

Research article

Camponotus punctulatus ant's demography: a temporal study across land-use types and spatial scales

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Abstract. Agricultural activities promote the explosion of diverse pest populations. In Argentina, the ant *Camponotus punctulatus* invades agricultural fields after production ceases. The temporal demography and spatial distribution of colonies of *C. punctulatus* were studied over a five year period using replicated plots of different land use types representing a gradient of increasing agricultural disturbance. We experimentally tested the hypothesis that the increase in *C. punctulatus* colony density was related to increasing levels of agricultural disturbance. Abandoned rice fields represented the situation with greatest disturbance. Sown pastures were intermediate. Natural grasslands represented no agricultural disturbance. The predictions were (1) the greater the soil disturbance produced by agriculture, the greater the susceptibility for invasion by *C. punctulatus*, (2) rice fields offers greater opportunities for establishment of colonizing species than sown pastures, and (3) disturbed land use areas that were more recently colonized as well as land use areas with greater soil disturbance will exhibit patterns of colony aggregation at a small scale but with time the patterns will become uniform. Initially, colonies in the abandoned rice fields had a higher annual mortality and larger turnover than in sown pastures. Over five years, abandoned rice fields sustained higher densities of colonies than sown pastures. The colonies were the largest and had the longest lifespans in abandoned ricefields. Natural grasslands had the lowest colony density, survivorship, and size but had variable levels of colonization. More than one type of spatial distribution was found in field replicates. At small spatial scales across disturbed land use types, replicates exhibited regular distributions. At greater spatial scales, spatial distributions were mostly random in sown pastures, there were many cases of

aggregation in rice fields, although some cases of uniform distributions were also found in all disturbed land uses. These results highlight significant intraspecific variation in ant demography across types of land use, space, and time, and show a clear predisposition of *C. punctulatus* to invade and successfully establish in the most disturbed land use types. Hypotheses that can account for the changes in demography across land use types are discussed.

Keywords: Abandoned rice fields, *Camponotus punctulatus*, natural grasslands, spatial distributions, sown pastures.

Introduction

In the Espinal Phytogeographical Region of Argentina (Carnevali, 1994), the natural grasslands of Corrientes Province, which have been used as cattle range since the last century, are being converted into new agroecosystems. Exotic grasses such as *Setaria sphacelata* and *Digitaria decumbens* are now planted for livestock forage. On larger farms, with the increased availability of artificial water reservoirs, paddy rice production is also becoming common. Concomitant with these practices has been an unusually large increase in numbers of nests belonging to the native ant *Camponotus punctulatus* (Mayr). In undisturbed sites, this ant species builds small mounds or nests underground at the base of tussocks, rosettes, or under rocks (Kusnezov, 1951). However, agricultural activities appear to have promoted an epigeic life history form with ants producing aboveground

mounds (Folgarait et al., 2002, for similar responses in flooded areas, see Lewis et al., 1991).

There are almost no studies directly examining how ant demography changes with different types of land use (for partial approximations on the topic see Diaz, 1991; Deslippe and Savolainen, 1994; Radford et al., 1995; Wang et al., 1996). Despite the fact that ant nests are relatively easy to map and follow their fates, few studies have addressed the issue of population dynamics through time (Chew, 1987; Keeler, 1993; Wiernasz and Cole, 1995; Gordon and Kulig, 1998; Adams and Tschinkel, 2001; Sanders and Gordon, 2004).

Most demographic studies of ant nests have focused on distribution patterns (Waloff and Blackith, 1962; Ryti and Case, 1986; Cushman et al., 1988; Johnson, 1992; Gordon and Kulig, 1996; Dillier and Wehner, 2004 to mention a few). The outcome of interactions among ant colonies ultimately should be reflected in the distributions of its colonies in space (Dillier and Wehner, 2004; Soares and Schoereder, 2001), even though the appropriate test may prove elusive (Adams and Tschinkel, 1995). Regular distributions are used to infer intraspecific and interspecific competition in models of homogeneous resource availability (Levings and Traniello, 1981; De Vita, 1979; Levings and Franks, 1982; Chew, 1987; Deslippe and Savolainen, 1995; Wiernasz and Cole, 1995). Conversely, competition could produce other non-regular distributions depending on the size distribution of individuals (Ryti and Case, 1992). However, there are other reasons besides competition, such as predation or resource distribution, that could lead to a similar regular spacing (Pielou, 1960; Ryti and Case, 1986; Deslippe and Savolainen, 1995). Aggregated nests may result from specialization on the same microhabitat, which is patchily distributed, or from colony budding (Herbers, 1994; Soares and Schoereder, 2001). It has been argued that spatial distributions are the results of recruitment, competition and mortality, at least on undisturbed environments (Wiernasz and Cole, 1995). Therefore studies of spatial distributions linked with other demographic parameters could shed more light in understanding those distributions. Recently, ecologists have also noted the importance of scale on distribution patterns, although this is rarely examined in this context (Wiernasz and Cole, 1995; Crist and Wiens, 1996; Theunis et al., 2005).

In this paper, we quantitatively document the dramatic increase of *C. punctulatus* colonies in agricultural fields of Northeastern Argentina. We experimentally test the hypothesis that the increase in *C. punctulatus* colony density is related to increasing levels of agricultural disturbance. We document the effect of land use and scale on ant spatial patterns across years. We followed colonization, survivorship/mortality, and density on different land uses through time. We tested the predictions that (1) the greater the soil disturbance produced by agriculture, the greater the susceptibility for invasion by *C. punctulatus*, because of the intrinsic abilities of *C. punctulatus* to

colonize, establish, and dominate disturbed ant communities (Folgarait and Gorosito; 2001, Gorosito and Folgarait, unpubl.) and because of the greater opportunities that disturbance events have for initiating a succession, (2) rice fields offer greater opportunities for establishment of colonizing species than sown pastures because of the removal of competitors and macrofauna (as more intense agricultural activities and flooding such as in rice cultivation removes all soil macrofauna (Folgarait et al., 2003; Folgarait and Gorosito, unpubl. results), leaving more space and resources available and (3) disturbed land use areas that were more recently colonized and land use areas with greater soil disturbance initially will exhibit patterns of colony aggregation at a small scale but with time the patterns will become more uniform reflecting a stable partitioning of the resource space. At larger scales, we do not have a priori expectations as colony distribution patterns could be related to other factors such as resource heterogeneity or/and dispersion than competition.

Material and methods

The system

Camponotus punctulatus has a very broad distribution across most areas of Argentina (Kusnezov, 1951). It usually lives hypogaeously in natural grasslands. However, in agriculturally disturbed sites from Corrientes, this ant shows a different life style. While *C. punctulatus* lives mostly below ground immediately after colonization, when the colonies mature, ca. 3 years later, the pattern reverses, and most of the ants are found aboveground, in mounds (Folgarait, 2004). The dramatic increase in above ground mound density in recently abandoned rice fields is accompanied by a concomitant increase in ant numbers and mound volume (Folgarait, 2004). Behavioral studies of aggression have demonstrated that each mound is a separate territorial colony (Martinez Ruiz Diaz and Folgarait, 2002). Despite the increase of colonies in agriculturally disturbed sites, *C. punctulatus* does not represent a direct threat to crops. It is neither herbivorous nor granivorous but omnivorous (Gorosito et al., 1997). Rather, after only a few years of colonization, a mechanical problem evolves. The hard-packed structure of the above ground nest, which grows tougher as the colony ages, becomes extremely resistant to erosion even after the death of the colony (Folgarait, 1998). The greatest nests have a ditch surrounding each mound, and these ditches become very deep at times, allowing water to accumulate in them (Gorosito et al., 2006). As time passes, the landscape is transformed into a moon-like surface, of tough, elevated ant mounds leaving little available space for cattle or horse movement.

In sown pastures, *C. punctulatus* negatively affects the abundance of other ant species of the community but not their richness (Folgarait and Gorosito, 2001). Additionally, *C. punctulatus* has been considered an ecosystem engineer (Folgarait, 1998) because it changes the composition of the soil microorganisms in individual nests (Gonzalez Polo et al., 2004), alters the mesofauna (Paris, 2000) and the plant community (Folgarait et al., 2002), and increases the fertility of the colony soil in comparison to soil away from the nests (Folgarait et al., 2002).

Invasion by *C. punctulatus* in abandoned rice fields is accompanied by a sudden increase in earthworms. Furthermore, both ants and earthworms change their diet from a C4 signature, typical of subtropical plants from natural grasslands of Corrientes, to a C3 signature responding to the cultivation of rice (Folgarait et al., 2003). *C. punctulatus*' carbon and nitrogen signature is more similar to that of

earthworms than to that of strictly carnivorous ants (Tayasu et al., 2002.). *C. punctulatus* is a pioneer species that rapidly invades agricultural fields (Gorosito and Folgarait, 2002, and in prep.) and current work is focused on better understanding the behavior and characteristics that facilitates this successful invasion of abandoned rice fields.

Study sites

The study was conducted in Mercedes Department, Province of Corrientes, Argentina (29°S, 58°W). The climate is wet sub-tropical, without a definite dry season; autumns (March and April) are rainy, springs (October and November) wet, and summers (December, January, and February) are hot and frequently wet. Mean annual precipitation is 1270 mm and mean annual temperature is 20.1°C. Air humidity is high (>73%) throughout the year (Fernández et al., 1993). Soils are primarily Brunizem hydromorphic soils developed on Triassic basalt and sandstone, with a large contribution of Pliocene fluvial clays (Purnell and Hein, 1969).

Sampling design

Data were gathered during July and August of every year from 1996 to 2000 (hereafter "96, 97, 98, 99, 00" respectively) in five different plot types reflecting land-use histories with a decreasing gradient of agricultural-soil disturbance. These plots included (1) abandoned rice fields where no cultivation had taken place for at least two years prior to 1996 (hereafter "rice2"); (2) abandoned rice fields where no cultivation has taken place for seven-eight years prior to 1996 (hereafter rice7); (3) pastures sown with *Setaria sphacelata* (hereafter "Setaria") seven-eight years ago; (4) pastures sown with *Digitaria decumbens* (hereafter "Pangola") seven-eight years ago; and (5) natural grasslands with no agricultural disturbance (equal to controls).

We had a series of land use types with a gradient of agricultural disturbance, from rice (highest) to *Digitaria* (lowest). The *Setaria* sown pastures were examples of intermediate disturbance. Natural grasslands had no agricultural disturbance so was used as a control. Rice is cultivated under flooding for part of the growing period after removing the natural vegetation, ploughing the land and leveling it; fields are abandoned after three consecutive years of growing rice and applying fertilizers. Fungicides may have been used in rice plots but insecticides are not known to have been applied. Sown pastures for cattle ranching were planted using machinery in the case of *Setaria*, or by hand for Pangola, after removing the vegetation and ploughing the land, with one application of fertilizer but no pesticides. Originally, the native grass, *Andropogon lateralis* dominated the natural grasslands and represents the situation with greatest plant biomass in space and time. The amount of vegetation and plant cover is lower at rice fields than at sown pastures, which generally covers all the ground. The region has had such a long history of cattle ranching that livestock have grazed even the natural grassland plots. Therefore our gradient represents only an agricultural-disturbance gradient and cattle disturbance was present in all our land types.

There were three to four replicate plots (each, at least of 1 ha), for each land-use type, with each replicate plot located at a different farm within the same region. Plots of different land-use types within the same farm were separated by 1 to 5 km whereas replicates of the same land-use type at different farms were separated by > 10 km. Two, 150-m long, 6-m wide, permanent transects, one N-S, and the other E-W, were laid out in each plot. Transects were placed in the middle of small plots (1 ha) or at least, >100 m from any border in greater plots (>1 ha).

Each year we counted and assigned coordinates for all colonies within a transect area using meter sticks and tapes perpendicular to each other (mounds at the edges of the transects were considered in the counts). Colonies that were active in consecutive years were considered survivors whereas those found only one year were considered to have subsequently died (Colonies were checked for activity by introducing a stick into the mound; if no ants came out, colonies were considered inactive). Colonies not present in the previous year were considered

new colonies. This species of ant does not seem to relocate its nests after establishment and does not remain dormant during the winter (Folgarait, unpubl. data). A subset of up to 20 colonies were tagged on each transect; for each mound we measured height, and maximum width with a meter stick (± 5 cm). Generally, mounds develop a cone shape as they grow; and at least for some species, there is a correlation between mound volume and time (King, 1981). We have shown that greater size volumes had greater number of ants, and probably corresponded to older colonies (Folgarait, 2004). Other ant species are present in fields invaded by *C. punctulatus*, most are hypogeous or build small mounds (Folgarait and Gorosito, 2001; Gorosito and Folgarait, unpubl.). By eye, the fields are largely monopolized by *C. punctulatus* as they occupy most of the aboveground space.

Statistical analyses

Demographic variables

Most of the demographic data (density of colonies, number of colonies surviving or dying from one year to the next, number of new colonies that colonized each year, and number of colonies that were born and died in the same year) consist of counts per area and are therefore Poisson variables. Consequently, we ran Poisson regressions to address the effect of land use and time on the demographic variables. Poisson regression is advantageous when fitting highly skewed distributions, however, it has a bias towards overdispersion which may lead to overestimates of test statistics such as deviance, chi square and p values (Allison, 2000). Preliminary analyses revealed that each of our dependent variables showed overdispersion (ratios of deviance/degrees of freedom much larger than 1). We addressed this problem by following the recommendation of Allison (2000) and used negative binomial regressions where the model is estimated by maximum likelihood. Because each plot was recorded at multiple points in time, and those observations may be correlated, we performed longitudinal analyses on the negative binomial regressions (similar to repeated measures in ANOVA) using a lag-1 autoregressive structure for the correlation matrix (Allison, 2000). We planned a priori contrasts to compare both rice histories, both pastures, rice and pastures, and to compare between years (In cases where there were too many zeros we were not able to run the contrasts.). Bonferroni's adjustment method for multiple comparisons with an experimentwise error rate of 0.05 or less was used (for land use comparisons alpha was 0.016 and for time comparisons alpha was 0.01) (Neter et al., 1985). These analyses were performed using SAS version 9.

After testing the assumptions required for ANOVA analyses, the volume of a cone, from the subset of measured colonies, was used as a surrogate for mound size for testing how mound size changed with land use across time. Repeated measure ANOVAs were run to test for replicate effects across time for mound size. Only anthills whose sizes were registered from 1996 to 2000 were included (dead anthills were not considered). Analyses were done using Statview for Windows, SAS Institute, version 5.0.

Spatial distributions

The spatial pattern of individual ant nests constitutes point-referenced data. The data were analyzed using the Ripley's $L(r)$ index that averages the number of nests within a distance r from a randomly chosen individual (Dale, 2000). The method is multi-scale because the function is estimated for increasing r values. Because the minimum inter-nest distance was 0.25 m we used this value as an increment for the distance lag r in all the Ripley's function analyses. The study plots, where all mounds were mapped, had a total length of 150 m and the computations were made up to 75 m. Because the distance to the nearest point could be strongly influenced by boundary effects, we have used a correction term (Ripley, 1977). If the Ripley's function $L(r) = 0$ the corresponding pattern was random, if $L(r) > 0$ the pattern was aggregated and if $L(r) < 0$ the pattern was regular. In order to test the null hypothesis of complete spatial randomness (CSR) we performed a large number of simulations of a Poisson process with density equal to that of the observed data set. For each randomization, the function $L(r)$

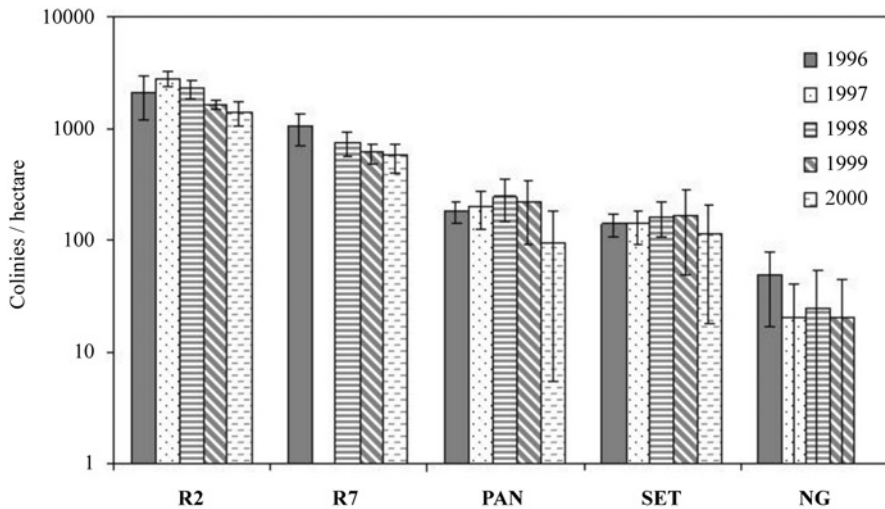


Figure 1. Mean and standard errors from the observed data of the density of anthills per hectare discriminated by year and land use type. R2=rice2, R7=rice7, PAN=Pangola, SET=Setaria, NG=natural grassland.

was calculated, and for every distance value r , a local confidence interval was built by the first percentile method. The $100(1-\alpha)\%$ confidence interval for the true value of $L(r)$ was given by the 2 values encompassing the central $100(1-\alpha)\%$ of this distribution. If the observed $L(r)$ was out of that interval, the null hypothesis (CSR) was rejected at the level of α . If the observed $L(r)$ value was higher than the upper bound, the spatial pattern was considered to be significantly aggregated, if the observed $L(r)$ value was below the lower bound then the pattern was significantly regular, if the observed $L(r)$ value was found in between the upper and lower bound, then the pattern was considered to be random. Throughout this study we used a risk $\alpha=5\%$. Computations were made using ADE-4 (Thioulouse et al., 1997) and a total of 1,000 randomizations were used for each of the 300 distance lags.

Results

Density

Each land use history had significantly higher colony density levels than the control (natural grassland). The estimated average number of colonies/ha across years was 2021.4 for rice2, 774.4 for rice7, 174.8 for pangola, 142.3 for setaria and 22 for natural grassland. Contrasts showed that rice2 had a higher density than rice7 ($X^2=5.11$, $p=0.023$), and rice land use types had significantly higher density than pastures ($X^2=11.23$, $p=0.0008$). Pangola did not differ from setaria ($X^2=0.38$, $p=0.538$). Also, each sampling year had a significantly higher density of colonies in comparison to the last sampling year (Table 1, Fig. 1). Colony density was very high in the first sampling (estimated mean for 96: 307.8 colonies/ha) and remained high (estimated mean for 97: 276.7 colonies/ha, for 98: 281.9, for 99: 244.5) until the fourth year. At that time, density started to decrease significantly (estimated mean for 00: 145.9 colonies/ha) (contrasts 96 Vs 97, 97 vs 98, 98 vs 99, all $p > 0.05$; contrast 99 vs 00 $p < 0.007$). The decline was found either when the analysis was done with all land use types together or separately (Folgarait, unpubl. results).

Size of anthills

Overall, mound volume changed significantly across land use types and through years (Table 2). Median mound volume increased in the following order across land use types: 0.117 m^3 for natural grassland $< 0.226 \text{ m}^3$ for rice2 $< 0.248 \text{ m}^3$ for pangola $< 0.309 \text{ m}^3$ for Setaria $< 0.469 \text{ m}^3$ for rice7. There was a significant interaction effect between land use type and time (Table 2). Mound volume increased in both abandoned rice fields over time indicating that these nests were still growing after ten years (Fig. 2). Mound volume in sown pastures, especially Setaria, was more variable across plots and years. Mound volume in the natural grassland remained relatively constant through time, except in 1996 and 1998 when greater colonization occurred and there were proportionally more young and smaller mounds than in other years.

Survivorship, mortality, mortality of younger than 1 year old colonies, and colonization

Each land use history had significantly higher annual colony survivorship from one year to the next in comparison to the natural grassland. Also, each sampling year had significantly greater survivorship of colonies in comparison to the last year of sampling (Table 1, Fig. 3). The estimated average percentage of colonies/ha that survived across years was 68.5% for rice2, 76.4% for rice7, 70.2% for pangola, 76.8% for setaria and 22.8% for natural grassland. Contrasts showed no significant differences in survivorship between land uses with agricultural disturbance. Survivorship levels across land uses were significantly higher for the period 97–98 (estimated average percentage 91%) and decreased later reaching a 34% for the last period 99–00 (Contrasts 96–97 VS 97–98 $p > 0.05$; 97–98 VS 98–99, 98–99 VS 99–00 $p < 0.04$ and 0.01 respectively).

Table 1. Longitudinal analyses of negative binomial regressions by land uses for density, colonization, % annual mortality and survivorship, and for % mortality of <1 year old anthills (for references see the text).

DENSITY				COLONIZATION		
Parameter	Estimate	Z	Pr < Z	Estimate	Z	Pr < Z
Intercept	0.8649	6.24	<0.0001	0.2700	0.77	0.4387
USE-R2	4.5197	33.66	<0.0001	4.3806	11.27	<0.0001
USE-R7	3.5602	31.29	<0.0001	2.7654	7.67	<0.0001
USE-P	2.0716	9.44	<0.0001	1.3825	2.57	0.0101
USE-S	1.8663	7.32	<0.0001	0.8144	1.79	0.0735
USE-NG	0.0000	–	–	0.0000	–	–
TIME-96	0.7463	3.69	0.0002			–
TIME-97	0.6397	4.08	<0.0001	0.3350	0.87	0.3832
TIME-98	0.6586	4.45	<0.0001	0.5207	1.79	0.0732
TIME-99	0.5162	3.29	0.0010	0.5099	1.61	0.1071
TIME-20	0.0000	–	–	0.0000	–	–
% ANNUAL MORTALITY				% ANNUAL SURVIVORSHIP		
Parameter	Estimate	Z	Pr < Z	Estimate	Z	Pr < Z
Intercept	4.8019	24.78	<0.0001	2.6008	9.24	<0.0001
USE-R2	–0.6857	–5.92	<0.0001	1.1000	3.92	<0.0001
USE-R7	–0.7588	–3.64	0.0003	1.2092	4.22	<0.0001
USE-P	–1.2057	–9.87	<0.0001	1.1239	3.94	<0.0001
USE-S	–1.2182	–2.81	0.0049	1.2147	3.97	<0.0001
USE-NG	0.0000	–	–	0.0000	–	–
TIME-96	–0.8563	–2.78	0.0054	0.6469	2.88	0.0040
TIME-97	–1.0244	–3.83	0.0001	0.9822	3.03	0.0025
TIME-98	–0.3324	–1.34	0.1816	0.4756	1.46	0.1446
TIME-99	0.0000	–	–	0.0000	–	–
% MORTALITY of <1 year old anthills						
Parameter	Estimate	Z	Pr < Z			
Intercept	4.0777	13.20	<0.0001			
USE-R2	–0.6366	–1.72	0.0853			
USE-R7	–0.7454	–1.98	0.0478			
USE-P	–1.5244	–3.61	0.0003			
USE-S	–1.3457	–3.77	0.0002			
USE-NG	0.0000	–	–			
TIME-97	–0.7955	–2.47	0.0136			
TIME-98	–0.2610	–1.00	0.3181			
TIME-99	0.0000	–	–			

Similarly, for annual mortality, each land use history was significantly different from the control (natural grassland), except *Setaria*, in that they had greater levels of colony mortality (Table 1, Fig. 3). Also mortality differed significantly across years in comparison to the last sampling year, when it was highest (56%). The period 98–99 was an exception (Table 1) as the estimated average percentage of mortality had increased to 40% whereas in previous years it was 20–23% (contrasts 97–98

VS 98–99, $p < 0.01$, 96–97 VS 97–98, 98–99 VS 99–00 $p > 0.05$).

Abandoned rice fields had similar estimated percentages of mortality of young colonies (on average 20% for younger than 1 year old) across years in comparison to the natural grassland (41%), whereas sown pastures had significantly lower (10%) (Table 1, Fig. 3). Contrasts showed significant differences between abandoned rice fields and sown pastures ($X^2 = 5.4$, $p = 0.02$) but not

Table 2. Repeated measures ANOVA for the volume of anthills.

Source	df	SS	MS	F	P
<i>Between Land Use</i>					
Between Use Type	4	38.66	9.66	73.69	0.0001
Error	418	54.82	0.131		
<i>Within Land Use</i>					
Time	3	1.78	0.59	49.39	0.0001
Land Use X Time	12	0.47	0.04	3.26	0.0001
Error (Time)	508	2.33	0.005		

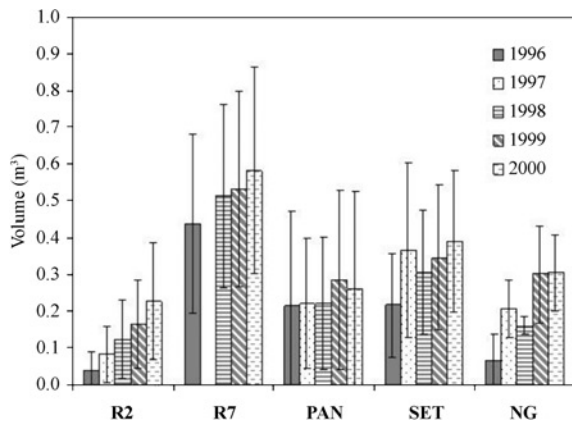


Figure 2. Mean and standard errors of the volume of anthills discriminated by year and land use type. R2 = rice2, R7 = rice7, PAN = Pangola, SET = Setaria, NG = natural grassland.

within any of either group ($p > 0.05$). Percentages of mortality increased with time from an estimated average of 11.3% for the period 96–97 to 25.2% for 99–00 (Table 1).

All land uses except Setaria exhibited significantly higher levels of colonization in comparison to the natural grasslands. No significant differences in levels of colonization were found for each year in comparison to the last sampling (Table 1, Fig. 3). The estimated average number of colonies/ha that colonized each land use type was 817.9 for rice2, 162.7 for rice7, 40.8 for pangola, 23.1 for setaria and 10.2 for the control or natural grassland. We were not able to run any contrast (see statistical analyses section).

Spatial distributions

Different spatial distributions were found at different scales (Fig. 4). In 55.8% and 24.2% of all the replicates studied (considering years individually), we found at least two and three, respectively, different spatial distributions for the same transect at different scales. All disturbed land use types showed uniform colony distributions throughout time at small distances, in general at less than 2 m for rice2, less than 3 m for rice7, than 8 m for

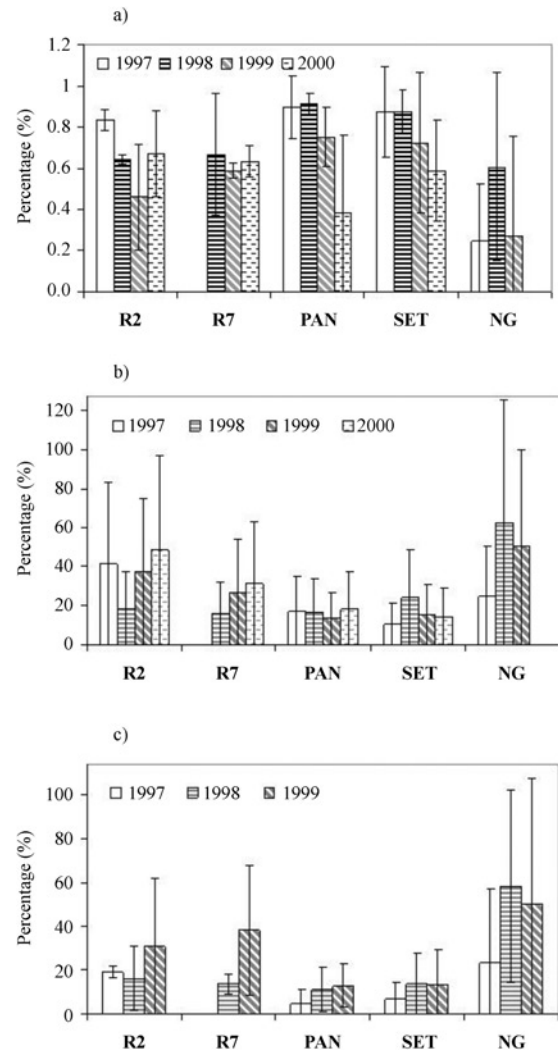


Figure 3. Mean and standard errors from the observed data, (a) the annual survivorship, (b) and the colonization of new anthills, (c) mortality of anthills younger than 1 year old discriminated by land use and by time. R2 = rice2, R7 = rice7, PAN = Pangola, SET = Setaria, NG = natural grassland.

Pangola, and less than 12 m for Setaria (we were not able to calculate the spatial distribution with reasonable confidence intervals for natural grasslands due to the low density of anthills). The percentage of regular distributions at small scales were greater for rice fields than sown pastures. At higher scales, aggregation or random distributions characterized abandoned rice fields whereas random distributions were mainly found in sown pastures. Some regularity was found across all land uses at the highest scale of comparison. In abandoned rice fields, clumped distributions became less common and random ones more common as time progressed. In both types of sown pastures, random distributions characterized the latter years of sampling. In Setaria regular distributions at small scales diminished in the last years whereas in Pangola low levels of regular distributions were found at the beginning as well as five years later.

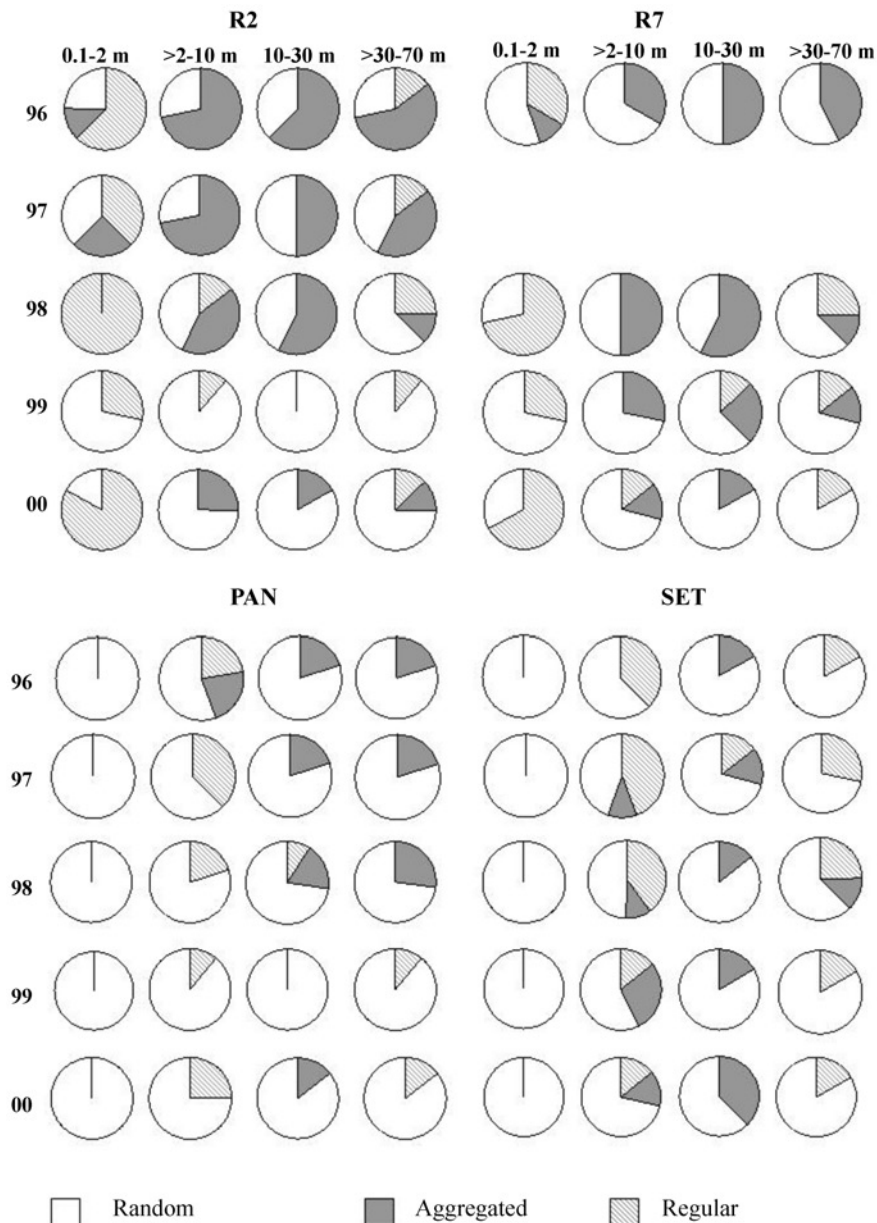


Figure 4. Percentage of transects with regular, aggregated, and random distributions at four different spatial scales and through time. Sample size for R2: 30, for R7: 24, for Pangola: 38, for Setaria: 28. Two or more distributions were assigned to the same scale if each distribution covered at least 40 percent of the scale under consideration.

Discussion

Dynamics of demographic parameters across and within land use types

This study established that land use types, as well as, time affected significantly the demographic parameters of *C. punctulatus*. Our results can be summarized by highlighting three patterns. 1) Opportunities for colonization and colony growth increased with the amount of previous agricultural disturbance and decreased with time since last disturbance. 2) Land use types with greater disturbance resembled each other more than those with lower disturbance whereas the control was completely different, and 3) Mound size was dependent on both land use

and time. Typically, land uses with a rice history had on average 8 times more density of colonies, which were smaller (rice 2) or bigger (rice 7), and had 2 times greater mortality of young colonies in comparison to sown pastures. Moreover, rice 2 and rice 7 had 80 and 30, respectively, times more new colonies (colonization on average across years) in comparison to natural grasslands.

Pastures had significantly lower density of colonies than abandoned rice fields but greater density than natural grasslands, with high survivorship for all age classes. Generally, mounds became larger through time but for similarly aged plots, rice-mounds were larger than those from pastures (Fig. 2). On the other hand, natural grasslands, with no agricultural disturbance, stood out with a unique pattern of extremely high levels of colony

mortality, reaching 100% in some replicates for less than 1 year old colonies. On average, mortality of young colonies was 2.7 times greater in natural grasslands than in disturbed land uses. As a result of this there was very low colony survivorship (28% or 3 times less), and variable levels of colonization (from 0% to 100% although in relative terms it was 26 times lower than in disturbed land uses).

Long abandoned rice fields seemed to reach their carrying capacity at around 600 anthills/ha after 12 years when all the anthills ($\sim 0.5 \text{ m}^3$ of size) were still active and growing. In contrast, the carrying capacity of similarly aged sown pastures approximated 200 anthills/ha. A high percentage of nests became inactive in sown pastures in the last years of sampling, and sometimes, nests of *C. punctulatus* were occupied secondarily by other ant species. This was especially the case in *Setaria*. Interestingly, in this land use the proportion of regular distributions at smaller scales diminished most likely because many of the nests became inactive (see next section). These results suggest the possibility that senescence starts after approximately 10 years in *C. punctulatus* in sown pastures. A 10 year lifespan is similar to that reported for other long-lasting ant species that build above ground mounds (Chew, 1987).

The effect of scale on the perception of spatial patterns

This study also found an effect of scale on spatial distributions. Field experiments, on abandonment rice plots, demonstrated that *C. punctulatus* colonies exhibit intraspecific aggression, at 2 as well as 10, years after abandonment (Martinez Ruiz Diaz and Folgarait, 2002; Folgarait, unpubl.). The uniform distributions at low spatial scales may represent the minimum spatial distances that these ants defend as territories. The size of this minimum distance changed with land use type, and was inversely correlated to colony density (i.e. smaller in rice plots and greater in pastures) and positively correlated to mound size (i.e. greater distances at sown pastures). In other ant species, a negative relationship between nest density and nest size-dependent spacing was found (Chew, 1987; Cushman et al., 1988). In R2 the average mounds were smaller than at other disturbed land uses. This could explain in part the higher density at R2 as food and space requirements are nest-size dependent. However, in the last sampling year, the average size of mounds from R2 (0.23 m^3) were similar to that found for similarly aged mounds in the first sampling year for both pasture types (0.22 m^3) even though the density was still 8.6 times larger in R2. In spite of this, regularity at smaller scales was retained at R2. On the other hand, the size of mounds of R7 in the first sampling year was twice of those from sown pastures (which were of similar age) and still showed regular distributions in the smallest scales. These comparative results on spatial distributions show that the carrying capacity is definitely higher in rice fields in

comparison to sown pastures. Probably an increased food resource allowed a greater packing of territorial colonies in rice fields (see next section).

The relationship between ant spatial distribution and scale has been examined only rarely (Wiernasz and Cole, 1995; Crist and Wiens, 1996; Theunis et al., 2005). In *Pogonomyrmex occidentalis*, spatial distributions changed with increasing neighbor distances. Regular patterns were found for 1st near neighbor distance; then there were regular or random patterns at increasing distances. By the 10th neighbor, at around 80 m distance, there was a pattern of aggregation (Crist and Wiens, 1996). Similarly, *C. punctulatus* nest spatial distribution changed with scale. At scales beyond the minimum neighbor distance, aggregation may represent neighborhoods of anthills reflecting good patches for ant establishment and maintenance, and/or hypothetical budding from recently formed nests (see next section). We have hypothesized that after 2–3 years of rice abandonment queens from the same nest split to each form a new colony (Folgarait, 2004). Although mature colonies are typically monogynous, cases of multiple queens founding a colony have been found and it is possible that non-related queens cooperate transitory at the colonization stage. This pattern has been found in other ants as well (Strassmann, 1989; Bernasconi and Strassmann, 1999; Sasaki et al., 2005). In fact, *C. punctulatus* queens collected in the field, immediately after their release, co-exist in the lab showing no aggression for long periods of time; this type of information has been used as an indication of queen tolerance (Provost and Cerdan, 1990). We speculate that co-founder queens and first cohorts of workers may not have developed their chemical templates (Folgarait, 2004) and during that period of chemical insignificance (Lenoir et al., 1999) the density of colonies in abandoned rice fields could be correlated with a lack of territoriality allowing a greater packing of colonies. Future studies at earlier stages of colonization will help to elucidate this point. As time progressed, in R2, the percentage of aggregation diminished significantly probably because budding was not the main mode of dispersion any longer when space and food are completely partitioned. On the contrary, regularity at greater scales could indicate landscape homogeneity and/or minimum distances between neighborhoods or patches.

Because we followed the fate of each plot for five years we were also able to explore if there were scale dependent changes in spatial distributions through abandoned time. Land use types with a dynamic demography, such as rice fields, drastically changed their spatial distributions through time in a scale dependent manner. We registered a reduction of aggregation at the first sampling years following colonization in R2. Probably this is related to a change of founding behavior from budding and polygyny to independent founding by monogynous queens (Folgarait, 2004). At one year's replicate of R2 (1997) we also found that colonization doubled which translated in the following year into a

single patch of aggregation at every scale beyond the smallest. However, this patch disappeared for the following years due to mortality in the most crowded areas of the transect. In sown pastures, on the other hand, with lower densities of anthills, spatial distributions changed little with time. Therefore, simultaneous analyses of temporal and spatial changes across scales can definitely help to understand the demography dynamics of ant species which their mode of funding and dispersion remains elusive.

Possible mechanisms to account for the successful invasion of C. punctulatus to agricultural lands

Possible reasons that account for the differences observed in *C. punctulatus* demography across land types imply competition and include the following: 1) *Resource based hypothesis*: recently abandoned rice fields represent situations of high productivity in terms of soil inputs of organic matter. In 1–2 years, this is translated into a drastic increase in earthworm numbers (Thomas et al., 2004) which could serve as a food source for hypogeous ants such as *C. punctulatus* (Folgarait et al., 2003). Our data on the carrying capacity and spatial distributions supports this hypothesis. Although we do not have data from sown pastures, we predict that lower amounts of resources are available after sowing the grasses because there is only one application of fertilizer and because less organic matter accumulates in the oxygenated soil, in comparison to rice fields (Tate, 1979). In natural grasslands, on the other extreme, most resources are already partitioned and used by the established soil community impeding a sudden increase of additional species. 2) *Succession hypothesis*: Abandoned rice fields may represent situations more similar to primary succession, sown pastures to secondary succession, and natural grasslands to climax communities. In situations of “primary succession”, all space and resources are available for pioneer species. *Camponotus punctulatus*, a pioneer species in abandoned rice fields according to pitfall data, is also the fastest at finding resources and monopolizing them, based on hundreds of baits (Gorosito and Folgarait, 2002 and data unpublished). As such, *C. punctulatus* seem to occupy abandoned rice fields first and/or more efficiently becoming the dominant species and changing the trajectory of the succession of the soil community in that land use type (Thomas et al., 2004; Gorosito et al., in prep.). In sown pastures, ants of many species remain in the soil even after plowing, allowing them to re-establish rapidly after the pasture is sown. In this case, new queens of *C. punctulatus* will need to compete with other ants already established and will be unable to completely monopolize the land. Finally, in natural grasslands, most resources are already allocated and partitioned by the species already present.

Implications

The results of this study, in concert with other work documenting important changes in vegetation, soil fertility and structure (Folgarait et al., 2002; Gorosito et al., 2006), and soil organisms (Paris 2000; Folgarait and Gorosito, 2001; Folgarait et al., 2003; Thomas et al., 2004; Gonzalez Polo et al., 2004) indicate that *C. punctulatus* is a highly successful invading (native) species of agricultural environments drastically modifying the landscape (Folgarait, 1998). We can predict that if intensive agriculture in the region continues, turning pristine grasslands into cultivated land, the dispersion and establishment of *C. punctulatus* ants will be difficult to stop, and long-lasting changes in the ecosystem should be expected.

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