

**Abstract** Species coexistence can reflect niche parti-



the fraction of the total bait occurrences for a species that were found in month  $i$ .

The Czechanowski index is a symmetric index of niche overlap, such that  $O_{12}=O_{21}$ . The index approaches 0 for species that share no resource states and approaches 1.0 for species pairs that have identical resource utilization distributions. To characterize the niche overlap patterns of the entire assemblage, we calculated the mean and variance of niche overlap among all unique pairs of species in the assemblage (Inger and Colwell 1977).

Next, we determined the statistical significance of the niche overlap patterns by comparing them with an appropriate null model, in which the observed utilization data were randomized among species. The data for each null model consists of a matrix in which the rows are species and the columns are resource states (months of the year, hours of the day, or individual bait stations within an hour). The entries in the matrix are the utilization of each resource state by each species. We used two kinds of randomization algorithms (RA) to test for non-random niche overlap patterns. Winemiller and Pianka (1990) have extensively analyzed these niche overlap models and have evaluated their performance on idealized data sets. For consistency, we used the same labels for the algorithms as Winemiller and Pianka (1990):

1. RA3. In this algorithm, the entries in each row of the utilization matrix were randomly reshuffled. This procedure retains the observed niche breadth of the species, but it allows utilization of any of the possible resource states. We used this algorithm for the analysis of spatial niche overlap. Although we used this algorithm in a preliminary analysis of temporal overlap, we do not believe that all resource states (different hours of a day or different months of a year) could necessarily be used by all species, even in the absence of species interactions.

Therefore it is not an appropriate null model for patterns of temporal niche overlap (see also Tokeshi 1986; Loreau 1989).

2. RA4. In this algorithm, only the non-zero entries in each row of the utilization matrix were randomly reshuffled. This procedure retains both the niche breadth of the species and the pattern of zero states. We used RA4 to analyze seasonal and diel patterns of niche overlap. Although RA4 is a somewhat conservative algorithm (Winemiller and Pianka 1990), it tended to produce higher expected niche overlap values with our data than did other alternative algorithms (RA1, RA2, RA3). Consequently, RA4 had the greatest chance of revealing significant patterns of reduced niche overlap.

For each data set, we randomized the utilization data according to algorithm RA3 or RA4 and created 1000 null assemblages. From these, we calculated the mean niche overlap of all possible species pairs and compared the observed mean to the distribution of simulated means. From these, we calculated the mean niche overlap of all possible species pairs as a community-level index of niche overlap. We compared this index to the histogram of 1000 indices that were calculated from the randomized data sets. We calculated the two-tailed probability values by tabulating the number of simulated niche overlaps that were greater or less than the observed overlap. Interspecific competition should cause mean niche overlap to be less than expected by chance, whereas abiotic constraints on activity, such as air temperature, might cause all species to have similar foraging patterns, so that observed niche overlap would be greater than expected.

We also tested for patterns in the variance, as well as the mean, of niche overlap. Inger and Colwell (1977) showed that if there is guild organization within the species assemblage, the variance in niche overlap will be greater than expected: species pairs within a

**Fig. 1**

guild will have unusually low niche overlap, whereas species pairs in different guilds will have unusually high niche overlap, leading to a large variance in niche overlap. In our data, these patterns might arise if there were a guild of night-foraging and day-foraging species, or if there were a guild of early-season and late-season foragers.

All simulations were carried out with EcoSim software (N.J. Gotelli and G.L. Entsminger, 1999, EcoSim: null model software for ecology, version 3.0, Aquired Intelligence Inc. and Kesity-Bear, <http://homepages.together.net/~gentsmin/ecosim.htm>). Although we used a two-tailed statistical test, we did not use any further adjustments such as a Bonferonni correction (Sokal and Rohlf 1981) for multiple tests because we were interested in the overall pattern of which data sets showed significance and which did not.

### Species associations

We examined pairwise Pearson product-moment correlations among species occurrences on both seasonal and diurnal time scales. We restricted this analysis to the four most abundant species (*Crematogaster punctulata*, *Lasius neoniger*, *Monomorium minimum*, and *Pheidole dentata*) so that there would be enough observations to make the statistical tests meaningful. Diel tests were restricted to the three warmest months (June, July, and August 1991) because these months had the highest ant abundances. We used partial correlation calculations to remove the effects of other species for each species pair tested. We also included ambient air temperature in the model to distinguish statistical associations of species with one another from associations of each species with ambient air temperature.

## Results

### Seasonal overlap

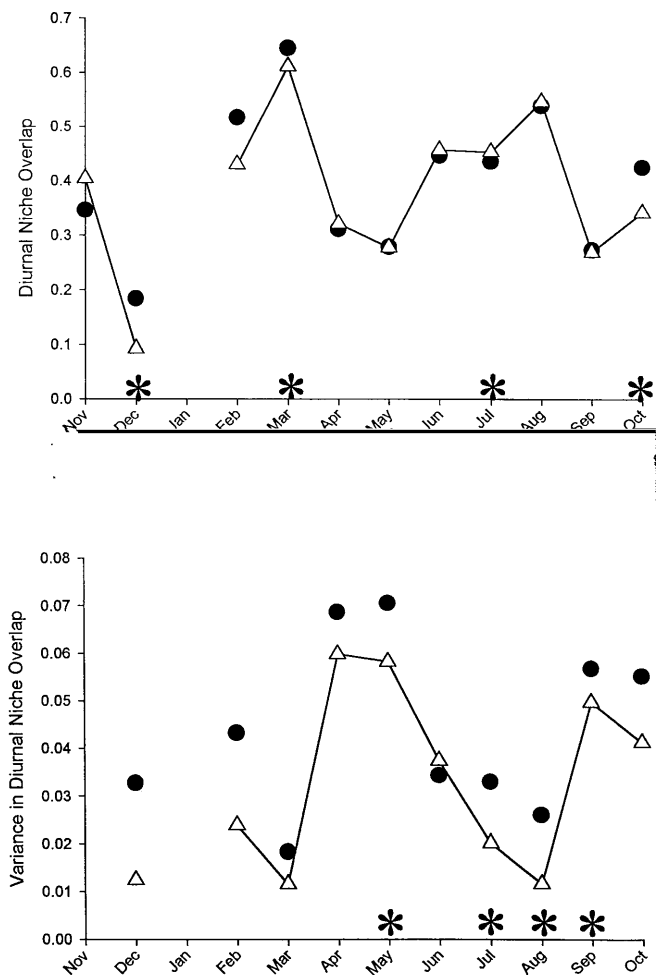
We recorded the presence of seven species during the year-long study, 4 of which were common (Fig. 1). In the unrestricted analysis of these data (RA3), seasonal niche overlap was significantly greater than expected, with few species foraging in the cooler months of the year. When the analysis was restricted to the months in which species were actually present (RA4), there was no evidence of non-random seasonal niche overlap. The variance of seasonal niche overlap also did not differ significantly from expected for RA3 and RA4 (Table 1).

### Diurnal overlap

On a 24-h time scale, there were three months (December, March, and October) in which diel niche overlap was significantly greater than expected, and one month (July) in which niche overlap was significantly less than expected (Fig. 2a). In all months except June, the variance of diel niche overlap was greater than expected, and the pattern was statistically significant in May, July, August, and September (Fig. 2b).

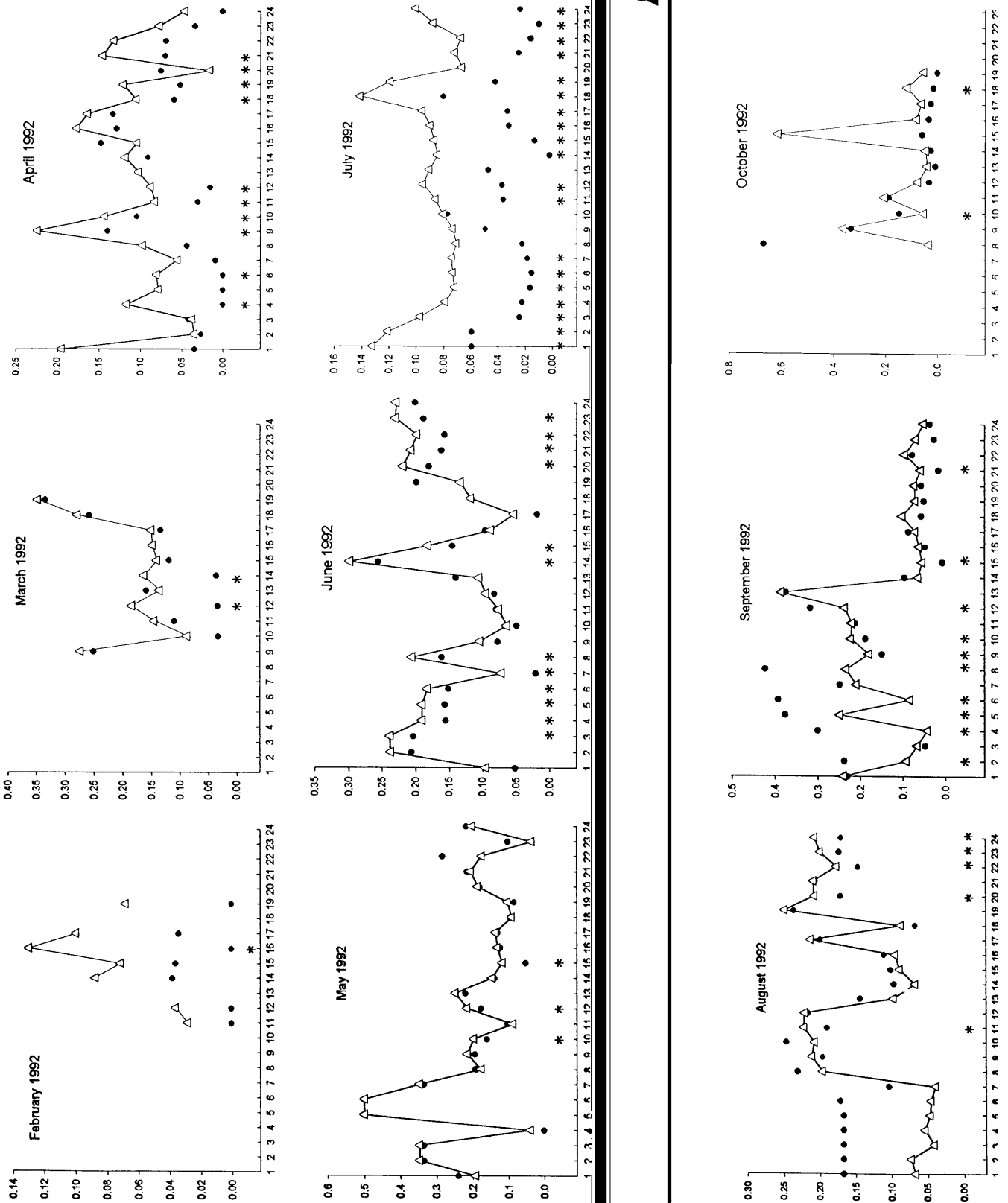
### Spatial overlap

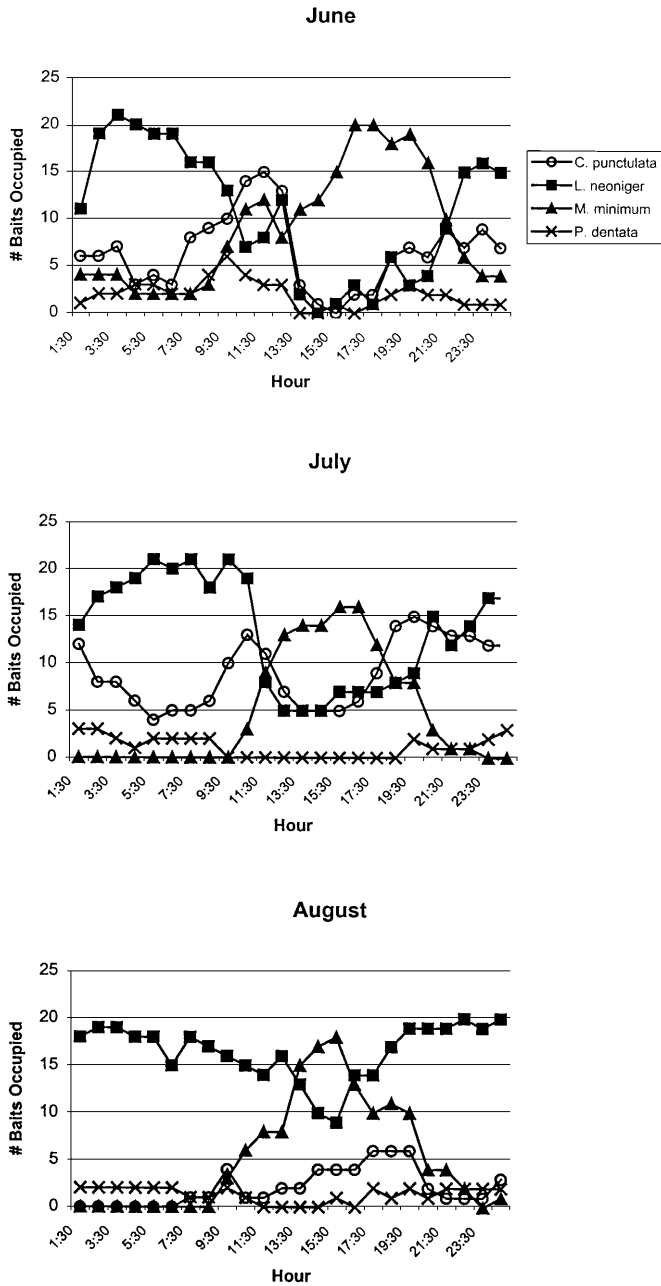
Both expected and observed overlap in spatial niches varied greatly among months and among hours of the



**Fig. 2a,b** Observed and expected diurnal niche overlap of ground-foraging ants. Each pair of points represents the diurnal niche overlap of foraging activity of ants recorded during a particular month. The open triangle is the expected niche overlap, calculated as the average niche overlap in 1000 randomized assemblages. The solid circle is the observed diurnal niche overlap in each month. An asterisk indicates an observed niche overlap that was significantly different from the null model ( $P$ )

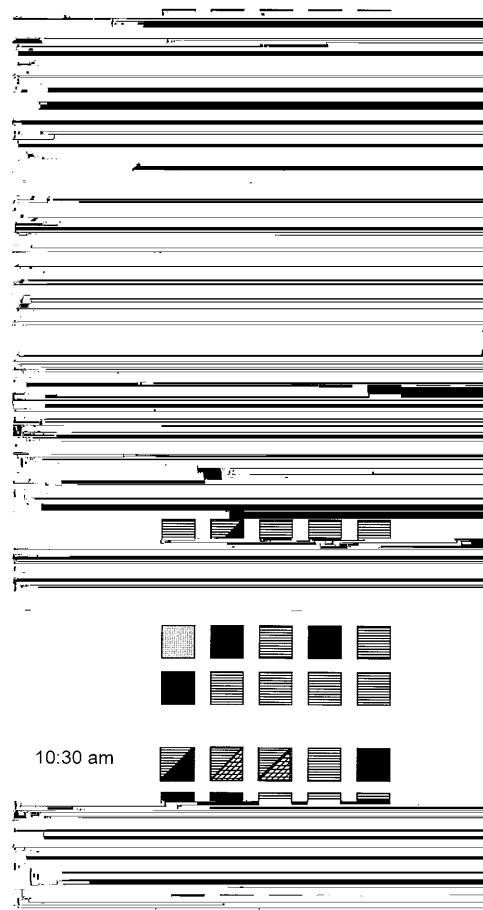
# SPATIALLY NICHE OVERLAP





**Fig. 4** Diel bait occupancy by the four most abundant species (*Crematogaster punctulata*, *Lasius neoniger*, *Monomorium minimum*, and *Pheidole dentata*). Each point represents the number of baits occupied by a species at each hour of the census. The maximum number of baits that could be occupied in each hour is 25

summarizes monthly and diel correlations between species pairs and between species and ambient air temperature. On the monthly time scale, occurrences of all species but *C. punctulata* were positively correlated with average ambient temperature; correlations between all



**Fig. 5** Each square represents a tuna fish bait in the 5 m×5 m grid, at three times of day during the July census. Modified from Gotelli and Graves (1996)

species pairs were non-significant. On the 24-h time scale the occurrences of *L. neoniger* and *P. dentata* were negatively correlated with ambient air temperature in all three months, whereas the occurrence of *M. minimum* was positively correlated with ambient air temperature. After partial correlation was used to remove the effects of air temperature and other species, there was a significant positive correlation between *P. dentata* and *L. neoniger*; also both species were negatively correlated with *M. minimum*. On the 24-h time scale, the occurrence of *C. punctulata* was uncorrelated with air temperature or the occurrence of other species.

**Discussion**

Niche partitioning in ant assemblages has been attributed to species temperature preferences (Talbot 1946; Lynch et al. 1980), humidity preferences (Talbot 1946; Levings and Traniello 1981), food availability (Bernstein 1979), and nest site availability (Herbers 1989), and competition (e.g., Davidson 1977; Hölldobler 1987; Human and Gordon 1996). The activity of one or two behaviorally dominant species may determine the activity patterns of less domi-

◀ **Fig. 3** Observed and expected spatial niche overlap of ground foraging ants. Each panel represents a different month of the year. Points represent the spatial overlap among baits calculated at different times of day. Symbols as in Fig. 2

nant species (Lynch et al. 1980; Fellers 1989; Andersen 1992). In our study, temperature appears to be an important determinant of temporal activity patterns. The activity of the two most abundant species correlated significantly but negatively, suggesting differing physiological preferences of these species. Similar patterns have been described for woodland ant assemblages (Lynch et al. 1980).

Nest site availability is probably not limiting in this grassland because all species found are ground-nesting (Albrecht 1995). Instead, spatial and temporal niche partitioning of foraging activity may permit coexistence. On a monthly time scale, there was little evidence of seasonal niche partitioning: all species showed a common pat-

In summary, we found little evidence of seasonal niche partitioning by ground-foraging ants. Instead, partitioning occurred on a diel time scale in which common species were active at different time of the day, and on a small spatial scale, in which species used food resources in a shifting spatial mosaic.

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