly rules can be predicted and tested: (1) among different communities within a region, species should co-occur less often than expected by chance (Diamond 1975), and (2) within each community, co-occurring species should differ in body size or morphology so that overlap in resource use, and therefore competition, is reduced (Brown & Wilson 1956). More specifically for ants, species with large colonies, the ability to mass-recruit, and aggressive territorial behavior should produce regular patterns, allowing some combinations of ant species, while excluding others (Diamond 1975, Levings & Traniello 1981, Hölldobler & Wilson 1990, Andersen & Patel 1994). Exclusion should be particularly apparent among ecologically similar, territorial species (Room 1971, Vepsäläinen & Pisarski 1982, Andersen & Patel 1994) at local scales. Examples in this fauna include the invasive fire ant, *Solenopsis invicta*, *Pheidole dentata*, and the dolichoderine *Forelius pruinosus*.

Methods

Upland ecosystems in north-central Florida are similar to those found throughout the southeastern coastal plain of the United States, with the exception of Florida Scrub, an ecosytem unique to the state (Myers & Ewel 1990). These ecosystems range from closed canopy, highly productive hardwood forests to completely open, low productivity herbaceous savannah. Using the ecosystem classification of Myers and Ewel (1990), I chose four of the most widespread natural upland Florida ecosystems for sampling: (1) temperate hardwood forests at the San Felasco Hammock State Park, (2) pine flatwoods at the Osceola National Forest, (3) high sandhill pine at the Katherine Ordway Biological Preserve, and (4) Florida scrub at the Archbold Biological Station. These represent some of the least-disturbed remaining native upland ecosystems in peninsular Florida. I also included a fifth category of a disturbed ecosystem, consisting of cleared fields. The plant communities in all localities were large enough to accommodate three, large (180 m) linear transects separated by at least 100 m from roads, fences, or edges (e.g., park boundaries or ecotones). For each ecosystem and for the region as a whole, sampling produced a nearly complete list of species along with their abundance (King & Porter 2005, King & Porter [In press]).

A complete description of the sampling methods can be found in King and Porter (2005 and [In press]). A combination of pitfall traps, litter sampling, hand collecting, and baiting captured a total of 94 species (King & Porter 2005). However, because hand collecting and baiting techniques are poor measures of relative abundance, and none of the methods effectively sampled arboreal species (King & Porter 2005), only the 76 ground-dwelling species sampled by pitfall or litter extraction were included in this analysis (Table 1). I did, however, use baiting data to assess the behavioral dominance and recruitment ability of species. Throughout the operation of baits, brief observations of the behavior of ants were made at baits. Behavioral dominance at baits was used in combination with combined pitfall and litter sample occurrences to compare the frequency of occurrence with behavioral dominance. Dominance was determined by the percentage of baits occupied per species. Percentage of baits occupied was then plotted with the percent occurrence in pitfall and litter samples for all species to compare patterns of behavioral dominance with their frequency of occurrence (a measure of relative abundance). Only species appearing in baits were used in this analysis. For some ecosystems the total percentage of baits occupied by all species exceeded 100% due to occasional co-occurrence of species at baits.

Table 1. The occurrence of 76 ant species in upland Florida ecosystems arranged alphabetically under subfamilies. Data are the number of samples in which workers occurred for each sampling method (P = pitfalls; L = litter extraction) within ecosystems. A total of 108 pitfall and litter samples were taken in each ecosystem. Introduced species are indicated by boldface type.

Species	Mass (mg)	Hardwood hammock	Florida scrub	Pine flatwoods	High pine	Field
Amblyoponinae						
Amblyopone pallipes (Haldeman)	0.616	1P, 5L	1P			
Dolichoderinae						
Dorymyrmex bossutus (Trager)	0.115*		3P		1P, 1L	
Dorymyrmex bureni (Trager)	0.189					49P, 12L
Dorymyrmex elegans (Trager)	0.190*		1P			
Dorymyrmex grandulus (Forel)	0.115				1P	
Forelius pruinosus (Roger)	0.061		5P, 2L	20P	31P, 10L	23P, 1L
Forelius sp. nov.	0.062*				6P, 1L	
Ecitoninae						
Neivamyrmex carolinensis (Emery)	0.153				2P	
Neivamyrmex opacithorax (Emery)	0.214				1P	
Neivamyrmex texanus Watkins	0.564				4P	1P
Formicinae						
Brachymyrmex sp. nov.	0.010*	1L				
Brachymyrmex depilis Emery	0.012	4L	3P, 12L	17P, 16L	2L	2P
Brachymyrmex obscurior Forel	0.043					5P, 6L
Camponotus castaneus (Latreille)	5.860	1P, 1L		1P		
Camponotus floridanus (Buckley)	3.463	1P, 2L	2P, 1L	20P, 7L		
Camponotus socius Roger	5.900*				4P	
Formica pallidefulva Latreille	1.717		3P, 7L	18P, 2L		
Formica schaufussi Mayr	2.062			5P		
Paratrechina arenivaga (Wheeler)	0.090		6P, 2L	2P	7P, 2L	2P
Paratrechina concinna Trager	0.047		3P	6P, 2L		2P, 1L
Paratrechina faisonensis (Forel)	0.084	4P, 26L		5P, 4L	5P, 1L	
Paratrechina parvula (Mayr)	0.052			20P, 13L	1L	11P, 2L
Paratrechina phantasma Trager	0.090*				6P	

continued

Table 1. Continued.

Species	Mass (mg)	Hardwood hammock	Florida scrub	Pine flatwoods	High pine	Field
Paratrechina wojciki Trager	0.035		9P, 23L	6P, 6L	3P, 7L	
Myrmicinae						
Aphaenogaster ashmeadi (Emery)	0.640*		3P, 2L		1P	
Aphaenogaster flemingi M.R. Smith	1.220*			1P		
Aphaenogaster floridana M.R. Smith	0.640				4P, 1L	3P, 1L
Aphaenogaster treatae Forel	0.759				1P	
***Cardiocondyla emeryi* Forel**	0.028*					19P, 9L
***Cardiocondyla nuda* (Mayr)**	0.028*					10P
***Cardiocondyla wroughtonii* (Forel)**	0.030*			2P		
Crematogaster atkinsoni Wheeler	0.416			2L		
Crematogaster minutissima Mayr	0.110		2L	1P, 1L		
Cyphomyrmex minutus Mayr	0.136*		1P, 3L			1L
***Cyphomyrmex rimosus* (Spinola)**	0.256	3P, 4L	3P, 1L	1P	1P, 3L	14P, 1L
Eurhopalothrix floridanus Brown & Kempf	0.136	8L	2L		1L	
Monomorium viride Brown	0.037			19P, 15L	3P, 3L	
Myrmecina americana Emery	0.268	2L				
Pheidole adrianoi Naves	0.031*				1P	
Pheidole dentata Mayr	0.077	33P, 45L	70P, 52L	52P, 19L	18P, 6L	23P, 5L
Pheidole dentigula M.R. Smith	0.030	31P, 87L	22P, 62L	2L		
Pheidole floridana Emery	0.027		38P, 39L	53P, 15L	13P, 18L	7P, 4L
Pheidole metallescens Emery	0.036		3P, 6L		21P, 15L	3P, 1L
***Pheidole moerens* Wheeler**	0.034	11P, 26L	6P, 2L	1P, 2L		6P, 12L
Pheidole morrisi Forel	0.090		4P, 1L	5P	19P, 2L	17P, 1L
Pogonomyrmex badius (Latreille)	2.778		1L		19P, 1L	2P
Pyramica bunki (Brown)	0.021*			1P		
Pyramica clypeata (Roger)	0.021*	1L				
Pyramica creightoni (M.R. Smith)	0.021*			2P		1L
Pyramica deyrupi Bolton	0.021*			2P, 4L		
Pyramica dietrichi (M.R. Smith)	0.021*			1L		
***Pyramica eggersi* (Emery)**	0.021	3L	4P, 4L			1L
Solenopsis geminata (Fabricius)	0.325				8P, 14L	26P, 6L
Solenopsis globularia (F. Smith)	0.075		1P, 2L			
***Solenopsis invicta* Buren**	0.360					11P, 7L
Solenopsis nickersoni Thompson	0.020	2P	19P, 28L	27P, 16L	6P, 9L	
Solenopsis pergandei Forel	0.025				6L	2P
Solenopsis abdita Thompson	0.020	3L			2P, 5L	
Solenopsis carolinensis Forel	0.025	73P, 101L	28P, 53L	63P, 59L	19P, 34L	5P, 12L
Solenopsis tennesseensis M.R. Smith	0.008	3P, 44L	1P, 50L	1P, 2L	1P, 20L	5L
Solenopsis tonsa Thompson	0.008*				1L	
***Strumigenys emmae* (Emery)**	0.053*		1L			
Strumigenys louisianae (Roger)	0.053	9P, 31L		1L	3L	3L
***Strumigenys rogeri* (Emery)**	0.027		1L			
Temnothorax palustris Deyrup & Cover	0.140*			1P, 5L		
Temnothorax pergandei Emery	0.168		10P, 13L	65P, 37L	8P, 13L	1L
Temnothorax texanus Wheeler	0.135				1P, 2L	
***Tetramorium simillimum* (F. Smith)**	0.058		1L			9P, 5L
Trachymyrmex septentrionalis (McCook)	0.380	5P, 6L	7P, 3L		5P, 2L	5P, 1L
Ponerinae						
Hypoponera inexorata (Wheeler)	0.070*	1L	1L	1L	1L	
Hypoponera opaciceps (Mayr)	0.068*	1L				
Hypoponera opacior (Forel)	0.068	12P, 88L	15L	11L	23L	1P, 2L
Odontomachus brunneus (Patton)	2.603	60P, 23L		42P, 12L	12P, 6L	
Odontomachus relictus Deyrup & Cover	1.813		23P, 7L			11P, 1L
***Odontomachus ruginodus* M.R. Smith**	1.851					4P
Ponera exotica M.R. Smith	0.060	6L				

*Approximate values (*see* text for details).

I measured the dry weight of workers of each species (Table 1). I measured dry mass as this is a central measure of size in ants and it covaries nearly isometrically with (accounts for) the size of head width and length, mouthparts, and limbs (Kaspari & Weiser 1999, Tschinkel *et al.* 2003, Weiser & Kaspari 2006). Body size is a viable measure to consider for analysis of ecological character displacement or ecological assortment as selection on size can lead to morphological divergence (changes in shape; Lande 1979, Mosimann & James 1979). For social insects there is evidence that selection and ecological assortment may operate on size (Whitford 1978, Chew & Chew 1980, Chew & DeVita 1980), particularly in the development of physical worker castes (Oster & Wilson 1978, Tschinkel *et al.* 2003). Furthermore, here I am assessing community-wide displacement of a character which may be important in ecological assortment across higher taxonomic levels (Strong *et al.* 1979) as opposed to morphological changes in body parts within a genus (e.g. Nipperess & Beattie 2004). Because the majority of species in this fauna are dietary generalists, there is no *a priori* reason to believe that, for example mandible size or shape is under selection. Instead, biomass is a proxy measure that accounts for (among other variables) the size of food particles workers can carry, the rate and distance at which workers will forage, and dessication resistance (all correlates of body size as well; Hood & Tschinkel 1990, Kaspari & Weiser 1999, Ness *et al.* 2004). In addition to this information, average dry worker biomass also provides a direct measure of the mass of individuals which can also be converted to colony biomass. In sum, worker dry biomass is a very important (and central) single measure of ant body size because it is fundamentally connected to ecological niche, population dynamics, evolutionary rates, and community structure.

For *Pheidole* species I used only the weight of minor workers, as majors were uncommon in samples. There were 23 species which were not weighed because they were mounted as vouchers. For these species, the body weight of a similar-sized species in the same genus was rounded to the nearest fraction (tenth, hundredth, thousandth) of a milligram and used as an approximation. The direction and magnitude of rounding was determined from the relative Weber's length (Brown 1953). This approach provides an approximation of unknown weight similar to other approaches (e.g., regressive relationships, Rogers *et al.* 1976, Kaspari & Weiser 1999). A majority of the unweighed species were rare, appearing in less than 1% of samples.

Analysis of co-occurrence

There were two scales at which co-occurrence hypotheses were tested: local and regional. For the regional scale, I tested the hypothesis that species occurred randomly with respect to ecosystem and all species were put into a species by habitat matrix, thus combining all of the transects (15) into one species list. At the local scale, to satisfy the spatial requirements of the co-occurrence hypotheses tested (and thus avoid pseudoreplication in a mensurative experiment, Hurlbert 1984), transects were separated by at least 1 km with the exception of two transects in San Felasco Hammock State park that were separated by 300 m. The spatial constraint on this hypothesis, that species co-occurrence patterns differed from random, must be at the scale at which individual colonies would exclude one another (no greater than several meters, even for largest colonies). While transects for any given ecosystem type were contained within one locality (e.g., Osceola National Forest), there were very large distances between them (1 km or more). This is crucial, because it means these large transects are spatially independent relative to the hypothesis tested, despite the fact that they are within the same "locality." Furthermore, I then averaged the results of these analyses in the meta-analysis (Table 2), effectively treating the (3) transects as replicates. Although ecosystem types could not be replicated within each locality because of the rarity of undisturbed native Florida ecosystems (Myers & Ewel 1990), transects were replicated 3 times within ecosystems. Thus, transects were sufficiently far apart to treat transects as replicates in analyzing local-scale co-occurrence patterns among species.

Ant assemblages were tested for random co-occurrence of species, following Gotelli and Ellison's (2002) random null hypothesis analytical approach. I analyzed occurrence data from pitfalls, litter samples and combined pitfall and litter data sets for each transect. However, for the local co-occurrence analyses I present and discuss only results from the pitfall data, as results obtained from analyses of the litter and combined data were nearly identical to the pitfall data. For the regional scale co-occurrence and body size analyses, I analyzed all species from litter and pitfall samples. The regional-scale data were organized as a presence-absence matrix with species (rows, $n = 76$) by sites (columns, $n = 15$). The local presence-absence matrix consisted of species (rows) by sample ($n = 36$). C-scores (Stone & Roberts 1990) provided a measure of co-occurrence within the matrices. Larger C-scores indicate that species occurred together less often than expected by chance, and may be an outcome of competition (Gotelli & Entsminger 2001). I generated a histogram of 10 000 *C*-scores from random null assemblages and used it to determine the exact tail probability for the observed *C*-score value (Gotelli & Ellison 2002). I analyzed each site occurrence matrix using three null models that use row and column constraints to test a variety of ecological scenarios: fixed-fixed, fixed-equiprobable, and weighted-fixed (detailed in Gotelli & Ellison 2002). In the fixed-fixed null model the row and column sums are preserved in the null community so that the number of species and species occurrences are the same as the observed community. In the fixed-equiprobable null model only the row sums are fixed and the columns (= sample points) are equiprobable. In the weighted-fixed null model the column totals are fixed but the frequency of each species is proportional to the total number of occurrences in pitfall samples within a site. As the fixed-equiprobable model treats all sites as equiprobable (a biologically unrealistic assumption at the regional scale where sites are different ecosystems), I analyzed the regional scale matrix using only the fixed-fixed and weighted-fixed models.

Table 2. Meta-analysis of exclusion or aggregation patterns of ants in pitfall traps at the local scale in upland ecosystems in Florida. After Bonferroni-correction for multiple tests, no sites showed significant aggregation or exclusion of species. “Lower tail” and “Upper tail” indicate the number of assemblages for which the observed *C*-score was respectively less than or greater than predicted by the null model. The number in parentheses indicates the number of sites with significant patterns ($P < 0.05$, one-tailed test). A one-sample *t*-test was used to test the hypothesis that the standardized effect size (SES) for the set of sites that comprise an ecosystem does not differ from zero. SES = $(I_{obs} - I_{sim})/s_{sim}$, where I_{sim} is the mean index of the simulated communities, s_{sim} is the standard deviation, and I_{obs} is the observed index. Bonferonni probabilities are corrected for all tests. Communities with little co-occurrence should frequently reject the null hypothesis in the upper tail, and the meta-analysis pattern would be an effect size significantly greater than zero.

Ecosystem	Model	Lower tail	Upper tail	Average effect size	SD of effect size	*t*	*P*	Bonferonni *P*
Hardwood hammock	Fixed–Fixed	3(0)	0(0)	–0.72	0.26	–4.80	0.04*	0.61
	Weighted–Fixed	3(3)	0(0)	–2.09	0.67	–5.42	0.03*	0.49
	Equiprobable–Fixed	2(0)	1(0)	> 0.01	0.57	> 0.01	1.00	1.00
Pine flatwoods	Fixed–Fixed	2(0)	1(0)	–0.19	1.37	–0.24	0.83	1.00
	Weighted–Fixed	3(3)	0(0)	–3.13	0.86	–6.30	0.02*	0.36
	Equiprobable–Fixed	3(0)	0(0)	–0.78	0.45	–2.96	0.10	1.00
Florida scrub	Fixed–Fixed	2(0)	1(0)	0.58	1.16	0.86	0.48	1.00
	Weighted–Fixed	3(3)	0(0)	–1.84	0.63	–5.06	0.04*	0.55
	Equiprobable–Fixed	2(0)	1(0)	–0.31	0.48	–1.11	0.38	1.00
High pine	Fixed–Fixed	0(0)	3(0)	0.82	0.61	2.32	0.15	1.00
	Weighted–Fixed	3(3)	0(0)	–2.12	0.57	–6.42	0.02*	0.35
	Equiprobable–Fixed	3(0)	0(0)	–0.69	0.86	–1.39	0.30	1.00
Field	Fixed–Fixed	0(0)	3(1)	2.09	2.63	1.37	0.30	1.00
	Weighted–Fixed	3(1)	0(0)	–1.40	0.35	–7.00	0.02*	0.30
	Equiprobable–Fixed	2(1)	1(1)	0.13	2.94	0.08	0.95	1.00

*Significant at $\alpha = 0.05$.

Analysis of body size overlap

If ecological character displacement (or assortment) exists, there should be little overlap of body sizes among coexisting species (Brown & Wilson 1956). To test for this overlap, I plotted mean worker ant weight on a log scale and calculated the ratio of body size of successive pairs of adjacent species. Here, again, there were two scales to consider: regional and local. The regional scale analysis was based on the full ground-dwelling species list (76 species from 15 transects). The local scale analysis consisted of the ground-dwelling species list for each ecosystem (generated from 3 transects in each ecosystem type) to include the full distribution of worker body size among co-occurring species within ecosystems. If there is little overlap in body size, then these ratios, averaged across the entire size range of species at either scale, should be constant. I therefore calculated the variance in these ratios (called “segment lengths”, σ^2_{sl}, *sensu* Gotelli & Ellison 2002) as an index of constancy in body size ratios. The variance of the observed ratios was compared with that of a null model composed of a histogram of 5000 ratios that were generated randomly. This histogram provided the exact tail probability for comparison with the observed value of the variance (Gotelli & Ellison 2002). A low value of the observed variance relative to a randomly assembled histogram indicates competitive structuring. I used four null models to generate the randomly constructed histogram within sites: uniform, equiprobable source pool, occurrence-weighted source pool, and abundance weighted source pool (detailed in Gotelli & Ellison 2002). The uniform null model uses the largest and smallest species to fix the endpoints of the distribution; the remainder ($n - 2$) species are chosen from a random, (log) uniform distribution within those limits. Species can be drawn multiple times. In the equiprobable model, each species on the list for a given ecosystem has the same chance of being drawn. Once a species is drawn it cannot be drawn again. In the occurrence-weighted model, species are also randomly drawn from the ecosystem species list; however, the relative probability that a species is drawn is proportional to the number of transects (1 to 3) in which it occurred. The abundance-weighted model is identical to the occurrence-weighted model except that the probabilities are calculated from the number of pitfalls or litter samples in which a species occurred (1–36). I used only the uniform model at the regional scale. Species co-occurrence patterns and body size ratios were examined using the program Ecosim (Gotelli & Entsminger 2001).

Results

At the regional scale upland ant assemblages had significantly less co-occurrence than expected by chance (large *C*-scores) for both the fixed-fixed and the weighted-fixed model (*C*-score > expected, $P < 0.01$, $P = 0.01$, respectively). Thus, there was some evidence for segregation of species among the different ecosystems but this pattern is not necessarily a result of competitive exclusion. Specifically, habitat selection may create these patterns. In contrast, at the local scale, there was no evidence of either aggregation or overdispersion, that is, species were associated randomly (Table 2). A few cases showed aggregation, but none were significant after Bonferonni correction. Even when species that were dominant or subordinate on baits were analyzed separately, they were associated randomly, and these associations were nearly identical to those for entire assemblages. No matter how the data were analyzed, there was little evidence of non-randomness of species co-occurrences.

Across the entire regional fauna, the body size of workers showed some evidence of non-random spacing. At the regional scale, body size overlap patterns appeared non-random with respect to a uniform draw of species (σ^2_{sl} < expected, $P < 0.01$). At the local scale, there was also limited evidence for non-random variance in segment length, that is, non-overlapping body sizes, among species weights (Table 3). The simple uniform model was significantly negative (evidence of even spacing of body weight) in all ecosystems. After Bonferonni correction, however, the uniform model was only significantly negative in the high pine and Florida scrub ecosystems. In contrast, the patterns of body size overlap appeared random when analyzed using equiprobable, occurrence weights, and abundance weights null models. In sum, these results provide some evidence that interspecific competition may affect the ant fauna at both the regional scale and at local scale by reducing the overlap of (at least one) species characteristics when species co-occur.

Baits were dominated by mass-recruiting species in all ecosystems, giving a biased estimate of their true abundance. A range of foraging strategies (e.g., "extirpators", "opportunists" and "insinuators", following Wilson 1971) were represented by species occurring in baits. A small number of mass-recruiting (extirpator), highly aggressive species occupied the most baits (Fig. 1). These species included *Pheidole dentata*, *Dorymyrmex bureni*, *Forelius pruinosus*, *S. invicta*, and *S. geminata*. *Pheidole dentata* was the most common species at baits, on average, in hardwood hammock (55%), Florida scrub (60%), and pine flatwoods (23%) ecosystems (Fig. 1). This species was most common in ecosystems with more ground cover and canopy cover. In more open high pine ecosystems *F. pruinosus* (23%) was the most common species at baits (Fig. 1). In the completely open fields, *D. bureni* (32%), *F. pruinosus* (21%), S. *geminata* (10%), and *S. invicta* (16%) occupied the most baits (Fig. 1). Opportunistic species and solitary foraging species that were often first to baits and easily displaced by mass-recruiting species (personal observation) were also common, including *Paratrechina faisonensis*, *Odontomachus brunneus*, and *Formica pallidefulva*. Species such as *S. carolinensis*, *P. metallescens*, and *Cardiocondyla* species often behaved as "insinuators," foraging individually or in small numbers even in the presence of mass recruiting species. Species were also plastic in their behavioral strategy — opportunistic or insinuator species occasionally mass recruited and excluded extirpator species (and vice versa).

Species at baits were among the most commonly occurring species within sites, but species occurring at baits only accounted for more

Table 3. Meta-analysis of body size overlap patterns of ants at the local scale in upland ecosystems in Florida. Communities with constant body size ratios should frequently reject the null hypothesis in the lower tail and the meta-analysis pattern would be an effect size significantly smaller than zero. Significant values after Bonferonni correction (in boldface) indicate some regularity (non-randomness) in body size patterns. The uniform model provided some evidence that species of similar body size do not co-occur in the same ecosystem.

Ecosystem	Model	Lower tail	Upper tail	Average effect size	SD of effect size	*t*	*P*	Bonferonni *P*
Hardwood hammock	Uniform	3(3)	0(0)	–1.97	0.21	–16.39	< 0.01*	**0.07**
	Equiprobable	2(1)	1(0)	–0.77	0.78	–1.71	0.23	1.00
	Occurrence weights	2(1)	1(0)	–0.77	0.78	–1.69	0.23	1.00
	Abundance weights	2(1)	1(0)	–0.76	0.80	–1.63	0.24	1.00
Pine flatwoods	Uniform	3(2)	0(0)	–1.54	0.26	–10.44	0.01*	**0.18**
	Equiprobable	0(0)	3(2)	9.10	6.61	2.39	0.14	1.00
	Occurrence weights	0(0)	3(2)	9.00	6.66	2.34	0.14	1.00
	Abundance weights	0(0)	3(2)	9.10	6.61	2.39	0.14	1.00
Florida scrub	Uniform	3(3)	0(0)	–1.96	0.05	–74.77	< 0.01*	**< 0.01***
	Equiprobable	1(0)	2(0)	0.72	1.14	1.09	0.39	1.00
	Occurrence weights	1(0)	2(0)	0.73	1.14	1.11	0.38	1.00
	Abundance weights	1(0)	2(0)	0.74	1.16	1.10	0.39	1.00
High pine	Uniform	3(3)	0(0)	–1.95	0.05	–71.56	< 0.01*	**< 0.01***
	Equiprobable	0(0)	3(0)	0.48	1.09	0.77	0.52	1.00
	Occurrence weights	0(0)	3(0)	0.45	1.03	0.75	0.53	1.00
	Abundance weights	0(0)	3(0)	0.45	1.01	0.77	0.52	1.00
Field	Uniform	3(2)	0(0)	–1.38	0.50	–4.72	0.04*	0.84
	Equiprobable	1(1)	2(1)	0.87	3.52	0.43	0.71	1.00
	Occurrence weights	1(1)	2(1)	0.96	3.53	0.47	0.69	1.00
	Abundance weights	1(1)	2(1)	0.98	3.71	0.46	0.69	1.00

*Significant at $\alpha = 0.05$.

than 50% of the total number of occurrences in hardwood hammock and pine flatwoods (Fig. 1, Totals). Additionally, the least diverse ecosystems as measured by baits were characterized by a relatively disproportionate dominance of baits by one or two species (*P. dentata* in hardwood hammock, *P. dentata* and *P. floridana* in Florida scrub). Typically, within ecosystems the mean percentage of baits a species occupied was between 25 and 50% (and in some case more) greater than the mean percentage of occurrences within ecosystems (Fig. 1). *S.* sp. nr. *carolinensis*, *P. dentigula*, and *Pogonomyrmex badius* were notable exceptions to this pattern as the mean percentage of baits they occupied was smaller than occurrences in pitfall and litter samples.

Although all of the ecosystems had a rich and diverse ant fauna, there were also large differences among them. Pitfall traps captured a total of 4142 ants litter samples 9418. This large number of specimens allowed me to detect 76 ground-dwelling ant species, and 94 species in total, across all of the sampled ecosystems, representing 70%–90% of the species present there (King & Porter 2005). The average number of species was highest in high pine sites (35 ± 7; mean ± 1 SD) followed by Florida scrub (29 ± 3), pine flatwoods (27 ± 6), hammock (21 ± 4) and field sites (20 ± 4). The richest genera were *Solenopsis* (10 species), *Pheidole* (7 species), *Camponotus* (6 species), *Paratrechina* (6 species) and *Pyramica* (6 species).

Discussion

Competitive asymmetry is generally believed to be the primary mechanism by which many behaviorally dominant species, including several exotic invasive species of ants, achieve dominance and affect other species (Vepsäläinen & Pisarski 1982, Savolainen & Vepsäläinen 1988, Hölldobler & Wilson 1990, Andersen & Patel 1994, Holway *et al.* 2002). This conceptual viewpoint has risen to prominence in the literature on invasive species, community organization, and social insect biology (Hölldobler & Wilson 1990 and references therein, Holway *et al.* 2002, LeBrun 2005). However, much of the

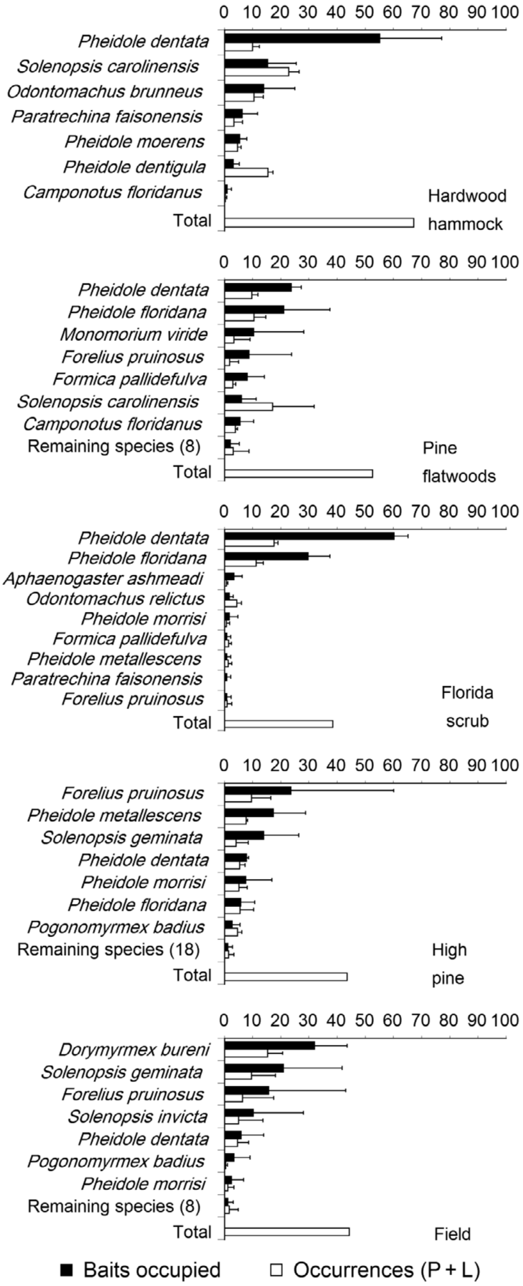

Fig. 1. Comparison of occurrence (%) of ant species at baits with their occurrence (%) in pitfall and litter samples. Bait values represent the average percentage of baits occupied across three replicate sites per ecosystem. Occurrence values represent the average percentage of occurrences for combined pitfall (P) and litter (L) samples per ecosystem. Total values (the bottom bar of each histogram) represent the average total percentage of occurrences, among all species occurrences in pitfall and litter samples, of species that occupied baits. Error bars represent one sample standard deviation.

evidence for this hypothesis involved overly broad extrapolation from baiting studies. Generally, this approach assumes that the outcomes of interactions at baits, which are relatively easy to observe, can be mapped simply onto conclusions about the role of competition in community assembly (e.g., LeBrun 2005, Parr *et al*. 2005). Our understanding of ant community ecology will benefit from additional experimental evidence (e.g., Gibb & Hochuli 2004, King & Tschinkel 2006) and community-wide tests for competition induced assembly rules (Gotelli & Ellison 2002, Ribas & Schoereder 2002). These approaches, including this study, have so far revealed a contrasting view that competition, at least in the form of competition hierarchies is not obviously impacting community-wide assembly patterns. Further studies of the same type conducted in a variety of ecosystems and regions are needed to validate this alternative view.

Again, competition theory predicts that when species compete, they should (1) co-occur less often than expected by chance among communities, and (2) within communities, the species that do co-occur should differ in morphology or body size, i.e., should exploit different resources (Brown & Wilson 1956, Diamond 1975). The co-occurrence patterns of ants I sampled provide only limited support for these predictions (Tables 2 and 3). However, the prediction that dominant, territorial ant species should strongly influence which species can coexist with them, and in what abundance at the local scale (Levings & Traniello 1981, Hölldobler & Wilson 1990) was not supported in any way. So, while there was some limited evidence that interspecific competition may, for example, structure these ant communities through ecological assortment by worker body size or even character displacement, the patterns suggest that it does not take the form of competition hierarchies in a specified, present-day locality (Vepsäläinen & Pisarski 1982, Cole 1983, Savolainen & Vepsäläinen 1988, Hölldobler & Wilson 1990, Andersen & Patel 1994).

At the regional scale, factors other than competitive exclusion can also limit species co-occurrence. Habitat preference, in particular, is clearly important in determining the distribution of a number of species. Among the species in this study, 5 species are endemic to these ecosystems in Florida (*D. bossutus*, *D. elegans*, *F. sp. nov.*, *O. relictus*, *P. phantasma*, *P. wojciki* and *P. adrianoi*) and are closely associated with (adapted to) bare, sandy areas in the xeric high pine and Florida scrub ecosystems. Similarly, there are species that only occur in more mesic areas such as pine flatwoods (*Temnothorax palustris*) and hardwood hammock (*Myrmecina americana*). Two likely mechanisms for such patterns are habitat preference (i.e., "habitat checkerboards") or historical, biogeographical influences ("historical checkerboards") which can also create the appearance of reduced species co-occurrence (Gotelli & McCabe 2002).

At the local scale, that is, at the scale at which ants potentially interact, species co-occurrence patterns were random or tended toward aggregation (Table 2). This was true even when co-occurrence among species at baits were examined (data not shown). Furthermore, despite the presence of numerous exotic, invasive species (e.g., *S. invicta*) in these ecosystems, there was no obvious effect of behaviorally dominant species on co-occurrence patterns. The limited impact and species characteristics of exotic ants in these ecosystems is fully examined elsewhere (King & Porter [In press]). These patterns of co-occurrence are similar to those documented for New England ant assemblages in forests and adjacent bogs where regional scale co-occurrence patterns were non-random and local scale co-occurrence patterns were random (Gotelli & Ellison 2002).

To date, the strongest evidence for interspecific competition within ant communities comes from numerous observations of pairs of related, ecologically similar species (e.g., Brown & Wilson 1956, Pontin 1961, 1963, Hölldobler & Wilson 1990). In contrast, testing for affects of competition across entire ant communities using null model analyses are relatively rare but have revealed no evidence for assembly rules dictated by competition (Simberloff 1983, Gotelli & Ellison 2002, Ribas & Schoereder 2002). Factors other than interspecific competition are probably more important in determining the assembly rules of these communities. For example, competition among colonies of the same species (intraspecific competition) may be the most important form of competition affecting the distribution and abundance of ant species (Ryti & Case 1986, 1988, 1992, Tschinkel 2006). Habitat type and disturbance have the greatest influence on the distribution of many species in this fauna (King & Tschinkel 2006, King & Porter [In press]). Additionally, the patterns of non-randomness in species spatial distributions at the local, within habitat scale that I observed might also arise from mechanisms other than competition, such as neutrality (Ulrich 2004, Bell 2005), spatial heterogeneity (Urban 2004), or differential migration ability (Molovsky & Bever 2002).

The patterns of co-occurrence and body size overlap in Florida's upland ant communities suggest that these ant communities differ little from other insect communities in that the impact of territorial, behaviorally dominant species is probably mediated by body size, trophic status, abiotic limitations, habitat preferences, and stochastic patterns of colonization (Herbers 1989, Kaspari 2001, Ribas & Schoereder 2002). For example, analyses of pairwise interactions among other insect taxa have also shown that the only competition between species that is apparent in "open" phytophagous insect communities occurs between similar, closely related species (Denno *et al.* 1995, Price 1997). Most ants (including some of the most abundant and behaviorally dominant species) are partly or wholly primary consumers (Tennant & Porter 1991, Tobin 1994, Davidson *et al.* 2003) and their patterns of relative abundance are often positively correlated with the productivity of the ecosystems they occupy (Kaspari *et al.* 2000, Kaspari 2001). The evidence for ecological assortment or character displacement by worker body size in this fauna suggests that this should be tested further and perhaps include colony size as well, in different habitats. So, while competition between species may result in ecological assortment (Strong *et al.* 1979, Dayan & Simberloff 2005) or character displacement (Brown & Wilson 1956) between similar species over long time spans and large areas, it does not appear to form competition hierarchies among species on the local scale at which ants actually interact.

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