

## Nineteen years of field data on ant communities (Hymenoptera: Formicidae): What can we learn?

Joan M. HERBERS



### Abstract

For 19 consecutive years I sampled litter-ant communities in three temperate deciduous forests in the northeastern USA (West Virginia, New York, Vermont). Cumulative species richness per site ranged from 13 to 16 species but had not reached a sampling asymptote at the southern-most site (West Virginia). Nest density varied seasonally, but was consistently higher in the two northern sites (New York and Vermont). In the Vermont site, nest density declined significantly over the 19 years, probably because of ongoing forest succession; studies of ant community shifts to infer large-scale phenomena such as global climate change must separate out such background temporal variation. We detected patchiness of ant nests at three spatial scales. The smallest-scale reflected colony subdivision (polydomy) whereas medium-scale and large-scale patchiness reflected habitat heterogeneity; differences between sites indicated effects at a larger regional scale as well. There was little evidence that competition between species affected co-occurrence or nest spacing. While resource competition and behavioral interactions predominate in many ant assemblages, their effects appear to be weak in temperate litter-ant assemblages.

**Key words:** Community structure, competition, patchiness, temporal variation.

Myrmecol. News 15: 43-52 (online 12 February 2011)  
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 1 September 2010; revision received 24 November 2010; accepted 26 November 2010

*Prof. Dr. Joan M. Herbers, Evolution, Ecology & Organismal Biology, Ohio State University, 484 W. 12<sup>th</sup> Avenue, Columbus, Ohio 43210, USA. E-mail: Herbers.4@osu.edu*

### Introduction

Ants are abundant, easy to observe in the field, and manifestly important to ecosystem function (HÖLDOBLER & WILSON 1990); their ubiquity and ease of study have made them a prime taxon for studies of community structure (LACH & al. 2009). A large literature shows that inferences about ant communities are highly dependent on spatial scale (BESTELMEYER & WIENS 2001, SOARES & al. 2001). Some authors report intensive work in a single locale (e.g., RYTI & CASE 1986, GOTELLI 1996) whereas others take a broader sweep across different ecosystems (e.g., KASPARI & al. 2000, BESTELMEYER & al. 2000, BESTELMEYER & WIENS 2001, GOTELLI & ELLISON 2002, LUBERTAZZI & TSCHINKEL 2003). Ant communities are subject to a multitude of factors that work at different scales, from local competition to latitudinal clines and continental weather patterns (GERAGHTY & al. 2007, ANDERSEN 2008, DUNN & al. 2009b).

By contrast, the temporal scale over which a study is performed tends to be extremely limited; while seasonality has been explicitly treated (HERBERS 1989, LINDSEY & SKINNER 2001, BARROW & PARR 2008), most studies of ant communities remain ecological snapshots. Long-term studies of individual species have provided important insight to population processes (ELMES 1987, GORDON & KULIG 1998, COLE & WIERNASZ 2002), but longitudinal studies of entire ant communities with sustained methodology are rare (SAMWAYS 1990). Here I report such a longitudinal community study, carried out in two geographic sites

over a span of 19 consecutive years, and compare inferences to those from a third site for which only snapshot data are available. Data collected in the same way across multiple years allow comparisons between geographic sites, within sites across years, and among seasons within those years. I show below that temporal scale can be as important as spatial scale for exploring community structure.

A large literature on ant communities treats both exploitative competition and interference competition (PARR & GIBB 2009), and the tension between these two forms has been encapsulated in the "discovery-dominance trade-off" hypothesis (DAVIDSON 1998, ADLER & al. 2007). The fundamental currencies for competitive interactions are food and shelter (BLÜTHGEN & FELDHAAR 2009), which themselves vary across habitats. Competition for space and its associated foraging area seems to predominate in arid environments (ANDERSEN 1986, RYTI & CASE 1992, BESTELMEYER 1997). By contrast, competition for nesting sites seems important in some tropical and temperate habitats (HERBERS 1989, BYRNE 1994, KASPARI 1996, SAGATA & al. 2010). In the tropics, litter-dwelling ant communities can be quite distinct from arboreal or ground-dwelling communities (YANOVIK & KASPARI 2000). Despite their ubiquity, then, ants respond to ecological variables differently across habitat types.

In previous papers (HERBERS 1985, 1989), I reported on species composition and nest spacing in two of the sites

Tab. 1: Sampling effort over years and seasons. Entries are the number of plots and total area of forest floor (in m<sup>2</sup>) cleared.

Site	Year	Spring	Summer	Autumn	Winter	Total
West Virginia	1988 1989	3, 147	3, 147	3, 147	3, 147	2 years 12 plots 588 m <sup>2</sup>
New York	1980 1981 1983 1984 1987 1988 1992 1993 1996 1998	5, 125 8, 200 1, 100 3, 147 3, 121 1, 49	10, 250 8, 200 3, 75 3, 147 3, 108 3, 121 12, 432	1, 25 4, 196 3, 108	3, 108	10 years 73 plots 2512 m <sup>2</sup>
Vermont	1985 1986 1987 1989 1990 1991 1992 1994 1995 1998	1, 25 3, 108  3, 108	5, 222 3, 121 5, 125 2, 98 3, 122 3, 108 12, 432 2, 72 4, 100	1, 36 2, 72 2, 72	3, 108	10 years 54 plots 1929 m <sup>2</sup>

considered here. The earlier papers, each based on a single year's data per site, established that for temperate deciduous forest ants, seasonality of nest spacing and species co-occurrences were pronounced. I interpreted those data in terms of complex colony structure, competition for scarce resources, and microhabitat preferences. With the database examined here I can re-examine whether those earlier inferences were supported over a longer time scale.

## Methods

The data reported here span 19 years and three sites. The West Virginia site (WV), located in Watoga State Park (Pocahontas County); the New York site (NY), on the E.N. Huyck Preserve (Albany County); and the Vermont site (VT) in Mallett's Bay State Park (Chittenden County) all contain temperate deciduous forests. The VT and NY sites have been described in detail elsewhere (HERBERS 1989), and the WV site is very similar to that studied by CULVER (1974). WV (38° N, 81° W, elevation 1000 m) became a State Park 80 years ago; NY (42° N, 74° W, elevation 600 m) has been a nature preserve for 90 years; VT (44° N, 73° W, elevation 30 m) was made a State Park only recently, but has been relatively undisturbed for 50 years. Each site has mixed deciduous-conifer forest with oaks more common in WV and VT relative to NY. Tree trunks were noticeably smaller in the VT site than the other two, which suggests the forest there was in an earlier successional state. The understory was least dense in NY, and VT was wetter than the other two. WV and NY are in mountainous regions, whereas VT is floodplain with escarpments. Reverse gradients in altitude and latitude across the sites yield similar weather conditions: average annual temperature is 7.1°C in WV, 7.1°C in NY, and 7.2°C in VT; average annual precipitation is 92 cm in WV, 90 cm in NY, and 86 cm in VT. The similar climates produce growing seasons of the same length, and sexuals appeared in ant nests at the same times of year across the sites. These

ecological similarities thus provide an opportunity for cross-site comparisons.

I restricted my collections to well-canopied second-growth forest, working within a total area of about 1000 hectares at each site and using one standard sampling technique over the years. Quadrats ranging in size from 25 m<sup>2</sup> to 100 m<sup>2</sup> were set up in the woods, separated by at least 10 meters. From year to year we located these quadrats randomly in the forests to minimize confounding spatial and temporal variation.

We cleared all plots to soil level. My field crews and I inspected cavities such as empty sticks, rolled leaves, and acorns, and also looked under every stone to find ant nests. When an ant nest was located, its position was marked. After the entire quadrat had been cleared, we mapped spatial locations of every ant nest contained therein. This method was exhaustive, and I am confident that we found every nest of litter-dwelling ants. It is likely that we missed some hypogaecic species (SCHMIDT & SOLAR 2010), and we almost surely missed arboreal ant nests. Even so, the consistency of our collecting methodology does allow for comparisons of the litter-ant community across years and sites. More than 5000 square meters in 138 plots were cleared. Sampling effort was not uniformly distributed across seasons, years or sites (Tab. 1). Sampling efforts were similar for the two northern sites (73 plots and 2512 m<sup>2</sup> in NY and 54 plots and 1919 m<sup>2</sup> in VT), but were substantially lower for the WV community (12 plots and 588 m<sup>2</sup> total). Data were collected over two years in WV versus ten years in NY and VT. Sampling in autumn and winter were thin, whereas efforts in spring and summer were more extensive. Plots were cleared from the WV site over one year only, in 1988 - 1989; these data constitute a "snapshot". Longitudinal data were collected from the NY site intermittently from 1980 through 1998, and from the VT site intermittently from 1985 through 1998. Thus two sites allow long-term investigation of community structure.

Tab. 2: Species lists for the three study sites (per FISHER & COVER 2007); incidence is measured as the proportion of all cleared plots upon which each species was found while abundance is measured as the proportion of all nests collected. Nest size classes: 1) small, with fewer than 25 workers; 2) medium, 25 - 75 workers; 3) large, 75 - 200 workers; 4) very large, more than 200 workers.

Species	West Virginia (12 plots, 410 nests)		New York (73 plots, 2894 nests)		Vermont (54 plots, 3532 nests)		Nest size
	Incidence	Abundance	Incidence	Abundance	Incidence	Abundance	
<i>Amblyopone pallipes</i> (HALDEMAN, 1844)	16.7%	0.5%	45.2%	2.5%	9.3%	0.1%	1
<i>Aphaenogaster rudis</i> ENZMANN, 1947	66.7%	14.6%	38.4%	1.7%	72.2%	5.7%	2
<i>Brachymyrmex depilis</i> EMERY, 1893	0		1.4%	0.1%	1.9%	0.2%	2
<i>Camponotus pennsylvanicus</i> DEGEER, 1773	25.0%	0.7%	6.8%	0.3%	13.0%	0.3%	3
<i>Formica neogagates</i> (VIERECK, 1903)	0		15.1%	0.5%	3.7%	0.1%	3
<i>Lasius alienus</i> (FOERSTER, 1850)	83.3%	6.6%	74.0%	10.4%	96.3%	22.1%	4
<i>Lasius nearcticus</i> (WHEELER, 1906)	0		68.5%	10.6%	33.3%	1.3%	4
<i>Lasius umbratus</i> (NYLANDER, 1846)	58.3%	5.6%	0		0		3
<i>Myrmecina americana</i> EMERY, 1895	58.3%	3.7%	8.2%	0.3%	24.1%	2.3%	1
<i>Myrmica americana</i> (WEBER, 1939)	0		9.6%	0.5%	5.6%	0.1%	2
<i>Myrmica punctiventris</i> ROGER, 1863	91.7%	27.1%	65.7%	12.8%	94.4%	29.0%	2
<i>Ponera pennsylvanica</i> BUCKLEY, 1866	8.3%	0.2%	0		0		1
<i>Protomognathus americanus</i> (EMERY, 1895)	58.3%	4.4%	43.8%	4.3%	27.8%	1.6%	2
<i>Stenamma diecki</i> (EMERY, 1895)	8.3%	0.2%	61.6%	5.8%	46.3%	2.7%	1
<i>Tapinoma sessile</i> (SAY, 1836)	16.7%	1.5%	0		7.4%	0.3%	2
<i>Temnothorax ambiguus</i> (EMERY, 1895)	0		15.1%	1.3%	46.3%	5.1%	2
<i>Temnothorax curvispinosus</i> (MAYR, 1866)	25.0%	4.9%	0		0		2
<i>Temnothorax longispinosus</i> (ROGER, 1863)	100.0%	30.0%	94.5%	49.1%	88.9%	29.1%	2
<i>Temnothorax</i> sp.	0		0		3.7%	0.2%	2

Ants were identified to species (FISHER & COVER 2007). Voucher specimens were deposited in the Zadock Thompson Natural History Collection at the University of Vermont, and at the Museum of Comparative Zoology Wheeler Collection at Harvard University.

The data reported below use the nest as a sampling unit. For several common species (in the genera *Temnothorax*, *Myrmica*, and *Lasius*) nests can be organized into larger family units termed polydomous colonies (HERBERS & GRIECO 1994, BANSCHBACH & HERBERS 1996a), and ambiguity concerning colony boundaries is problematic for understanding biological interactions (DEBOUT & al. 2007). Even so, detailed work has shown that for *Temnothorax longispinosus* and *Myrmica punctiventris*, the local nest rather than the larger colony is the functional ecological unit (HERBERS & STUART 1996, BANSCHBACH & HERBERS 1999). Thus inferences about community structure can be made by consideration of nest-level ecological data, and we interpret our results in light of colony polydomy.

Estimates of species diversity were computed for each site by the program EstimateS (viceroy.eeb.uconn.edu/estimates). Sample coverage was assessed by performing 50 randomizations of the species-by-plot incidence data to generate standard errors. Two classes of estimators exist, the first based on relative abundance of each species in the sample and a second based on presence / absence. Incidence-based estimators circumvent the problems of identifying what constitutes a colony in polydomous species (since each is counted only once in a plot) yet they lose consider-

able ecological information afforded by numerical abundance data. I report both classes below and make interpretations accordingly.

To examine the scale of patchiness in these communities, I first examined differences in species occurrences and abundance between plots in each site. That approach implies a scale greater than 1000 m<sup>2</sup>. To examine patchiness at smaller scales, I applied blocked quadrat methods to nest spatial distributions on two large plots (each 100 m<sup>2</sup>). The method of choice, random paired quadrat variances (GOODALL 1974), relies on very large quadrats to achieve adequate sample sizes. Since my largest quadrats were only 100 m<sup>2</sup>, I used instead the paired quadrat variance method (LUDWIG 1979). This approach measures the variance in density as larger and larger contiguous blocks of habitat form the unit of sampling. I therefore calculated nest density for blocks ranging from 1-m<sup>2</sup> doubling throughout to 64 m<sup>2</sup>, via sliding windows. Any peaks in the distribution of density variance with increasing block size indicate patchiness (LUDWIG 1979). Thus decomposition of the variance in density according to block size allows one to make inferences about the ecological scale at which patchiness is important.

## Results

### Overall description of the communities

Table 2 gives a synopsis of data collected throughout this study. Overall, 19 ant species were collected across the three sites. Table 2 reports both incidences (proportion of

all plots on which they occurred) and relative frequencies (proportion of all nests that were collected). Nine species occurred in all three sites, and the two northern communities shared 14 species. Examination of the species lists shows that the WV community was the least like any other; it contained nine unique species, whereas VT contained two unique species and NY none. Even so, the most common species in each of the sites were *Temnothorax longispinus*, *Lasius alienus*, and *Myrmica punctiventris*. I compared incidence of individual species between NY and VT by contingency table analysis. Those results (G-tests, with Bonferroni correction for multiple tests) showed that four species had significantly higher incidence in VT (*Aphaenogaster rudis*, *Temnothorax ambiguus*, *Lasius alienus*, and *Myrmica punctiventris*) whereas two had higher incidence in NY (*Amblyopone pallipes* and *Lasius nearcticus*). Species that were relatively rare in one site were rare in all: The abundance ranks of the nine species occurring across all three sites were strongly concordant (Kendall's coefficient  $W = 0.774$ ,  $P = 0.02$ ). Therefore the similarities in species composition across sites outweighed the differences.

Figure 1 shows species accumulation curves, and they strongly suggest that I under-sampled the WV community. However, the asymptotes for NY and VT show they were sampled virtually to exhaustion. I used EstimateS to generate standard deviations for estimated total species numbers as a function of sampling effort. The Chao-2 estimates in Figure 2 leveled off quickly and had reduced variance with sampling effort for NY ( $S_{est} = 13$ ) and VT ( $S_{est} = 16$ ). By contrast, our limited sampling in WV yielded an estimate of 14 species, but the data gave neither a clear asymptote nor smaller variance with increased sampling effort (Fig. 2). The analysis suggested that as many as three species were missing from our WV samples, but only one species was missing from the NY and VT lists. Thus inferences about the WV community are less robust than for the NY or VT community. The log-series  $\alpha$  estimate of diversity was 2.56 in WV, 1.93 in NY, and 2.17 in VT. The Simpson and Shannon diversity indices likewise gave values lowest in NY and highest in WV. Despite considerable argument about the intrinsic meaning of diversity indices (MAGURRAN 1988), all consistently showed that diversity was lowest in New York and highest in West Virginia.

### Ecological importance of individual species

My basic datum is the ant nest. Yet number of nests is insufficient to describe community dynamics because species vary in colony size and worker body size. Thus a species with few nests in an area can have a disproportionate effect if those nests are very large, if the ants themselves are aggressive, or if they quickly recruit to food sources (DAVIDSON 1998). Table 2 includes an indication of nest size for the species in my three study sites. Colony sizes ranged from the very small and cryptic nests of *Amblyopone pallipes* to the relatively large and diffuse nests of *Lasius alienus*. Even the largest nests in these forests, though, are dwarfed by species such as fire ants and army ants that can have colonies several orders of magnitude larger.

Previous work has demonstrated geographic variation in nest and colony size for at least three of the species in Table 2. The acorn ant *Temnothorax longispinosus* has smaller nests in WV than in NY and VT, as does its so-

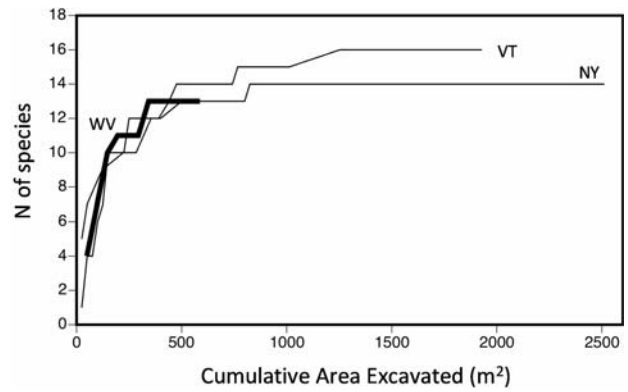


Fig. 1: Species accumulation curves. WV = West Virginia; NY = New York; VT = Vermont.

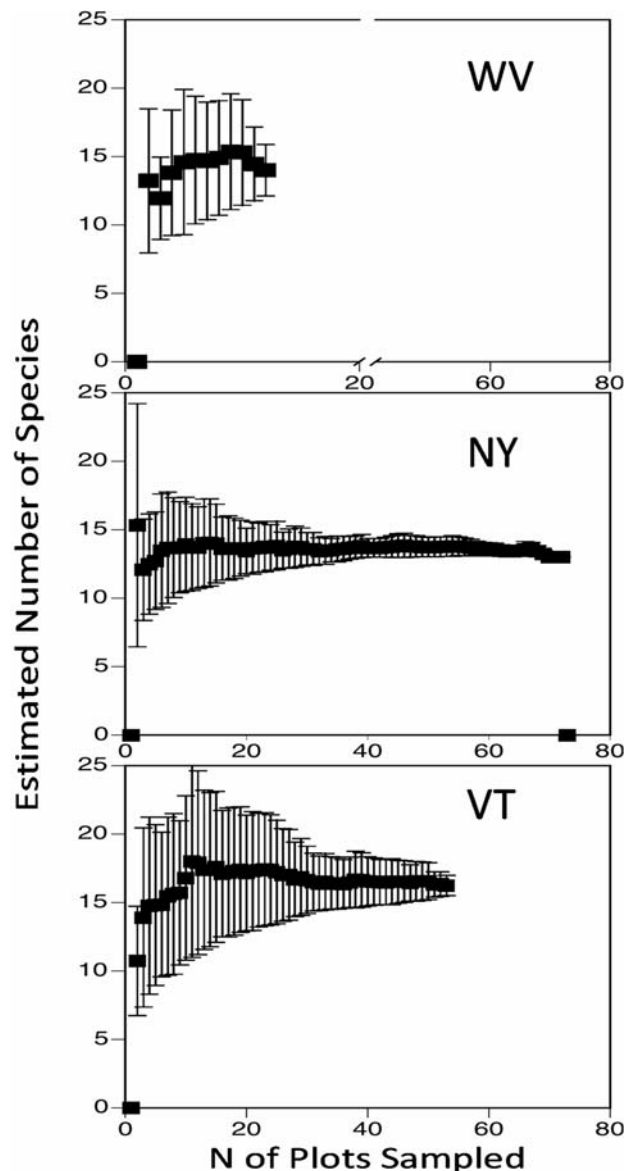


Fig. 2: Estimates of species number (given here for the Chao-2 estimator) converged with increasing sample size, especially for NY and VT. Estimates of  $S$  and their standard errors were computed by the program Estimate-S; abbreviations as in Figure 1.

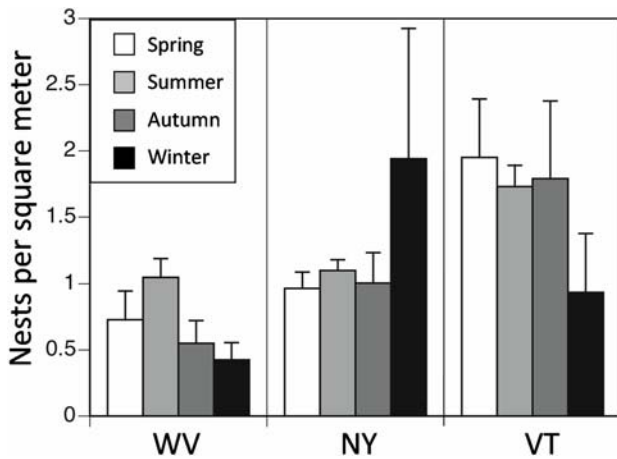


Fig. 3: Density of ant nests across seasons in the three sites. Abbreviations as in Figure 1.

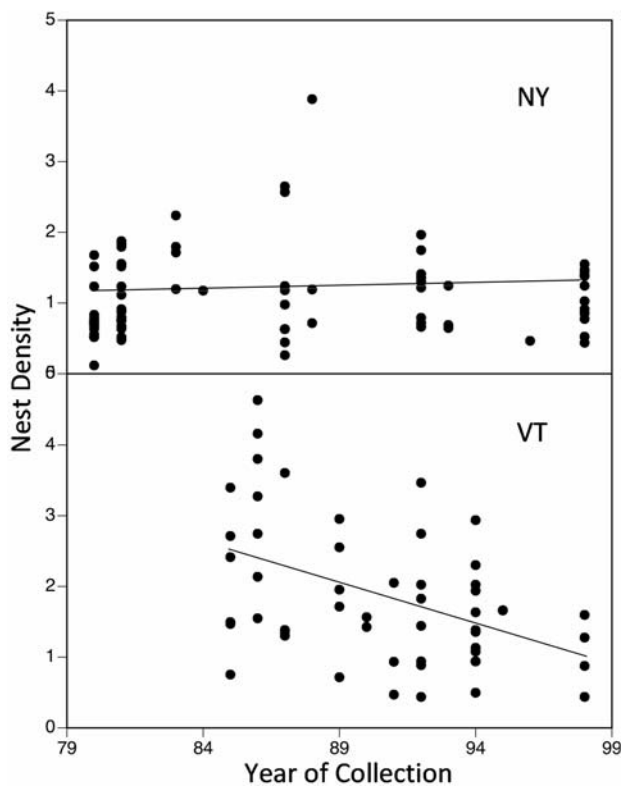


Fig. 4: Nest density over the years of the study; each point represents one plot. The least-squares regression lines are superimposed on the data; the regression was significant in VT but not in NY. Abbreviations as in Figure 1.

cial parasite, *Protomognathus americanus* (see HERBERS & FOITZIK 2002). Perhaps most interesting is *Myrmica punctiventris*, which differs in virtually every aspect of its social organization between NY and VT. For that species, colony size is no different, but nest size differs strongly between the sites. In NY colonies tend to occupy only one nesting site, whereas in VT they are fractionated into several different nesting sites (BANSCHBACH & HERBERS 1996a). The net result of these differences is spatial patchiness of this species in NY and ubiquity in VT (Tab. 2). Thus comparisons across sites are confounded by differences in colony and / or nest size for some of the species.

### Nest density

Because sampling effort and plot sizes were variable (Tab. 1), I converted absolute numbers of nests into densities. Overall, there were 0.69 ant nests / m<sup>2</sup> in WV, 1.10 in NY, and 1.82 in VT, but those densities varied considerably from plot to plot within a site, between sites, and across years. Average nest density was lower in WV and highest in VT (Fig. 3; ANOVA with orthogonal contrasts;  $P < 0.05$ ), but there were no consistent seasonal shifts in nest density and no interaction between site and season (two-way ANOVA; effect of site  $P < 0.01$ ; effect of season and interaction effect, both  $P > 0.05$ ). Therefore, I pooled density data across seasons within a site to examine long-term trends.

The NY and VT data span 19 and 14 years, respectively, and over the whole community, nest density in VT declined significantly over that period (Fig. 4; regression coefficient =  $-0.113 \pm 0.032$  nests / year;  $P < 0.001$ ); no such effect was observed for NY (slope =  $0.006 \pm 0.011$  nests / year;  $P > 0.05$ ). The decline in Vermont was observed in each of the four seasons, and was not an artifact of differential sampling across years there. Rather, the composite effect (Fig. 4) reflected declining nest density for individual species: Regression coefficients were negative for eight of nine species (binomial  $P < 0.0001$ ) and significantly so for *Temnothorax longispinosus* and *Lasius alienus* (regression analysis with Bonferroni corrections,  $P < 0.05$ ). I separated the nests into incipient colonies (i.e., those with a queen and brood but no workers) and mature nests (having workers). Negative slopes again were obtained ( $-0.008$ ,  $P = 0.002$  for incipient colonies;  $-0.105$ ,  $P = 0.0013$  for mature nests). The decline in ant nest density in VT was a community-wide phenomenon. Furthermore, our last measurements showed density there was similar to that measured in NY throughout our sampling.

A decline in nest density might produce increased distances between neighboring nests, and so I examined distance to nearest neighbor and to nearest conspecific neighbor for the spring and summer data (Fig. 5). In both sites, the distance to nearest neighbor increased over time (regression analysis; slope = 0.38 cm per year in NY,  $P = 0.002$ ; in VT, slope = 0.96 cm / year;  $P < 0.0001$ ), and the increase was faster in VT than in NY (analysis of covariance; effect of site,  $P < 0.0005$ ). Thus in both sites, the spacing between ant nests increased over time, but that increase was shallow in NY and almost three times steeper in VT. Distance to nearest conspecific neighbor (Fig. 5) likewise increased (NY slope = 1.16 cm / year and VT slope = 0.95, both  $P < 0.0001$ ). Multiple regression showed that in NY the increase in distance to nearest conspecific was responsible for the temporal change in distance to nearest neighbor: The year effect became statistically insignificant when distance to nearest conspecific was factored out ( $P < 0.05$ ). By contrast, the VT data showed that distance to nearest neighbor increased over the years, even when distance to nearest conspecific was factored out ( $P < 0.0001$ ). Therefore the entire community was not spacing out over time in NY, but rather subunits of polydomous colonies were. In Vermont, however, the entire ant community spaced out increasingly over the years, including species with polydomous colonies.

I examined the neighbor-distance data for individual species as well. In NY, regressions of distance to nearest



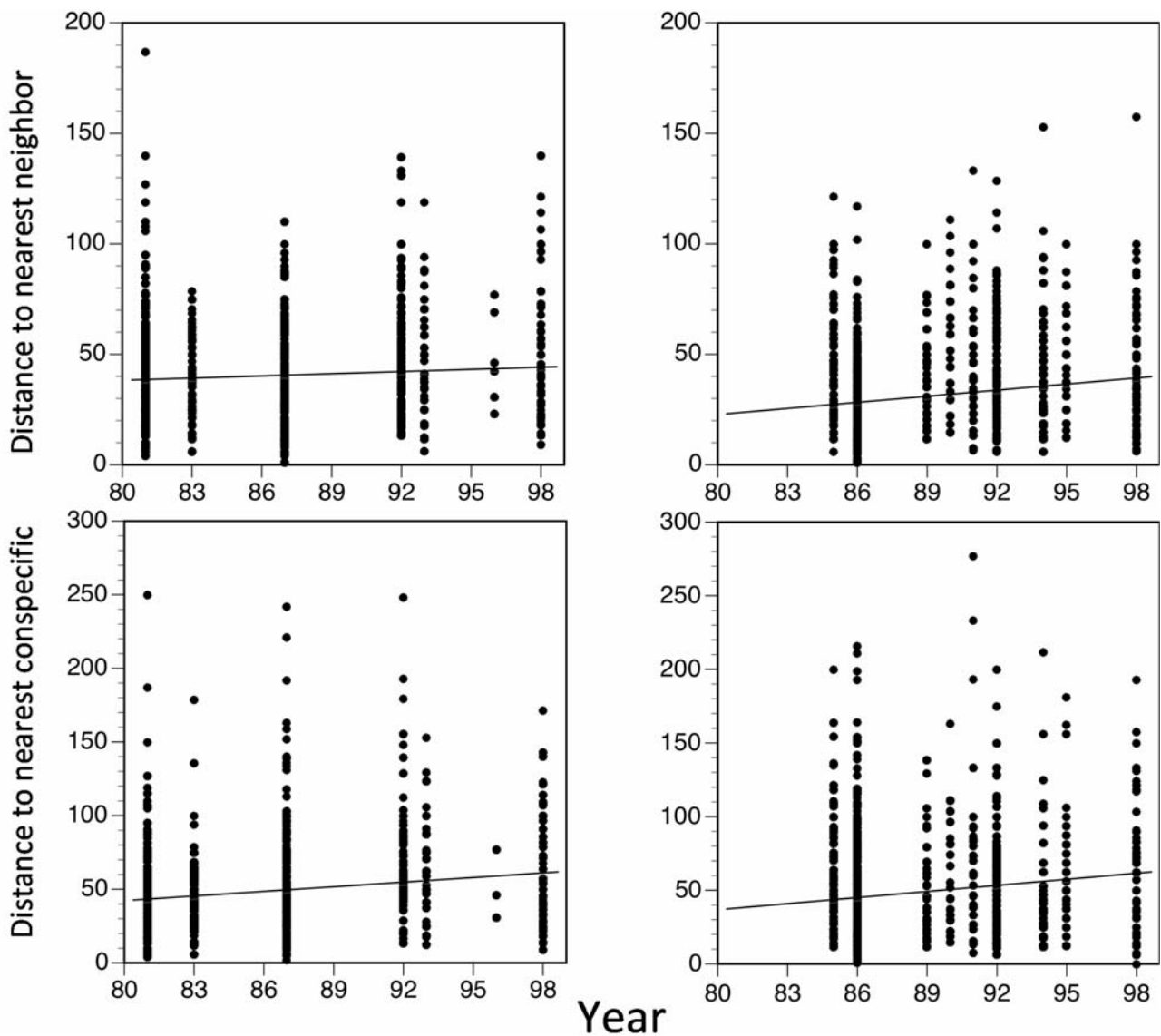


Fig. 5: Distances to nearest neighbor and nearest conspecific increased over the course of this study in both northern sites. Data on the left side represent NY and those on the right VT. Each point gives data for one species on one plot. The least-squares regression lines are superimposed on the data. Abbreviations as in Figure 1.

neighbor on time showed a positive slope for six of eight species (binomial  $P = 0.11$ ) whereas for VT all nine species increased in distance to neighbor over time (binomial  $P = 0.002$ ). Distance to nearest conspecific increased over time for three of six species in NY (binomial  $P = 0.50$ ) and six of eight species in VT ( $P = 0.11$ ). Together, the density and neighbor distance results confirm long-term decline in ant nest numbers in VT but not in NY.

### Spatial patchiness

The incidence data (Tab. 2) indicate patchiness at scales exceeding  $100 \text{ m}^2$ . Presence / absence information for individual plots shows that the tiny acorn ant *Temnothorax longispinosus* was virtually ubiquitous in these sites whereas other species occurred in only a subset of the cleared plots. Incidence and abundance were strongly correlated within each site (Tab. 2; Spearman's rank correlations,  $P < 0.001$  in each site); that is, rare species tended to have spotty distributions while common species were abundant on most

plots. I examined patchiness explicitly by computing for each species the Poisson expectations for numbers of nests per plot. The Poisson is characterized by having its variance equal to the mean; thus the ratio of variance to mean from a sample indicates dispersion: Values greater than 1.0 indicated under-dispersion (aggregation) whereas values less than 1.0 indicated over-dispersion (HERBERS 1986). Because the Poisson distribution fits rare events, the approach allowed me to examine whether species with incidences below 0.5 were simply rare or were instead patchily distributed: Patchy species by definition were locally abundant but found irregularly. For this analysis, I used data only from plots collected in spring and summer, since many of these species spend the winter below-ground (HERBERS 1989). The results (corrected for multiple tests) showed that four species in NY (*Lasius alienus*, *Lasius nearcticus*, *Myrmica punctiventris*, and *Protomognathus americanus*) were truly patchily-distributed. In VT, three different species were patchily distributed (*Aphaenogaster rudis*, *Tem-*

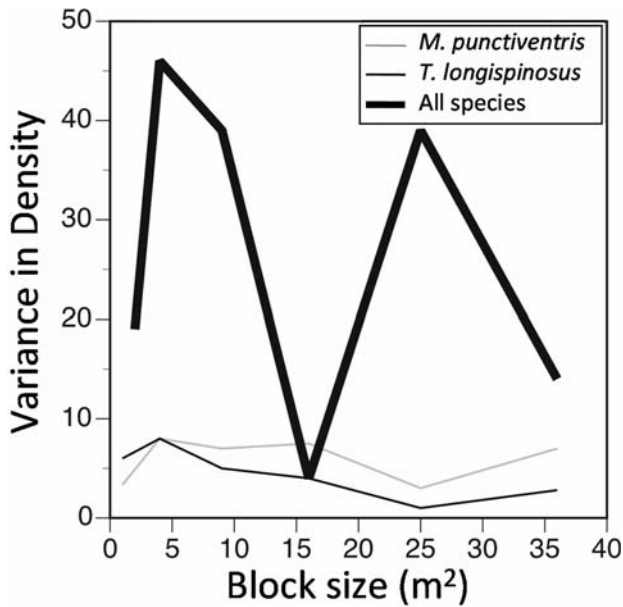


Fig. 6: Results of paired-quadrat-variance analysis. Peaks in the distribution of variance with increasing sampling units (block size) indicate the scale of patchiness in a spatial distribution.

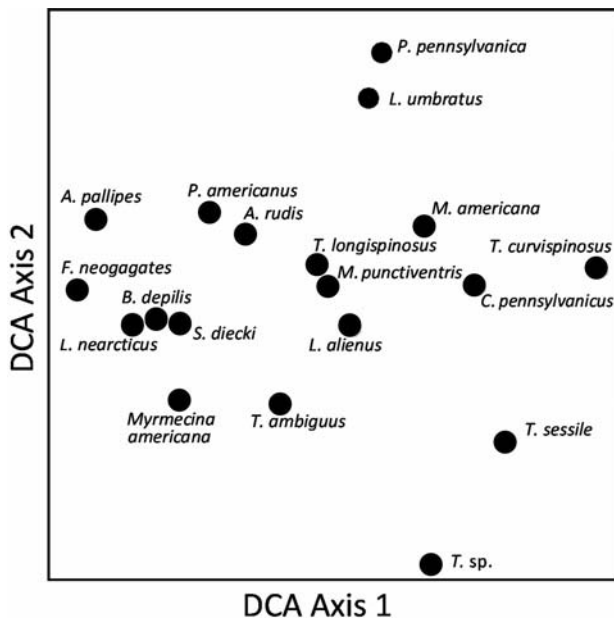


Fig. 7: Results of detrended correspondence analysis (DCA) on the abundances of ant species within plots.

*nothorax ambiguus*, and *Stenammina diecki*). For these patchy species there was an excess of plots with either zero or many nests.

Incidence data therefore showed that some ant species were patchily distributed at a large scale. I also looked for evidence of patchiness on a smaller scale, within a given plot. Nests in NY and VT were aggregated in space (HERBERS 1985, HERBERS 1989) and in each site nests were closer to each other than chance expectation (G-tests based on the Poisson distribution;  $P < 0.01$  for NY, VT, and WV). Community-wide nest aggregation reflects two factors. Some species have spatially subdivided (polydomous) col-

onies, such that one family unit is spread over multiple nesting sites; this leads to local nest clustering at a fine scale. Second, microhabitat patchiness is important for these ants, many of which use plant cavities for nesting sites (HERBERS 1989). Both quality and quantity of these cavities reflect the overhead canopy. Under oaks, acorns predominate on the forest floor while beech trees in the canopy provide an abundance of hollow twigs; by contrast, suitable nest sites are scarce under hemlocks. Thus two factors, polydomy and habitat heterogeneity, should produce patchiness at different scales, both smaller than the patchiness we uncovered from incidence data across entire plots.

To disentangle the two scales that occurred within plots, I looked explicitly for indications of scale in the spatial data via paired quadrat variance methods (LUDWIG 1979). Three separate analyses were run: one for each of the two most common species, *Temnothorax longispinosus* and *Myrmica punctiventris* (which have polydomous colonies), and a third for the entire ant community. Ant nest density was much more variable when all species were included than when the two most common species were analyzed separately (Fig. 6); this result simply reflects that common species are common everywhere, and thus have low variance in density. More importantly, the curves for the two species known to be polydomous yielded peaks in variance at about 4 - 5 meters, the scale on which polydomy has been previously established. Over all species (Fig. 6), one peak corresponded to patch size of about five square meters, and a second peak to 25 square meters. Thus three scales of patchiness appear important in this community.

#### Species composition and co-occurrence over time

Previous analysis showed that some species pairs were nearest neighbors more often than chance expectation (HERBERS 1989), a pattern that seemed to reflect habitat variation. To examine this hypothesis more systematically, I subjected the presence-absence data of species on plots to a detrended correspondence analysis (DCA). The results (Fig. 7) show that species ordered surprisingly uniformly in DCA space. As expected, species collected only in one site (e.g., *Ponera coarctata* and *Lasius umbratus* in West Virginia, *Temnothorax* sp. in Vermont) were outliers. When I examined presence-absence data separately for the three sites, important differences emerged. A variance ratio test was consistent with independent placement of species on plots for West Virginia ( $VR = 1.77$ ,  $P > 0.05$ ) but there were clear indications that co-occurrences were nonrandom in New York ( $VR = 1.72$ ,  $P < 0.001$ ) and Vermont ( $VR = 3.19$ ,  $P < 0.001$ ). Contingency table analysis of pairwise species combinations (corrected for experiment-wide error) yielded three pairs that co-occurred more often than chance expectation: [*Amblyopone pallipes* - *Lasius nearcticus*]; [*Temnothorax ambiguus* - *Myrmica americana*]; and [*Aphaenogaster rudis* - *Myrmica americana*] and only one pair less often than chance expectation [*Formica neogagates* - *Myrmica americana*]. A different approach was to look for correlations of abundances for species pairs (correcting for multiple tests by the sequential Bonferroni procedure). Densities of two pairs were negatively correlated [*T. longispinosus* - *T. ambiguus*] and [*T. longispinosus* - *L. nearcticus*] while the densities of a third pair were positively correlated [*L. alienus* - *T. ambiguus*]. Overall, then, pooling presence-absence data gave evidence of nonran-

dom species co-occurrences, but the contributions of individual species pairs towards the overall pattern were weak. I examined these data to ascertain whether long-term trends in overall nest density (Fig. 6) were accompanied by shifts in species composition or use of space. Neither the species lists nor relative abundances of individual species changed systematically over the years in NY or VT; similarly, I detected no changes in species co-occurrences over time. Thus the decline of ant nest density in VT (Fig. 6) was not accompanied by long-term shifts in species composition or relative abundance.

## Discussion

Long-term studies of individual species have revealed important insights to ant population ecology and life history (COLE & WIERNASZ 2002, TSCHINKEL 2006), but our work sets a record for longitudinal study of entire ant communities. Seasonal shifts in nest density and spacing are important in litter-ant communities (HERBERS 1989), and the current analysis shows that long-term temporal changes can be important as well. A striking decline in overall nest density at the Vermont site was accompanied by reduced density of individual species and associated shifts in nest spacing; furthermore, these long-term density changes occurred for both young and mature colonies. Altogether, the evidence strongly suggested a large-scale force operating at that site. One possibility is a long-term environmental disturbance. While the disturbance hypothesis cannot be ruled out, no putative causal agent is immediately apparent to explain why only VT should be affected: for example, acid rain and global climate change are not unique to that site. Rather, I suspect the long-term decline in nest density there represents successional change. The New York and West Virginia forests were last logged about 100 years ago, while the Vermont site was last logged about 50 years ago, and long-term changes in nest density there are most likely related to community age. Indeed, the succession hypothesis is supported by the most recent nest density measurement in Vermont (Fig. 6), which is nearly identical to the density that has been stable for 19 years in New York. Even so, concurrent shifts in species composition, incidence, or co-occurrence did not occur over the years. If my hypothesis is correct, then it sheds light on successional dynamics: Apparently in these litter-ant communities succession operates chiefly to reduce population sizes rather than species composition.

In addition to providing information on succession dynamics, long-term studies provide insights about sampling efficacy and use of space. Because the WV site was sampled only in two years, the data were inadequate to fully characterize the resident ant community (Fig. 2). Similarly, my earlier analyses of snapshot data from VT and NY (HERBERS 1989) were unable to adequately explore patchy distributions or species co-occurrence. Therefore large datasets acquired over time can provide insight to fundamental ecological questions.

The data reported here were collected as an adjunct to detailed studies of evolutionary ecology for some common species. Those studies, of *Temnothorax longispinosus* and *Myrmica punctiventris* (see BACKUS 1995, BANSCHBACH & HERBERS 1996b, HERBERS & BANSCHBACH 1999), have confirmed that food is severely limiting in the VT site but may be less of a constraint in NY and WV (HERBERS &

STUART 1996, DEHEER & al. 2001). Competition for nesting sites also seems important for these ants, most of which are cavity dwellers (BANSCHBACH & HERBERS 1999, BACKUS & al. 2006). Further, we have induced dramatic shifts in the colony organization of these two focal species by manipulating nest site density (HERBERS 1986, DEHEER & al. 2001). Over the years, then, we have amassed strong evidence of intraspecific and possibly interspecific competition over resource use in common species.

We are left with a conundrum: While intensive studies of individual species showed clearly that ants compete for resources, there was virtually no signal here of such competition: Nest spacing patterns were aggregated rather than over-dispersed, and species did not form clusters in multivariate space. These results are consistent with other studies of litter-dwelling ant communities. YANOVIK & KASPARI (2000) explicitly compared forager overlap and interactions at baits in tropical leaf litter and in the canopies overhead; their work shows that litter ants are subject to more environmental heterogeneity than their arboreal neighbors. Similarly, SOARES & al. (2001) found no signal of strong competition from a comparison of local to regional species richness for Australian litter ants. Thus litter communities give at best a weak signal of interspecific competition; those wanting to study competitive interactions from nest-spacing data should work in other systems.

Sampling methods and subsequent data analysis must be designed with specific questions in mind (BESTELMEYER & al. 2000, DELABIE & al. 2000, ELLISON & al. 2007). For litter-ant communities, colony-level collecting is a preferred method (DUNN & al. 2009b), and the quadrat-based collections allowed me to examine nest density and dispersion as a function of spatial scale. Indeed, we found patchiness at three scales. The prevalence of polydomous colonies produced structure at a small scale (about 5 m<sup>2</sup>) whereas microhabitat heterogeneity produced patchiness at a larger scale (25 m<sup>2</sup>). The sheer quantity of data accrued over 19 years thus allowed me to untangle the effects of polydomy from habitat selection, a problem that plagues other studies of nest spacing (DEBOUT & al. 2007). Uncovering the scale of 25 m<sup>2</sup> is particularly satisfying, because at the outset I chose 25 square meters as the minimum quadrat size for study; thus my biological intuition was born out by quantitative analysis.

Larger-scale spatial effects (at least 100 m<sup>2</sup>) were implicated by the substantial variation among plots cleared at the same time, and comparisons among sites suggested a regional scale is important for these ants as well. A striking regional effect was that overall ant-nest density was substantially lower in West Virginia (Fig. 3). What drives differences in nest density between the southern-most and two more northern sites is not clear, but those differences have important consequences for social structure of the ants living there. For example, the abundant species *Temnothorax longispinosus* has monogynous colonies in West Virginia but polygynous colonies in the northern sites, accompanied by important life-history shifts between populations as well (HERBERS & STUART 1996). Its social parasite, *Protomognathus americanus*, also shows geographic variation linked to the differing densities of its host species (HERBERS & FOITZIK 2002). Regional effects are likewise suggested by comparisons of our data to those collected in similar habitats. Species lists and relative abundances for



ant communities from the northern state of New England to the southern tier of mixed hardwood forests (CULVER 1974, LYNCH 1981, FELLERS 1987, GIBBS & al. 2003, LESSARD & al. 2007) show variation in species composition across regions. Even so, the number of species in North American second-growth forests appears consistently within 15 - 30 species. In comparison to other major habitats, then, temperate deciduous forests have relatively low ant diversity (LUBERTAZZI & TSCHINKEL 2003).

Long-term data are hard-won, and it is not surprising that such studies are rare. Yet the explicit temporal-spatial dimensionality of these data allows exploration of questions that are otherwise impossible. As ecologists work to understand the importance of long-term effects such as invasive species (KRUSHELNYCKY & al. 2009) and global climate change (DUNN & al. 2009a), they must predicate their work on an understanding of the underlying long-term dynamics of natural communities.

### Acknowledgements

My lab group has assisted in all phases of this work over the years. In particular, I thank undergraduates Mark Wilkinson, Carol Tucker, Michael Cunningham, Eric Choiniere, and Linda Bisson; graduate students Vickie Backus, Laura Snyder, Jonathan Leonard, Dave Webb, Joe Fontaine, and Tim Judd; postdocs Robin Stuart, Valerie Banschbach, Susanne Foitzik, Chris DeHeer, and Rum Blatrix; and technicians Ron Spicer and Linda Prince. I have benefited from the gracious advice of colleagues for ideas and analysis suggestions; Nick Gotelli and Brandon Bestelmeyer have strongly influenced my thinking concerning ant communities. Finally, this work has been generously supported by grants from the National Science Foundation, Vermont EPSCoR, and the E.N. Huyck Preserve.

### References

- ADLER, F.R., LEBRUN, E.G. & FEENER, D.H. 2007: Maintaining diversity in an ant community: modeling, extending, and testing the dominance-discovery trade-off. – *American Naturalist* 169: 323-333.
- ANDERSEN, A.N. 1986: Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in south-eastern Australia. – *Australian Journal of Zoology* 34: 53-64.
- ANDERSEN, A.N. 2008: Not enough niches: non-equilibrium processes promoting species coexistence in diverse ant communities. – *Austral Ecology* 33: 211-220.
- BACKUS, V.L. 1995: Rules for allocation in a temperate forest ant: demography, natural selection, and queen-worker conflict. – *American Naturalist* 145: 775-796.
- BACKUS, V.L., DEHEER, C. & HERBERS, J.M. 2006: Change in movement and subdivision of *Myrmica punctiventris* (Hymenoptera: Formicidae) colonies in north temperate forests is related to a long-term shift in social organization. – *Insectes Sociaux* 53: 156-160.
- BANSCHBACH, V.S. & HERBERS, J.M. 1996a: Complex colony structure in social insects. I. Ecological determinants and genetic consequences. – *Evolution* 50: 285-297.
- BANSCHBACH, V.S. & HERBERS, J.M. 1996b: Complex colony structure in social insects. II. Reproduction, queen-worker conflict, and levels of selection. – *Evolution* 50: 298-307.
- BANSCHBACH, V.S. & HERBERS, J.M. 1999: Nest movements and population spatial structure of the forest ant *Myrmica punctiventris* (Hymenoptera: Formicidae). – *Annals of the Entomological Society of America* 92: 414-423.
- BARROW, L. & PARR, C.L. 2008: A preliminary investigation of temporal patterns in semiarid ant communities: variation with habitat type. – *Austral Ecology* 33: 653-662.
- BESTELMEYER, B.T. 1997: Stress tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. – *Journal of Arid Environments* 35: 297-310.
- BESTELMEYER, B.T., AGOSTI, D., ALONSO, L., BRANDAO, C.R., BROWN, W.J.H., DELABIE, J.H.C. & SILVERSTRE, R. 2000: Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. In: AGOSTI, D., MAJER, J., ALONSO, J.L. & SCHULTZ, T.R. (Eds.): *Ants: standard methods for measuring and monitoring biodiversity*. – Smithsonian Institution Press, Washington, DC, pp. 122-144.
- BESTELMEYER, B.T. & WIENS, J.A. 2001: Local and regional-scale responses of ant diversity to a semiarid biome transition. – *Ecography* 24: 381-392.
- BLÜTHGEN, N. & FELDHAAR, H. 2009 [2010]: Food and shelter: how resources influence ant ecology. In: LACH, L., PARR, C.L. & ABBOTT, K.L. (Eds.): *Ant ecology*. – Oxford University Press, Oxford, UK, pp. 115-136.
- BYRNE, M.M. 1994: Ecology of twig-dwelling ants in a wet lowland tropical forest. – *Biotropica* 26: 61-72.
- COLE, B.J. & WIERNASZ, D.C. 2002: Recruitment limitation and population density in the harvester ant, *Pogonomyrmex occidentalis*. – *Ecology* 83: 1433-1442.
- CULVER, D.C. 1974: Species packing in Caribbean and north temperate ant communities. – *Ecology* 55: 974-988.
- DAVIDSON, D.W. 1998: Resource discovery versus resource dominance in ants: a functional mechanism for breaking the trade-off. – *Ecological Entomology* 23: 484-490.
- DEBOUT, G., SCHATZ, B., ELIAS, M. & MCKEY, D. 2007: Polydomy in ants: what we know, what we think we know, and what remains to be done. – *Biological Journal of the Linnean Society* 90: 319-348.
- DEHEER, C.J., BACKUS, V.L. & HERBERS, J.M. 2001: Context dependency of sociogenetic response to ecological variation in the ant *Myrmica punctiventris*. – *Behavioral Ecology and Sociobiology* 49: 375-386.
- DELABIE, J.H.C., FISHER, B.L., MAJER, J.D. & WRIGHT, A.W. 2000: Sampling effort and choice of methods. In: AGOSTI, D., MAJER, J., ALONSO, L. & SCHULTZ, T.R. (Eds.): *Ants: standard methods for measuring and monitoring biodiversity*. – Smithsonian Institution Press, Washington, DC, pp. 145-154.
- DUNN, R.R., AGOSTI, D., ANDERSON, A.N., ARNANA, X., BRUHL, C.A., CERDA, X., ELLISON, A.A., FISHER, B.L., FITZPATRICK, M.C., GIBB, H., GOTELLI, N.J., GOVE, A.D., GUENARD, B., JANDA, M., KASPARI, M., LAURENT, E.J., LESSARD, J.-P., LONGINO, J.T., MAJER, J.D., MENKE, S.B., MCGLYNN, T.P., PARR, C.L., PHILPOTT, S.M., PFEIFFER, M., RETANA, J., SUAREZ, A.V., VASCONCELOS, H.L., WEISER, M.D. & SANDERS, N.J. 2009a: Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. – *Ecology Letters* 12: 324-333.
- DUNN, R.R., GUENARD, B., WEISER, M.D. & SANDERS, N.J. 2009b [2010]: Geographic gradients. In: LACH, L., PARR, C.L. & ABBOTT, K.L. (Eds.): *Ant ecology*. – Oxford University Press, Oxford, UK, pp. 38-57.
- ELLISON, A.M., RECORD, S., ARGUELLO, A. & GOTELLI, N.J. 2007: Rapid inventory of the ant assemblage in a temperate hardwood forest: species composition and assessment of sampling methods. – *Environmental Entomology* 36: 766-775.
- ELMES, G.W. 1987: Temporal variation in colony populations of the ant *Myrmica sulcinodis*. II. Sexual production and sex ratios. – *Journal of Animal Ecology* 56: 573-583.

- FELLERS, J.H. 1987: Interference and exploitation in a guild of woodland ants. – *Ecology* 68: 1466-1478.
- FISHER, B.L. & COVER, S.P. 2007: *Ants of North America*. – University of California Press, Berkeley, CA, 194 pp.
- GERAGHTY, M.J., DUNN, R.R. & SANDERS, N.J. 2007: Body size, colony size, and range size in ants (Hymenoptera: Formicidae): Are patterns along elevational and latitudinal gradients consistent with Bergmann's Rule? – *Myrmecological News* 10: 51-58.
- GIBBS, M.M., LAMBDIN, P.L., GRANT, J.F. & SAXTON, A.M. 2003: Ground-inhabiting ants collected in a mixed hardwood southern Appalachian forest in eastern Tennessee. – *Journal of the Tennessee Academy of Science* 78: 45-49.
- GOODALL, D.W. 1974: A new method for the analysis of spatial pattern by random pairing of quadrats. – *Vegetatio* 29: 135-146.
- GORDON, D.M. & KULIG, A. 1998: The effect of neighbours on the mortality of harvester ant colonies. – *Journal of Animal Ecology* 67: 141-148.
- GOTELLI, N.J. 1996: Ant community structure: effects of predatory ant lions. – *Ecology* 77: 630-638.
- GOTELLI, N.J. & ELLISON, A.M. 2002: Biogeography at a regional scale: determinants of ant species density in New England bogs and forests. – *Ecology* 83: 1604-1609.
- HERBERS, J.M. 1985: Seasonal structuring of a north temperate ant community. – *Insectes Sociaux* 32: 224-240.
- HERBERS, J.M. 1986: Nest site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. – *Behavioral Ecology and Sociobiology* 19: 115-122.
- HERBERS, J.M. 1989: Community structure in north temperate ants: temporal and spatial variation. – *Oecologia* 81: 201-211.
- HERBERS, J.M. & BANSCHBACH, V.S. 1999: Plasticity of social organization in a forest ant species. – *Behavioral Ecology and Sociobiology* 45: 451-465.
- HERBERS, J.M. & FOITZIK, S. 2002: The ecology of slavemaking ants and their hosts in north temperate forests. – *Ecology* 83: 148-163.
- HERBERS, J.M. & GRIECO, S. 1994: Population structure of *Leptothorax ambiguus*, a facultatively polygynous and polydomous ant species. – *Journal of Evolutionary Biology* 7: 581-598.
- HERBERS, J.M. & STUART, R.J. 1996: Multiple queens in ant nests: impact on genetic structure and inclusive fitness. – *American Naturalist* 147: 161-187.
- HÖLDOBLER, B. & WILSON, E.O. 1990: *The ants*. – Harvard University Press, Cambridge, MA, 732 pp.
- KASPARI, M. 1996: Litter ant patchiness at the 1-m<sup>2</sup> scale: disturbance dynamics in three Neotropical forests. – *Oecologia* 107: 265-273.
- KASPARI, M., O'DONNELL, S. & KERCHER, J.R. 2000: Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. – *American Naturalist* 155: 280-293.
- KRUSHELNYCKY, P.D., HOLWAY, D.A. & LEBRUN, E.G. 2009 [2010]: Invasion processes and causes of success. In: LACH, L., PARR, C.L. & ABBOTT, K.L. (Eds.): *Ant ecology*. – Oxford University Press, Oxford, UK, pp. 245-260.
- LACH, L., PARR, C.L. & ABBOTT, K.L. (Eds.) 2009 [2010]: *Ant ecology*. – Oxford University Press, Oxford, UK, 424 pp.
- LESSARD, J.-P., DUNN, R.R., PARKER, C.R. & SANDERS, N.K. 2007: Rarity and diversity in forest ant assemblages of Great Smoky Mountains National Park. – *Southeastern Naturalist* 1: 215-238.
- LINDSEY, P.A. & SKINNER, J.D. 2001: Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. – *Journal of Arid Environments* 48: 551-568.
- LUBERTAZZI, D. & TSCHINKEL, W.R. 2003: Ant community change across a ground vegetation gradient in north Florida's longleaf pine flatwoods. – *Journal of Insect Science* 3: 21-38.
- LUDWIG, J.A. 1979: A test of different quadrat variance methods for the analysis of spatial pattern. In: CORMACK, R.M. & ORD, J.K. (Eds.): *Spatial and temporal analysis in ecology*. – International Co-operative Publishing House, Fairland, MD, pp. 289-304.
- LYNCH, J.F. 1981: Seasonal, successional, and vertical segregation in a Maryland ant community. – *Oikos* 37: 183-198.
- MAGURRAN, A. 1988: *Ecological diversity and its measurement*. – Princeton University Press, Princeton, NJ, 179 pp.
- PARR, C.L. & GIBB, H. 2009 [2010]: Competition and the role of dominant ants. In: LACH, L., PARR, C.L. & ABBOTT, K.L. (Eds.): *Ant ecology*. – Oxford University Press, Oxford, UK, pp. 77-96.
- RYTI, R.T. & CASE, T.J. 1986: Overdispersion of ant colonies: a test of hypotheses. – *Oecologia* 69: 446-453.
- RYTI, R.T. & CASE, T.J. 1992: The role of neighborhood competition in the spacing and diversity of ant communities. – *American Naturalist* 139: 355-374.
- SAGATA, K., MACK, A.L., WRIGHT, D.D. & LESTER, P.J. 2010: The influence of nest availability on the abundance and diversity of twig-dwelling ants in a Papua New Guinea forest. – *Insectes Sociaux* 57: 333-341.
- SAMWAYS, M.J. 1990: Species temporal variability: epigeaic ant assemblages and management for abundance and scarcity. – *Oecologia* 84: 482-490.
- SCHMIDT, F.A. & SOLAR, R.R.C. 2010: Hypogaic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna. – *Insectes Sociaux* 57: 261-266.
- SOARES, S.M., SCHOEREDER, J.H. & DESOUZA, O.G. 2001: Processes involved in species saturation of ground-dwelling ant communities (Hymenoptera, Formicidae). – *Australian Journal of Ecology* 26: 187-192.
- TSCHINKEL, W.R. 2006: *The fire ants*. – Harvard University Press, Cambridge, MA, 723 pp.
- YANOVIK, S.P. & KASPARI, M. 2000: Community structure and the habitat templet: ants in the tropical forest canopy and litter. – *Oikos* 89: 259-266.