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Belowground space occupation and partitioning in an ant community during succession

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Abstract. In this study we analyze the successional strategies for belowground space occupation and partitioning in Mediterranean ant communities on fallow land. Three successional sequences were established, by means of a number of plots representing disturbance patches with different surrounding matrices (forests, uncultivated and cultivated land). The belowground extension of the colonies was mapped on a grid of squares. The amount of space occupied by the ant colonies increased during the three successional sequences. The colonies increased significantly in number but not in size in areas surrounded by uncultivated or cultivated land. The contrary occurred when the surrounding matrix was composed of forest (significant increase in size but not in number). Finally, those study areas with an expectedly higher propagule flux (founding queens) from the surrounding matrix (mosaic of uncultivated fields and forest) showed a significant increase in overlapping on the space of neighbouring colonies. The analysis of the colony size of the most abundant species showed that each maintains a certain colony size, which did not vary among the areas studied. The proportion of mature species (characteristic of later successional stages) is greater in areas with a more mature surrounding matrix. Species composition is suggested to be a key factor in explaining the different strategies developed by ant communities in their colonization of disturbance patches.

INTRODUCTION

Ecological succession is commonly used to analyze the temporal dynamics of ecological communities (Drury & Nisbet, 1973; MacMahon, 1980; Peet & Christensen, 1980). Most studies, however, pertain to plant communities (see, e.g., Austin, 1980; Bornkamn, 1981; Collins & Adams, 1983; Lepš, 1987). Animal communities have not received such attention. Although the latter are often considered causal factors which explain some aspect of plant succession (Austin et al., 1981; Tilman, 1983; Brown, 1984; Gibson et al., 1987), few works deal strictly with their own successional dynamics (Anderson, 1975; Taylor & Woiwod, 1980; May, 1982; Glowazinski & Weiner, 1983). This is certainly the case with ants: there are studies of their influence on succession in pastures (Jonkman, 1978; Fowler & Haines, 1983) or of the response of a single species to different successional stages, as defined by vegetation (Carroll & Risch, 1984; Blanton & Ewel, 1985), but little work has been done on the specific dynamics of ant communities during succession (Lynch, 1981; Boomsma & van Loon, 1982; Chew, 1987; Gallé, 1991).

Many types of disturbance, whether of natural or anthropogenic origin, may initiate a successional process, since the disappearance of the original community has consequently provided an "empty" space for colonization (Horn, 1974; Levin & Paine, 1974; Davis, 1986; Forman & Godron, 1986). Fields abandoned after ploughing are often used to study this process of secondary succession (Bazzaz, 1975; Reichhardt, 1982; Lepš, 1987). Such fields are readily found in nearly every landscape transformed by man and allow a temporal series of plots to be established, according to their time of abandonment. This "static approach", or space-for-time substitution, has been proposed and employed as a practical alternative to long-term studies of succession (Austin, 1977; Pickett, 1989). It is, moreover, the only effective way to study the successional processes foreseen by this research, considering the destructive sampling method needed to obtain the data (see below).

This methodological approach was thus used to study the temporal dynamics of Mediterranean ant communities on fallow land in central Spain. Topics related to succession which have been studied previously include the spatial organization of communities (Zorrilla et al., 1986; Acosta et al., 1988; Serrano et al., 1988; Serrano & Acosta, in press), changes in species composition in relation to diet, foraging behaviour and the size of individuals (Serrano et al., 1987), and the characterization of directionality in the successional process of ant communities (Gomá et al., 1988).

The present study analyzes the strategies of occupation and partitioning of belowground space in these Mediterranean ant communities during succession, focussing especially on the role of the surrounding matrix in the colonization process. Although the partitioning of space because of competition is a common topic in ant ecology (see, e.g., reviews of Hölldobler & Lumsden, 1980; Levings & Traniello, 1981), all such studies have dealt with aboveground processes, mainly the competition for space due to the establishment of foraging areas for the exploitation of food resources. Certain processes in belowground competition for space have been found to occur in the root systems of plants (e.g., Cody, 1986; Smith, 1986), and may also be studied in ants. Galleries and chambers constitute the equivalent of a "root" system in ant colonies, although this subterranean network is, in most cases, developed to provide not access to food resources, but instead refuge and space for brood rearing and food storage. These latter are the motives that we assume drive ants to compete in the belowground partitioning of space.

Both the number and size (inferred from external evidence) of ant nests have been found to vary with different trends among time series (Francoeur & Pépin, 1978; Jonkman, 1979; Klimetzek, 1981; Chew, 1987). However, there are no analyses of what community-level consequences variation in these parameters may have for the partitioning of space. Studies of this kind have only been conducted theoretically on the growth of individual plants (e.g., Pacala, 1986). The purpose of the present investigation is to analyze how these parameters (number and size of nests) are involved in the occupation of belowground space by an ant community colonizing disturbance patches, and to assess the influence exerted in this process by the degree of maturity of the surrounding matrix.

MATERIALS AND METHODS

This study was conducted in three areas of central Spain, where vegetal climax is made up of Holm oak (*Quercus rotundifolia* Lam.) "dehesas" or open woodlands (Bellot, 1978). All were composed, to a greater or lesser extent, of a mosaic of abandoned cereal fields with a prior homogenization consequent to cropping techniques, practically identical in all Mediterranean regions of Spain. Each area contained a number of plots of different abandonment ages, and constituted an independent temporal series. The plots represented disturbance patches, and were surrounded by a matrix (Forman & Godron, 1986) that depended on the area. The areas were selected according to a sequence of increasing maturity in the surrounding matrix of the plots, from cereal crops up to "dehesa". The areas (identified by localities and provinces) were the following:

1. Sabiote (Jaén province). Six plots with 1, 2, 4, 6, 8 and 26 years since their last ploughing. Surrounding matrix of cultivated fields of cereal crops.

2. Valdelaguna (Madrid province). Four plots with 3, 8, 13 and 17 years since their last ploughing. Surrounding matrix of uncultivated fallow lands of varying abandonment ages.

3. Arganda (Madrid province). Two plots with 14 and 30 years since their last ploughing. Surrounding matrix of "dehesa".

The plots of each series were near to each other, within a radius of less than 500 m.

A number of 4 x 4 m squares were selected in each plot: five squares in each Sabiote plot, four in Valdelaguna, and eight and nine, respectively, in the two Arganda plots. Each square was subdivided into 64 units of 0.5 x 0.5 m by means of a grid. These subdivisions were the spatial sampling units. The terrain was excavated to a depth of 50 cm, and the presence of ant colonies in each spatial sampling unit was recorded. "Presence" was recorded when individuals of a species were detected inside a gallery. When galleries were not visible (due to the process of excavation and/or the small size of the galleries of some species) the criterion was instead the presence of a large number of specimens. Sampling work was performed between July and August, 1991.

The strategies of occupation and partitioning of space were investigated according to the following parameters, which were estimated independently of species composition:

(i) Number of colonies. One colony is spatially defined as the group of all contiguous spatial sampling units with presence of the same species. Field observations validate this definition, because none of the nests occupying several contiguous sampling units showed any discontinuity in the presence of galleries or groups of individuals (as explained above), and no cases were observed where there was more than one colony of the same species within a single sampling unit. The number of colonies was calculated per square.

(ii) Colony size. Estimated as the number of spatial sampling units occupied by each colony.

(iii) Space occupied. Defined as the total number of spatial sampling units occupied in a square.

(iv) Overlapping colonies. Defined as the ratio between the number of spatial sampling units occupied by more than one species and the total number of spatial sampling units occupied in a square. A colony was considered to be occupying a spatial sampling unit when either the whole or a part of the colony was included in the unit. The total number of these overlapped sampling units was 197; 86% of which were occupied by two species, and the remaining 14% occupied by three species.

Given that all data were counts and were ranked, the changes in these parameters for each successional sequence were tested using Kruskal-Wallis and U Mann-Whitney tests (Sachs, 1982). Number of colonies, space occupied, and overlapping of colonies were compared using average values of mean ranks per square, while colony size was compared employing mean ranks per plot.

The colony size of those species sufficiently represented in each study area were also compared amongst areas and species by means of Kruskal-Wallis and U Mann-Whitney tests.

Some of the species found in this study were classified as characteristic of the mature stages of succession (hereafter referred to as "mature" species), according to the results of previous studies of succession in fallow lands and "dehesas" in central Spain (Zorrilla et al., 1986; Gomá et al., 1988; Serrano et al., 1988). The proportion of mature species in relation to the total number of species present was estimated for each study area.

RESULTS AND DISCUSSION

A total of 28 species belonging to 13 different genera were found in the 12 sampling plots. The names of species and the number of colonies found in each plot are given in Table 1.

Results of the tests on space occupied, number, size and overlapping of colonies in the successional sequences are summarized in Table 2. The belowground space occupied in the plots increased significantly in the three successional series (Table 2), probably as a result of the colonization process, to which all the disturbance patches are subjected (e.g., Gloaguen & Gautier, 1981; Davis, 1986). If, however, we examine how the space is occupied, two different strategies can be outlined (Fig. 1).

TABLE. 1. Species found in the three study areas. (M) = "Mature" species (see Methods section). Numbers in each species file indicate the number of colonies in each plot. Numbers under the heading of each study area indicate years of abandonment (time since last ploughing) of each plot.

Species	Sabiote						Valdelaguna				Arganda	
	1	2	4	6	8	26	3	8	13	17	14	30
Hypoponera eduardi (Forel)	–	–	–	–	–	–	–	–	–	1	–	–
Aphaenogaster gibbosa (Latr.)	2	–	–	–	–	1	1	–	10	6	–	15
Aphaenogaster iberica Em. (M)	–	–	–	–	–	–	–	–	–	–	2	–
Aphaenogaster senilis Mayr	1	1	1	2	1	3	1	–	2	3	–	–
Aphaenogaster dulcinea Sants. (M)	–	–	–	–	–	–	–	–	–	10	–	–
Crematogaster auberti Em. (M)	–	–	–	–	–	–	9	9	19	17	12	34
Leptothorax fuentei Sants.	–	–	–	–	–	3	–	–	–	19	–	2
Lepthotorax cervantesi Sants.	–	–	–	–	–	–	–	–	–	–	–	1
Messor barbatus (L.) (M)	1	–	4	7	–	9	–	1	–	6	2	7
Messor capitatus (Latr.) (M)	–	–	–	–	–	–	–	2	–	3	–	1
Messor structor (Latr.)	9	4	–	–	3	4	12	14	20	15	–	–
Pheidole pallidula (Nyl.) (M)	–	6	7	5	7	2	–	–	1	–	–	–
Strongylognatus caeciliae Forel	–	–	–	–	–	–	–	–	–	1	–	–
Tetramorium hispanicum Em.	–	–	–	–	–	–	6	13	–	–	4	8
Tetramorium semilaeve André	11	–	9	8	1	17	14	4	7	12	21	–
Camponotus aethiops (Latr.)	–	–	–	–	–	–	–	–	5	2	–	–
Camponotus foreli Em. (M)	–	–	–	–	–	–	–	2	1	1	1	5
Camponotus sylvaticus (Ol.) (M)	–	–	–	–	–	–	–	–	–	–	2	–
Cataglyphis iberica Em.	–	–	–	–	–	–	–	–	–	–	2	–
Cataglyphis viaticoides (André)	–	–	–	1	–	–	–	–	–	–	–	–
Lasius flavus (Fabr.)	1	–	–	–	–	1	–	–	–	–	–	–
Lasius niger (L.)	–	–	1	–	1	–	–	–	–	–	–	–
Plagiolepis pygmaea (Latr.)	–	–	–	–	–	–	–	5	10	12	–	3
Plagiolepis schmitzi Forel (M)	1	2	10	1	–	–	–	1	–	–	14	14
Proformica ferreri Bond.	–	–	–	–	–	–	6	22	5	–	–	–
Tapinoma erraticum (Latr.)	–	–	–	–	–	–	–	–	1	4	–	–
Tapinoma nigerrimum (Nyl.)	13	6	4	5	3	6	10	–	–	–	27	–
Tapinoma simrothi Krausse	–	–	–	–	–	–	–	–	–	1	–	–
Total number of colonies	39	19	36	29	16	46	59	73	81	113	87	90

The number of colonies increased significantly in the two study areas with less mature surrounding matrices (Sabiote and Valdelaguna; cultivated and uncultivated fallow lands), but there was no significant trend in colony size (Table 2). This indicates that the belowground space is occupied by a growing number of colonies that do not spread spatially during the successional process. Conversely, the number of colonies does not increase in Arganda (Table 2), where the disturbance patches have the most mature surrounding matrix ("dehesas"). Since the amount of belowground space occupied also increases in these patches, a compensatory mechanism acting to secure occupation of this space is foreseeable. In effect, the size of the colonies increases significantly in the successional series of Arganda (Table 2), so that belowground space is thus occupied by colonies that spread spatially during the colonization of ploughed patches.

There is a significant increase in colony overlapping in the Arganda and Valdelaguna plots (Table 2). As mentioned in the Methods section, overlapping might be due to the

TABLE. 2. Results of the ranked tests of space occupied and number, size, and overlapping of colonies in the three successional sequences. Numbers under the heading of each study area indicate years of abandonment (time since last ploughing) of each plot. Real averages are given in number of spatial sampling units (squares of 0.5 x 0.5 m). K-W = Kruskal-Wallis test. U = Mann-Whitney test. N.S. = not significant.

Locality	Parameter	Test	N	Plots mean ranks (and real averages)						Statistic	p
				1	2	4	6	8	26		
Sabiote	No. colonies	K-W	30	17.9 (7.8)	9.5 (4.2)	17.4 (7.2)	13.5 (5.8)	8.6 (4.0)	26.1 (11.6)	H = 13.69	< 0.5
	Colony size	K-W	201	92.3 (1.36)	100.3 (1.43)	94.1 (1.39)	113.1 (1.65)	92.6 (1.4)	108.4 (2.25)	H = 6.29	N.S.
	Space occupied	K-W	30	15.3 (9.8)	10.6 (6.2)	16.2 (9.4)	14.2 (8.6)	9.0 (5.6)	27.7 (24.2)	H = 14.15	< 0.05
	Overlapping	K-W	30	17.4 (0.06)	11.0 (0.02)	15.2 (0.06)	16.8 (0.1)	9.0 (0.0)	23.6 (0.11)	H = 10.53	N.S.

Locality	Parameter	Test	N	Plots mean ranks (and real averages)				Statistic	p
				3	8	13	17		
Valdelaguna	No. colonies	K-W	16	3.0 (14.7)	6.7 (18.5)	10.0 (21.5)	14.2 (30.2)	H = 12.22	< 0.01
	Colony size	K-W	312	155.8 (1.93)	147.8 (2.06)	151.4 (2.26)	165.7 (2.34)	H = 2.69	N.S.
	Space occupied	K-W	16	3.6 (23.2)	7.6 (31.0)	9.4 (34.5)	13.4 (43.2)	H = 8.70	< 0.05
	Overlapping	K-W	16	4.5 (0.11)	6.5 (0.18)	9.0 (0.24)	14.0 (0.40)	H = 8.91	< 0.05

Locality	Parameter	Test	N	Plots mean ranks (and real averages)		Statistic	p
				14	30		
Arganda	No. colonies	U	17	8.4 (9.8)	9.6 (11.4)	Z = 0.48	N.S.
	Colony size	U	179	79.7 (1.38)	100.2 (2.06)	Z = 3.19	< 0.001
	Space occupied	U	17	7.0 (13.0)	11.2 (20.0)	Z = 1.73	< 0.5
	Overlapping	U	17	6.9 (0.05)	11.3 (0.14)	Z = 1.85	< 0.5

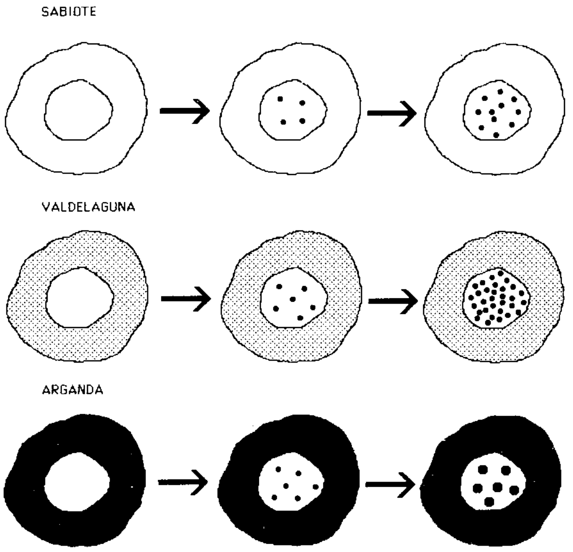

Fig. 1. Model of evolution of the colonization processes in the three study areas. Inner and outer surfaces represent the disturbance patch and surrounding matrix, respectively. The type of matrix is indicated as follows: white = cereal crops, grey = fallow lands with differing abandonment age, black = "dehesa" (open woodlands). Dots represent ant colonies, regardless of species. Numbers and sizes of colonies do not correspond to real values but are simplified to highlight whether or not they increase significantly over the successional sequence. Colonization processes are symbolized as three stages from left to right, constituting an ideal successional sequence for all study areas, in order to simplify comparison.

presence of several whole colonies or parts of them in the same spatial sampling unit. In addition, we found cases of overlapping colonies of two or three different species within the same spatial unit. If our findings on the strategies of belowground occupation in these two areas are correct, the increase in overlapping is due to different processes in each. The sharing of a single spatial unit by whole colonies and the presence of more colonies in each unit should be proportionately larger in Valdelaguna (where the colonies increase in number) than in Arganda (where they increase in size). This prediction is supported by the proportion of overlapped spatial units found in each study area. Whole colonies occupy 11% of the overlapped units of Valdelaguna, but only 6% of those in Arganda. The percentage of these overlapped units having three species present is also greater in Valdelaguna (18%) than in Arganda (3%). The flux of colonizing propagules (foundress queens) from outside the patch is expected to be greater in the plots of these two areas, compared to those of Sabiote, where there is no significant trend in colony overlapping over successional time (Table 2). The latter area has a surrounding matrix composed of cultivated fields, and the propagules that reach it must travel from more distant areas. In fact, the spatial sampling units in Sabiote with some presence of any species only represent 17% of the total number of sampling units, compared to 25% and 52% for Arganda and Valdelaguna, respectively.

Some studies have demonstrated the major importance of competition for nesting places to the spatial structuring of ant communities (Brian, 1952; Brian et al., 1966; Levings & Franks, 1982). Colonies may increase or decrease their spatial area or even disappear as a result of competitive interaction (Scherba, 1963; Francoeur & Pépin, 1978; Klimetzek, 1981; Chew, 1987). Although we have not assessed the proportion of land covered by ant nests in its effect on competitive interactions among the colonies found in our study areas (which requires further study), we assume that the land coverage in these areas is sufficient to stimulate such competitive effects. Nielsen (1986), studying a four-species ant community, found territory to be a limiting factor for nest size in an area where 15% of the land was covered by nests (a lower percentage than the minimum found in our study areas).

Nevertheless, competitive interaction depends not only on the density of colonies but also on the complex network of relations between species in the ant assemblages. For example, the intensity of competition varies with the relationship between the species involved (Levings & Franks, 1982; Hölldobler, 1976; Hölldobler & Wilson, 1977), and some species prevail over others because they are better adapted to the environmental conditions of a certain site (Boomsma & De Vries, 1980; Doncaster, 1981; Samways, 1983; Assing, 1986). These conditions may change over time and have been proven to encourage species substitution, leading to the categorization of species as "pioneer" or "mature" (Boomsma & van Loon, 1982; Zorrilla et al., 1986; Serrano et al., 1988).

Therefore, if the belowground growth of colonies is assumed to be constrained by the same condition as that in aboveground areas (Levings & Traniello, 1981), then the species composition of an ant community is a key factor in explaining changes in the number and size of nests. The way these changes occur depends on the different interactions entailed by different interacting species. Given that the species invading the empty patch after disturbance will vary according to the nature of the surrounding matrix (Forman & Godron, 1986; Gomá et al., 1988; Serrano et al., 1988), a tentative explanation for the strategies followed by the ant communities considered here could lie in the species composition determined by each type of matrix. Mature species are expected to preferentially employ strategies that ensure a higher colony survival rate, and may thus increase the size of their colonies over time. A more mature matrix probably contains a larger proportion of mature species, and consequently will send more propagules of these species to the patch that is to be colonized.

If this occurs in the ant communities studied here, a larger proportion of mature species would be expected in Arganda, as compared to Valdelaguna and Sabiote, since the former has the most mature matrix, and is the only one which shows an increase in colony size over successional time. The data on the proportion of mature species within each study area agree with this hypothesis. The mature species (see Methods section) present were *Aphaenogaster iberica*, *Aphaenogaster dulcinea*, *Messor barbarus*, *Messor capitatus*, *Pheidole pallidula*, *Crematogaster auberti*, *Camponotus foreli*, *Camponotus sylvaticus*, and *Plagiolepis schmitzi* (Table 1), constituting 47% of the species found in Arganda, but only 33% and 25% of those in Valdelaguna and Sabiote, respectively. However, the relationship of this proportion with area age is likely smaller, since, for example, the most mature plot from Sabiote (26 years) had a smaller proportion of mature species (22%) than the earlier plot from Arganda (14 years; 50%).

Furthermore, the hypothesis that the species composition of a community is the factor determining strategies for the occupation of belowground space is likewise supported by the data on the colony size of a certain species in the different study areas. The colony size of the following species, both mature and immature, was compared over the three areas: *Aphaenogaster gibbosa*, *Crematogaster auberti*, *Messor barbarus*, *Tetramorium hispanicum*, *Tetramorium semilaeve*, *Plagiolepis schmitzi*, and *Tapinoma nigerrimum*. No species showed a significantly different colony size from one study area to another (Table 3), although the species did differ significantly among themselves in colony size (Table 4). If each species has its own colony size, which does not vary with changing areas, the differences in the strategies for space occupation of these ant communities during succession cannot be attributed to differences in the belowground colony spreading of each species in the different sites, but are instead likely to be related to species composition. This process of space occupation might be conceived as the result of more or less "mature" species composition, which would be superimposed over the change from pioneer to mature communities that takes place in each successional sequence.

Table. 3. Results of ranked tests performed to compare the colony size of different species between two or three of the study areas, according to information available. K-W = Kruskal-Wallis test (for those species sufficiently represented in the three study areas). U = Mann-Whitney test (for those species sufficiently represented in only two study areas). N. S. = not significant.

Species	Test	N	Statistic	p
Aphaenogaster gibbosa	U	32	Z = –0.465	N.S.
Crematogaster auberti	U	88	Z = –0.486	N.S.
Messor barbatus	K-W	37	H = 2.702	N.S.
Plagiolepis schmitzi	U	31	Z = –1.589	N.S.
Tapinoma nigerrimum	K-W	90	H = 0.991	N.S.
Tetramorium hispanicum	U	43	Z = –0.38	N.S.
Tetramorium semilaeve	K-W	74	H = 4.496	N.S.

Table. 4. Results of the ranked Kruskal-Wallis test (K-W) performed to compare colony size among those species sufficiently represented. Real averages are given in number of spatial sampling units (squares of 0.5 x 0.5 m).

Parameter	Test	N	Statistic	p
Colony size	K-W	407	H = 15.253	< 0.05

Species	N	Mean ranks (and real averages)
Aphaenogaster gibbosa	32	184.44 (1.4)
Crematogaster auberti	100	217.65 (2.3)
Messor barbatus	37	247.41 (2.8)
Plagiolepis schmitzi	43	181.42 (1.3)
Tapinoma nigerrimum	74	183.70 (1.8)
Tetramorium hispanicum	31	212.58 (2.8)
Tetramorium semilaeve	90	202.47 (1.7)

Although the ultimate causes of the development of different strategies of belowground space occupation need to be investigated thoroughly and require further research, this study demonstrates that such strategies exist at the level of an entire ant community, and shows the possible role of the surrounding matrix, as a source of species, in explaining these processes.

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