

Ant Community Structure in Citrus Orchards in the Mediterranean Basin: Impoverishment as a Consequence of Habitat Homogeneity

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ABSTRACT This study analyzes the structure and composition of ant communities in citrus orchards in Catalonia (northeast Spain) and compares them with the ant fauna found in natural communities of the region. In the citrus orchards considered in this study, the most abundant species were *Lasius niger* and *Pheidole pallidula*, which are behaviorally dominant species. Two other dominant species, *Linepithema humile* and *Tetramorium caespitum*, were also abundant, although only in one orchard. Species richness and diversity in the studied orchards were low compared with natural communities: although in orchards, there were few species and low diversity values, in natural communities, the number of species was higher and diversity also increased. This reduction of species richness and diversity was not modified by edge effects: only light and local differences were found between the inner part of the orchards and the orchard margins, and differences among orchards were greater than differences between inner parts and edges. The activity peaks of the different ant species actively foraging on these citrus orchards were distributed throughout the whole activity period of ants. Overall, the composition of ant communities present in the citrus orchards of this study was extremely poor. This agrees with the fact that monocultures are ecosystems associated with an inevitable loss of biodiversity and abundance of insect populations.

KEY WORDS ant community, citrus orchard, dominance, seasonality, Mediterranean region

The abundance and ecological dominance of ants make them the most important contributors to the biodiversity of many habitats (Hölldobler and Wilson 1990). In natural communities, interspecific competition has long occupied a preeminent position among factors affecting composition and diversity of ant communities (Andersen 1992, Cerdá et al. 1997). In completely contrasted regions of the world, strongly competitive ants behave similarly by excluding other potential competitors from their territory and reducing the foraging success of subordinate species (Andersen 1992, Andersen and Patel 1994). In managed ecosystems, such as agricultural lands, where ants are both pests and pest control agents, because they prey on honeydew-producing homoptera but also take care of them (protecting them against predators) and harvest the sugar-rich honeydew to feed their colonies (Stevens et al. 1998, James et al. 1999), interspecific competition also plays a role in shaping ant communities (Human and Gordon 1996, Roth et al. 1994). In these cases, changes from natural systems to agricultural ones may result in a significant decrease in diversity of ground-foraging ants (Roth et al. 1994, Perfecto and Snelling 1995), because habitat disturbance loses the rare species and promotes the common ones.

Then, reduced vegetation structure may lead to lower diversity and increased dominance (Bestelmeyer and Wiens 1996).

A particular situation occurs in Mediterranean ant communities, where resistance to physical factors reduces the occurrence of competition (Cerdá et al. 1998a). Dominants are heat-intolerant species that are restricted largely by physical conditions, whereas subordinates are heat-tolerant species that are active over a wider range of temperatures (Cerdá et al. 1997, 1998b). In this scenario, vegetation cover, through the percentage of shade created by the canopy, has proved to be a good predictor of the structure of Mediterranean ground ant communities (Retana and Cerdá 2000): in open sites, temperature rather than interspecific competition primarily determines the temporal activity patterns (Cerdá et al. 1998a), with dominants decreasing and subordinates increasing their relative abundance from spring to summer (Cros et al. 1997, Retana and Cerdá 2000); in forest sites, dominant species are not affected by high temperatures and exclude many subordinate species (Retana and Cerdá 2000). However, there is scarce information on the effects of anthropogenic change, i.e., agricultural culture, on the structure and function of ant communities in these Mediterranean conditions, with temperature conditioning more than competition the coexistence of dominant and subordinate species (Cerdá et al. 1998a).

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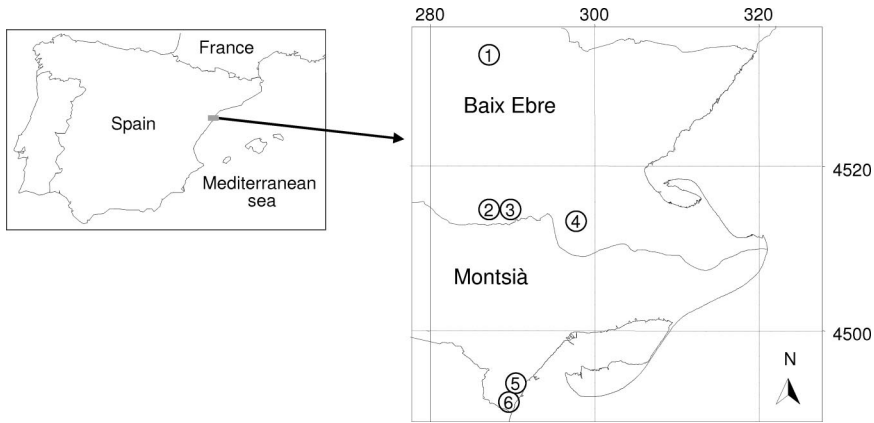


Fig. 1. Geographical location of the six orchards sampled in the regions of Baix Ebre and Montsià regions (Tarragona, NE Spain). Citrus orchards: 1, Benifallet; 2, Mianes; 3, Xalet; 4, Frudelta; 5, Palmeres; 6, Xeminavel.

Ants are a major component of the citrus orchard floor fauna, and their effects, abundance, and species composition have been deeply studied throughout the world (Samways 1983, James et al. 1997, Stevens et al. 1998). They have been considered a major indirect pest in these orchards (James et al. 1999, Urbaneja et al. 2004, but see Van Mele and Cuc 2000) because they are attracted into the trees by the honeydew excreted by soft scales, mealybugs, and aphids. In the Mediterranean basin, the economic importance of citrus orchards is very large. This work reports on the characteristics of ground foraging ant communities in citrus orchards in Catalonia (northeast Spain). The aim of this study was to analyze the structure and composition of ant communities in different citrus orchards with different characteristics and management practices and to compare them with the ant fauna found in natural communities of the region.

Materials and Methods

Study Sites. The study was carried out in Baix Ebre and Montsià regions (southern Catalonia, northeast Spain; Fig. 1). The climate is semiarid (according to the Thornwaite index), with mean annual temperature of 16–18°C and mean annual precipitation of 500–700 mm, concentrated between October and May. The study sites were six citrus orchards (*Citrus sinensis* L., cultivar Navelina) under different management and plantation practices (Table 1): age of

trees ranged between 25 and 50 yr, and orchards also differed in percent canopy cover, the use or not of machinery for labor activities, the presence or not of weeds, and the different abundance of stones. The aim of choosing these different orchards was to gain some insight into how the ant community changed under the different management types. No pesticides for pest control were spread in any of the orchards in the 3–4 yr previous to the sampling.

Sampling. To sample ants within each site, 16 pitfall traps were placed in each orchard: 8 in the inner part of the orchard and 8 in the orchard margin. These traps were distributed at 0.5–1 m from citrus trees, with 5-m spacing between traps. Pitfall traps were 6-cm-diameter, 7-cm-deep plastic vials partially filled with water, ethanol 70%, and soap. They were laid on the ground during seven sampling periods, i.e., once a month from April to October. In each sampling period, traps were operated for 7 d. The contents of the traps of the inner part and the traps of the margin of each orchard in each sampling period were lumped separately to obtain two different samples per orchard. The content of pitfall traps was analyzed in the laboratory to the species' level. Voucher specimens of the species found have been placed on the collection of the Autonomous University of Barcelona.

The indexes used to examine community structure of the different orchards were *S* (species richness), *H* (Shannon's diversity index), and *F* (Hill's ratio evenness index). The Shannon index of diversity (*H*) was estimated as: $H = -\sum(p_i \log_e p_i)$, where p_i is the

Table 1. Main characteristics of the citrus orchards considered in this study

Orchard	Location	Age of trees (yr)	Plantation frame (m)	Percent canopy cover	Labor activities	Weed presence	Stoniness
Benifallet	Benifallet (Baix Ebre)	30	4.5 by 4.5	44	With machinery	Very high	Low
Frudelta	Aldea (Baix Ebre)	25	5 by 5	36	None	High	High
Les Palmeres	Alcanar (Montsià)	25	5 by 3	54	With machinery	Nil	High
Mianes	Vinallop (Baix Ebre)	25	4.5 by 4.5	50	None	Nil	Low
Xalet	Vinallop (Baix Ebre)	25	4.5 by 4.5	46	None	Nil	Low
Xeminavel	Alcanar (Montsià)	50	5 by 5	65	None	Nil	High

Table 2. Composition of the ant fauna sampled in the six orchards considered in this study

Species	No. total ants	Total percent	Benifallet	Frudelta	Les Palmeres	Mianes	Xalet	XemiNavel
<i>Lasius niger</i> L.	36,870	89.46	57.79	9.24	81.94	98.33	98.11	40.34
<i>Pheidole pallidula</i> (Nylander)	3,014	7.31	11.91	21.12	17.71	1.44	1.77	59.10
<i>Linepithema humile</i> (Mayr)	584	1.42	0.00	39.41	0.00	0.00	0.00	0.00
<i>Plagiolepis schmitzii</i> Forel	512	1.24	0.00	30.16	0.15	0.18	0.08	0.56
<i>Tetramorium caespitum</i> L.	138	0.33	20.29	0.00	0.00	0.00	0.00	0.00
<i>Formica cunicularia</i> Latreille	49	0.12	7.21	0.00	0.00	0.00	0.00	0.00
<i>Messor barbarus</i> L.	16	0.04	2.35	0.00	0.00	0.00	0.00	0.00
<i>Aphaenogaster senilis</i> Mayr	10	0.02	0.00	0.00	0.21	0.00	0.00	0.00
<i>Tapinoma nigerrimum</i> (Nylander)	9	0.02	0.00	0.00	0.00	0.04	0.00	0.00
<i>Camponotus foreli</i> (Emery)	7	0.02	0.00	0.00	0.00	0.01	0.04	0.00
<i>Myrmica scabrinodis</i> Nylander	1	0.00	0.15	0.00	0.00	0.00	0.00	0.00
<i>Hypoponera eduardi</i> (Forel)	1	0.00	0.15	0.00	0.00	0.00	0.00	0.00
<i>Camponotus pilicornis</i> (Roger)	1	0.00	0.15	0.00	0.00	0.00	0.00	0.00
<i>Diplorhoptum robusta</i> Bernard	1	0.00	0.00	0.07	0.00	0.00	0.00	0.00
No. ants	41,213		680	1,482	4,805	21,083	11,014	2,149
PSI inner part-edge	0.96		0.90	0.83	0.74	0.98	0.95	0.73

No. total ants indicates the no. of ants collected in 16 pitfall traps during 48 h.

Values of each orchard are expressed as relative abundance (%). Proportional similarity index (PSI) values between the catches in the edge and the inner part of each orchard (and overall) are also shown.

proportion of workers of the *i*th species in traps during the period of time considered. The modified Hill's ratio (*F*) was also calculated as: $F = (1/\sum(p_i^2)) - 1 / (e^H - 1)$, where *H* is the Shannon diversity index. To quantify patterns of species composition similarity between each given pair of sampled orchards, a proportional similarity index (PSI) based on the Colwell and Futuyma (1971) proportional overlap index was calculated: $PSI_{ih} = 1 - 0.5\sum|p_{ij} - p_{hj}|$, where p_{ij} is the abundance of species *j* in the orchard *i*, and p_{hj} is the abundance of the same species in the orchard *h*.

Resampling Procedure. To estimate the number of total expected species in each orchard community, we used a sample-based randomization procedure from EstimateS (Colwell 2006). Within each orchard and from empirical data of 16 samples, sample order was randomized 50 times, and the mean and SD of richness (*S*) was computed for each value of number of samples (between 1 and 16). Chao1 estimator of species richness was computed for total expected species. Chao1 is a simple estimator of the true number of species in an assemblage based on the number of rare species in the sample (Colwell and Coddington 1994). The Chao1 bias correction was selected for all orchards except Benifallet. In Benifallet, orchard data gave a Chao estimated coefficient of variation for abundance distribution >0.5 and, in this case, the procedure recommended to recompute Chao1 is the classic instead the bias-corrected option (Colwell 2006).

To compare richness and diversity between the inner part and the edge of orchards, we computed species accumulation (rarefaction) curves using EstimateS (Colwell 2006). We computed sample-based rarefaction curves from empirical data of eight samples (sample order was randomized 50 times) of the inner part and the edge part of each orchard. We computed the expected richness function Mao Tau and their 95% CI curves and the Shannon diversity

index mean (and SD) from 50 randomizations of sample order from EstimateS (Colwell 2006).

Statistical Analysis. Statistical analyses were performed with the SAS package (SAS Institute 1999). To analyze differences in variables at the community level (total number of ants, number of species, species diversity, and Hill's ratio evenness) between the inner part and the edge of the orchards, random effects were required to be included in the analyses, and linear mixed models were performed. First, to test differences between the inner part and edge in all orchards considered together, data included different measures of the same orchard; these measures were correlated within each orchard. This covariance structure was handled by introducing the variable "orchard" as random effects into the statistical analyses. Then, to test differences in the same variables within each orchard, data included two measures of each month; these measures were correlated within each month, and the variable "month" was introduced as random effect into the analyses. Normality of dependent variables was always tested before fitting statistical models; when different distributions of error were possible, the one that minimized the deviance of the model was selected (Herrera 2000). It was used either as generalized linear mixed models with Poisson or Gamma distributions with log link function (hereafter $GLMM_{POISSON}$ and $GLMM_{GAMMA}$) or general linear mixed models with normal distribution and identity link function (hereafter $GLMM_{NORMAL}$). GLMM computations were performed with the procedure MIXED and the macro program GLIMMIX in SAS v.8.2 (SAS Institute 1999).

Results

Differences of Ant Communities Between and Within Citrus Orchards. The total number of ants sampled at pitfall traps was 41,213. Table 2 lists the 14 ant species recorded at the six orchards. *Lasius niger*

Table 3. Values of different community parameters calculated from ants catches at pitfall traps in the six citrus orchards (top) and in other natural Mediterranean communities (bottom) from Catalonia

Study site	Vegetation type	Richness (S)	Diversity (H)	Evenness (Hill's F)
Frudelta	Citrus orchard	5	1.28	0.90
Benifallet	Citrus orchard	8	1.20	0.66
Les Palmeres	Citrus orchard	4	0.49	0.66
Mianes	Citrus orchard	5	0.09	0.35
Xalet	Citrus orchard	4	0.10	0.37
XemiNavel	Citrus orchard	3	0.71	0.93
Serra de Collcerola	Shrubland	7	1.60	0.67
Canet de Mar	Grassland	12	1.98	0.65
Canet de Mar	Open holm oak forest	15	1.60	0.43
Canet de Mar	Open pine forest	15	1.40	0.30
Serra de l'Obac	Forest gap	15	1.24	0.72
Serra de l'Obac	Open holm oak forest	11	1.48	0.62
Serra de l'Obac	Holm oak forest	13	1.48	0.74
Portbou	Grassland	10	1.74	0.64
Portbou	Shrubland	8	1.40	0.46
Portbou	Open mixed forest	8	1.49	0.56

The location of natural communities is given in Retana and Cerdà (2000).

and *Pheidole pallidula* contributed 89 and 7%, respectively, to the total number of ants and were the only species present in all six orchards. *Plagiolepis schmitzii* was present in five orchards, *Camponotus foreli* in two orchards, and the other 10 species were found only in one orchard each. *L. niger* was the most abundant species in four orchards, and *P. pallidula* and *Linepithema humile* were the most abundant in one orchard each.

The highest number of ants was found in two orchards, Xalet and Mianes, mainly because of the extremely high number of *L. niger* workers collected (the two orchards with >98% of pitfall catches belonging to this species; Table 2). Species richness ranged from three to eight species (Table 3). These low numbers of species in citrus orchards do not seem to be caused by an incomplete sampling procedure. Values of Chao1 estimators of total expected species in each orchard were exactly the same to those of observed richness in all orchards except in Benifallet, where Chao1 estimated 11 expected species versus only 8 observed species in the field.

Species diversity was highest in Benifallet and Frudelta (Table 3), the two orchards with highest weed presence (Table 1). A significant negative relationship was observed between diversity and total number of ants collected per orchard (Spearman's $r_s = -0.94$, $P = 0.035$, $n = 6$): the highest diversity values (in Benifallet and Frudelta orchards) were paired with very low values of number of ants caught in pitfall traps, whereas Xalet and Mianes, with the highest values of number of ants, had the lowest diversity values. The Hill's ratio (Table 3) was also lowest in Xalet and Mianes, because of the important presence of *L. niger*.

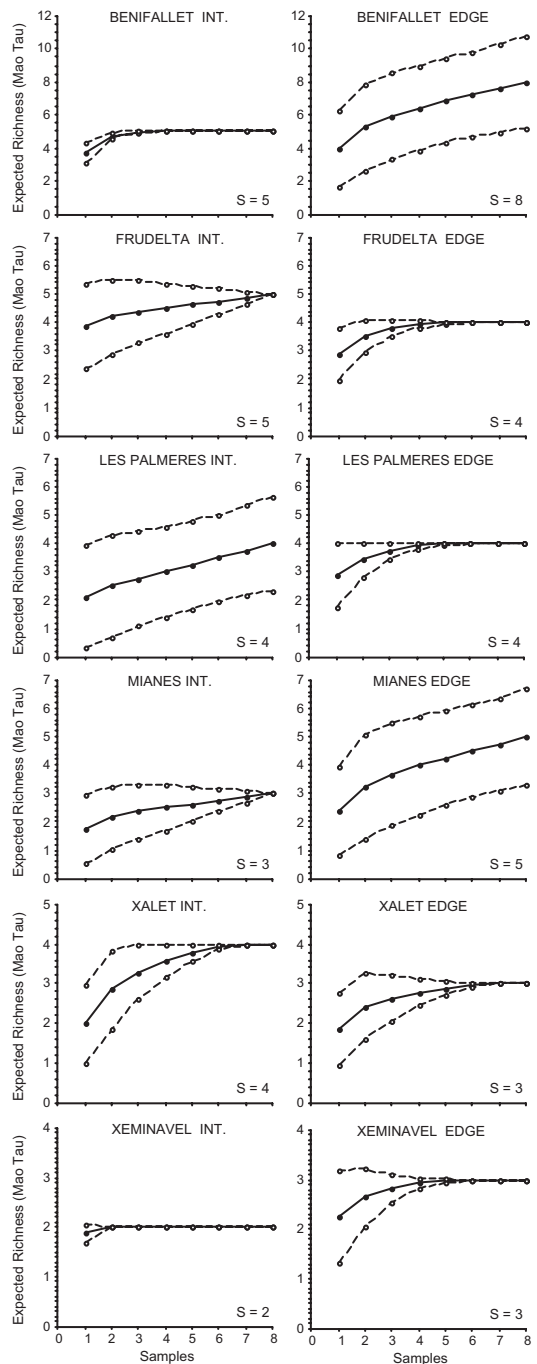


Fig. 2. Sample-based rarefaction curves of the inner part (INT) and the edge part (EDGE) in each orchard (sample order was randomized 50 times). Values are the expected richness function Mao Tau and their 95% CI. Observed richness (S) is given for each case.

When considering all the orchards together, the comparison between the inner part and the edge of the orchards gave no significant differences in total number of ants (GLMM_{GAMMA}, $F_{1,77} = 0.0$, $P = 0.99$),

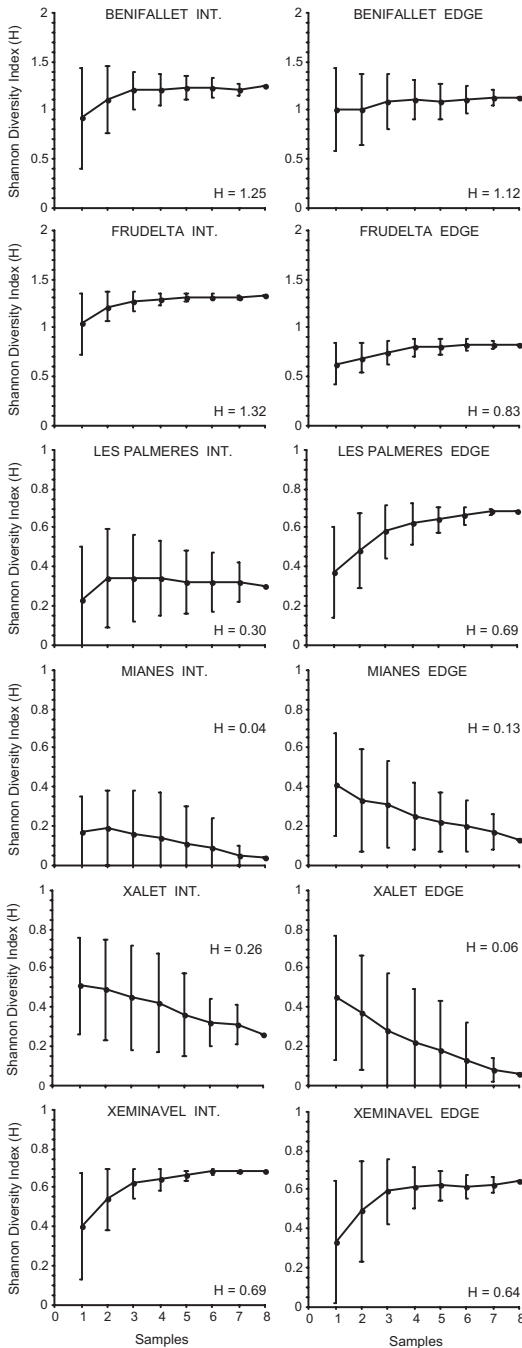


Fig. 3. Diversity curves of the inner part (INT) and the edge part (EDGE) in each orchard. Values are the Shannon diversity index mean (error bars: SD) from 50 randomizations of sample order. Observed Shannon's diversity (H) is given for each case.

species richness (GLMM_{POISSON}, $F_{1,77} = 0.95, P = 0.33$), species richness (GLMM_{NORMAL}, $F_{1,77} = 0.19, P = 0.66$), Pielou's evenness (GLMM_{NORMAL}, $F_{1,77} = 0.66, P = 0.42$), and Hill's ratio evenness (GLMM_{NORMAL}, $F_{1,77} = 0.89, P = 0.35$). However, when analyzing the

Table 4. Proportional similarity index in ant composition between the different orchards considered in this study

Orchard	Frudelta	Mianes	Les Palmeres	Xalet	Xeminavel
Benifallet	0.21	0.59	0.70	0.60	0.52
Frudelta		0.11	0.27	0.11	0.31
Mianes			0.84	0.99	0.42
Les Palmeres				0.84	0.58
Xalet					0.42

same community parameters within each orchard (see Statistical analysis section), some significant differences were found between the inner part and the edge in two orchards. In Mianes, there were significant differences for the total number of ants (GLMM_{GAMMA}, $F_{1,6} = 7.12, P = 0.04$), species richness (GLMM_{POISSON}, $F_{1,6} = 6.54, P = 0.04$), species diversity (GLMM_{NORMAL}, $F_{1,6} = 7.22, P = 0.04$), and Hill's ratio (GLMM_{NORMAL}, $F_{1,6} = 7.71, P = 0.03$), with higher values in the edge than in the inner part of the orchard for all these variables. In the Frudelta orchard, there were significant differences only for total number of ants (GLMM_{GAMMA}, $F_{1,6} = 50.43, P = 0.0004$) and species richness (GLMM_{POISSON}, $F_{1,6} = 8.80, P = 0.025$), with higher values in the inner part than in the edge of the orchard (probably associated to the high presence of the invasive *L. humile* in the edge).

Because GLM do not remove the effects of abundance, a rarefaction approach was also used to compare edge versus interior orchard samples. Figure 2 shows the sample-based rarefaction curves of the two types of samples in each orchard. There was not a clear pattern, with some orchards showing higher richness values in the edge and others in the inner part. In most cases (9 of 12), the expected richness values (Mao Tau function) from resampling were similar to the observed richness (S) values. Figure 3 shows the diversity curves of the inner and the edge part in each orchard from 50 randomizations of sample order. Again, there was not one pattern, with one orchard with higher diversity in the inner part, another with higher diversity in the edge, and others with similar diversity in the inner part and the edge.

The total value of similarity (PSI) between inner and edge of all orchards considered together was 0.96 (Table 2); PSI values for each orchard were always higher than 0.70. The similarity of species composition between orchards ranged widely, between 0.11 and 0.99 (Table 4). In general, PSI values were >0.5, and the most different orchard was Frudelta (the only with presence of *L. humile*), with PSI values <0.31 with the others.

Seasonality of Ants in Citrus Orchards. The highest abundance of ant workers collected in traps (pooling the six orchards together) was found in April (Fig. 4A), with the highest presence of *L. niger* on the ground. These values decrease progressively throughout the year, especially from April to May and from June to July. The lowest values were found in October, when many species started the prehibernation period.

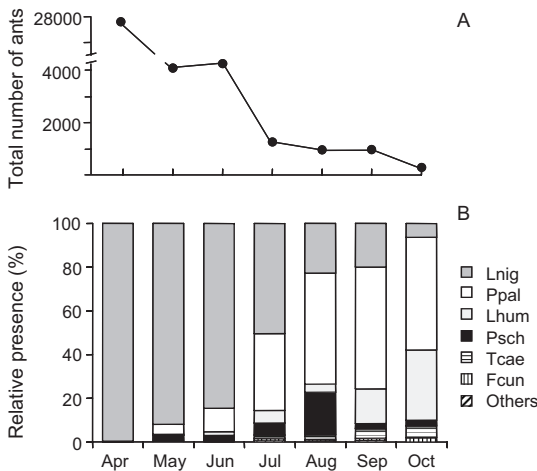


Fig. 4. Seasonal variations in (A) the total number of ants (pooling the results obtained in the six orchard) and (B) relative frequency of the different ant species collected in pitfall traps in the different monthly samplings. Lnig, *Lasius niger*; Ppal, *Pheidole pallidula*; Lhum, *Linepithema humile*; Psch, *Plagiolepis schmitzii*; Tcae, *Tetramorium caespitum*; Fcun, *Formica cunicularia*. Others include eight species with <0.1% of catches in pitfall traps.

Figure 4B shows the relative abundance of the different ant species throughout the activity period, from April to October. *L. niger* was the most abundant species from April to June, but its presence decreased in summer. *P. pallidula* was the most abundant species from August to October (but its absolute values were considerably smaller than those of *L. niger* in spring). The relative abundance of *P. schmitzii* increased from May to August, whereas that of *L. humile* was highest in September and October.

Citrus Orchards and Natural Mediterranean Ant Communities. Table 3 shows some community variables of the six studied citrus orchards and of other natural Mediterranean communities from Catalonia. All the natural communities are situated relatively near the coast and provide a wide spectrum of different vegetation types: from the degraded grasslands to the well-preserved holm oak and pine forest. The first difference between natural and orchard ant communities was the number of species: whereas in orchards, there were only few species, ranging from 3 to 8 species (but only one orchard with >5 species), in natural communities, the number of species was always higher than 7 (and only three communities had <10 species). Diversity (Shannon's index) was also higher in natural communities (with most of values ranging from 1.40 to 1.98, and one exception with 1.24) than in orchards (values ranging from 0.09 to 1.28), with only two orchards (Benifallet and Frudelta) having diversity values similar to the lowest natural community value. The Hill's ratio was very variable in both orchard and natural communities (Table 3), ranging from 0.35 to 0.93 in orchards and from 0.30 to 0.74 in natural communities.

Discussion

In the citrus orchards considered in this study, the most abundant species were *L. niger* and *P. pallidula*, which are behaviorally dominant species in the Mediterranean region (Cerdá et al. 1997, 1998a, b). Two other dominant species, *L. humile* and *Tetramorium caespitum*, were also abundant, although only in one orchard (Table 2). *L. niger* is a top level species (Hölldobler and Wilson 1990), which defends nests and foraging areas as absolute territories. Its diet is mainly based on honeydew from aphids that they protect against enemies (Stadler 2004). *P. pallidula* is a Mediterranean scavenger ant able to dominate food resources by means of an efficient mass recruitment system (Cerdá et al. 1998b). *L. humile*, the Argentine ant, is a tramp species that also exploits Homopteran honeydew and typically invades Mediterranean habitats, where it has a very negative effect on the local ant fauna (Suarez et al. 1998). *T. caespitum* also defends nest and food resources (Hölldobler and Wilson 1990). Only one subordinate species, the small and cryptic *P. schmitzii*, was abundant in the ant communities studied. The presence of particularly abundant and competitive ants may profoundly affect both the species composition and abundance of other ants in the community (Cammell et al. 1996, Cerdá et al. 1998a, Retana and Cerdá 2000). These dominant species behave similarly to those of other regions of the world by reducing the foraging success of subordinate species and even contributing to the disappearance of certain species (Human and Gordon 1996).

The consequence of this impoverishment of the ant fauna is the low values of species richness and diversity in the studied orchards compared with natural communities (Retana and Cerdá 2000, Arnan et al. 2006). In open Mediterranean habitats, climatic axes seems to have a primary role in community structure (Cerdá et al. 1997). Areas that are exposed to wind and direct sunlight are expected to be drier and warmer and to have wider temperature extremes than those that are protected by a canopy cover (Retana and Cerdá 2000). In open habitats, the different resistance of dominants and subordinates to physical factors reduces the occurrence of competition (Cerdá et al. 1997). Thus, heat-intolerant dominants and heat-tolerant subordinates are abundant during different periods of the day (Cros et al. 1997), and this increases species diversity. In the orchards considered in this study, vegetation cover of citrus trees (36–65%; Table 1) is not as high as in forests (70–90%; Retana and Cerdá 2000, Arnan et al. 2006) but still reduces the presence of heat-tolerant species and favors the increment of heat-intolerant dominant species. Moreover, other reason suggested by different authors (Room 1975, Perfecto and Snelling 1995) for the decrease of diversity of ground-foraging ants is the reduction of vegetation structure. In these agricultural habitats, the reduction in vegetation structure caused by management also determines the reduction of species richness and the increment of dominant species. Thus, in the two orchards with the highest presence of

understory vegetation under the citrus trees, i.e., with higher vegetation complexity, species richness and diversity are also considerably higher than in those with no presence of understory vegetation (Table 2). Other studies have also shown that changes from traditional agroforestry systems to monoculture, simplified systems may result in a significant decrease of diversity of ground-foraging ants (Roth et al. 1994, Perfecto and Snelling 1995, Cammell et al. 1996), whereas the opposite pattern, i.e., progressive land abandonment, leads to an increase in ant richness and abundance. It has been suggested that a possible explanation for the observed pattern of biodiversity loss in these monoculture systems is that food availability considerably decreases in these habitats (Perfecto and Snelling 1995) and, consequently, niche availability for species is reduced.

This reduction of species richness and diversity was not modified by edge effects. The importance of edges has received increased recognition (Fagan et al. 1999, Bolger et al. 2000), because of the modification of physical gradients in light, moisture, and wind velocity or variations in food availability, and some evidences of edge effects have been shown in ant communities in agricultural habitats (Samways 1983, Roth et al. 1994, Peck et al. 1998). In Germany, *L. niger* shows significantly higher nest abundance at the edges compared with the center of different agricultural sites (Dauber and Wolters 2004). However, in our case, only slight and local differences were found between the inner part of the orchards and the orchard margins. Differences among orchards are probably greater than differences between the inner part and the edge.

The results of this study are in accordance with other studies on the seasonal activity of Mediterranean ant communities (Cros et al. 1997). The activity peaks of the different ant species actively foraging on these citrus orchards are distributed throughout the whole activity period of ants in the Mediterranean basin, which goes from early spring to autumn. Thus, the most abundant species, *L. niger*, has the peak activity at the beginning of the season, whereas *P. pallidula* (and to a lesser extent, *L. humile* and *T. caespitum*, which were only present in one orchard each) was active primarily in late summer and autumn. This temporal partitioning of the habitat by dominant species contrasts with the spatial partitioning of the habitat in tropical forests, where dominant species spread out into a mosaic with mutually exclusive territories that cover from one to several trees each throughout the whole year (Room 1971, Samways 1983, Hölldobler and Wilson 1990).

Overall, the composition of ant communities present in the citrus orchards of this study is extremely poor, even more than the values given for other orchard and arable lands in the Iberian Peninsula (Cammell et al. 1996, Gómez et al. 2003), and considerably more than unproductive or disturbed areas (Bestelmeyer and Wiens 1996, Hoffmann 2000). This should not be a surprise because monocultures are ecosystems in which one of the main goals of ecosystem managers is to purposefully reduce biodiversity as much as possi-

ble (Vandermeer and Perfecto 1997). Pesticides, herbicides, and other substances bring an inevitable loss of biodiversity. In general, the disturbance of natural vegetation, by human activities such as agriculture, has a very significant effect on soil communities, reducing the diversity and density of these populations. Vandermeer and Perfecto (1997) described, in other tropical monocultures, a dramatic loss in ants (and other insect groups) as the "modernization" and technification of the system proceeded. In the Mediterranean ant communities studied here, this reduction in species richness determines, following the "dominance-impoverishment rule" proposed by Hölldobler and Wilson (1990), that the more likely the community is to be dominated behaviorally by few dominant species, which also contribute in reducing the presence of subordinate or opportunistic ants (Andersen 1992, Davidson 1998, Retana and Cerdá 2000).

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