

Invasion of *Camponotus punctulatus* ants in sown pastures: consequences for ant activity and diversity

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ABSTRACT. Agricultural activity in NE Argentina promotes the demographic explosion of the ant *Camponotus punctulatus* Mayr. We compared ant activity between a natural grassland and a neighbouring sown pasture in north-eastern Argentina during 24 h periods during three different times in the year. We offered sugar and tuna baits to ants in order to assess ant foraging activity. We set pitfalls during the summer to quantify ant activity independently of their responses to food resources. We also used bait and pitfall data to estimate ant diversity. *C. punctulatus* was the single ant species present at baits in the sown pasture. Significantly greater numbers of *C. punctulatus* in comparison to other ants were found at pitfalls at the agriculturally-disturbed plot when compared with the natural grassland, although no differences in ant species richness were observed between plots. *C. punctulatus* was active throughout the day. Foraging of the ant community differed significantly between the sown pasture and the natural grassland. Foraging activity of *C. punctulatus* and all other ant species exhibited opposite patterns in the natural grassland. The successful establishment of *C. punctulatus* after agricultural disturbance seemed to have a negative effect on the foraging patterns of the ant community through a change in the relative abundance of ant species.

RESUMEN. Invasión de *Camponotus punctulatus* en pasturas: consecuencias sobre la actividad y diversidad de la comunidad de hormigas: La actividad agrícola promueve la explosión demográfica de la hormiga *Camponotus punctulatus* Mayr en el NE de la Argentina. Comparamos la actividad de las hormigas entre un pastizal natural y una pastura implantada lindante, en Mercedes, Corrientes, durante períodos de 24 h en tres momentos del año. Colocamos cebos de azúcar y de atún para registrar la actividad de alimentación de las hormigas. Pusimos trampas de caída en el verano para cuantificar la actividad de las hormigas independientemente de los recursos alimenticios. Utilizamos los datos obtenidos de los cebos y de las trampas de caída para determinar la diversidad de hormigas. *C. punctulatus* fue la única especie presente en los cebos de las pasturas. Un número significativamente mayor de individuos de *C. punctulatus*, en comparación con individuos de otras especies de hormigas, fue encontrado en los potreros con disturbio agrícola en comparación con el pastizal natural, aunque la riqueza se mantuvo similar entre sitios según los resultados obtenidos en las trampas de caída. *C. punctulatus* estuvo activa durante todo el día. La actividad de alimentación de la comunidad de hormigas varió significativamente entre la pastura y el pastizal. *C. punctulatus* mostró patrones de actividad de alimentación opuestos al de las otras especies de hormigas en el pastizal. El establecimiento exitoso de *C. punctulatus* después del disturbio agrícola parece tener un efecto negativo sobre el patrón de alimentación de la comunidad de hormigas, a través de una alteración en la abundancia relativa de las especies.

INTRODUCTION

Human disturbances of natural environments can produce important changes in biodiversity and, therefore, in the interspecific relationships that structure and modulate the

functioning of a community (Lubchenco et al. 1991; Primack 1992; Solbrig 1992; Lavelle et al. 1997; Folgarait 1998; Hector et al. 1999, Sala et al. 2000). Ants appear to be very sensitive to human impact, but also have a great recovery capacity (Folgarait 1998). For these reasons, ants have been used as bioindicators of res-

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toration efforts in rehabilitated mined sites (Majer 1983; Andersen 1990, 1993) as well as biomonitors of metal accumulation (Maavara et al. 1994; Rabitsch 1997).

Although comparisons between paired-sites with and without agricultural disturbance is one of the first necessary steps for addressing the impact of agriculture on biodiversity, few studies have investigated ant biodiversity simultaneously in agroecosystems in comparison to controls (Roth et al. 1994; Lobry de Bruyn 1999). A reduction in ant biodiversity may have profound consequences on ecosystem functioning because of the important role of ants as ecosystem engineers (Folgarait 1998). Most agricultural practices reduce ant diversity, although they may produce an overall increase in ant abundance due to the dominance of aggressive ants or exotic species (Room 1975; Andersen & McKaige 1987; Williams 1994). Sown pastures, in particular, seem to have a less drastic effect than crops in reducing invertebrate diversity (Lavelle et al. 1997) including ant diversity (Folgarait 1998).

In the case of *Camponotus punctulatus* Mayr, agricultural activities have favoured its establishment and dispersion in North-eastern Argentina (Folgarait et al., in press). Nowadays, it is very difficult to find in this region an agriculturally-disturbed field without great densities of mounds of these ants. On average, 170–270 mounds/ha are found at sown pastures of *Setaria sphacelata* and *Digitaria decumbens*, respectively, whereas natural grasslands without agriculture have on average 10–50 mounds/ha. Furthermore, sown pastures have larger *C. punctulatus* anthills (average 1.25 m diameter and 0.45 m height) than do natural grasslands, where most of the nests are smaller or inactive (average 0.65 m of diameter and 0.10 m of height) (unpubl. data). These ants also change the floristic composition and edaphic characteristics of the soil on the mounds (Folgarait et al., in press). Because of the patterns described, we hypothesised that the increase of *C. punctulatus* anthills — mediated by agricultural disturbance — might have a negative effect on the rest of the ant community at the sown pastures. Specifically, in this study we compared ant foraging activity and ant diversity of sown pastures with neighbouring paired natural grasslands at three times of the year.

METHODS

Study area

Field work was carried out at Mercedes (29°S; 58°W), Corrientes Province, Argentina. The climate is sub-tropical and lacks a definite dry season; autumns are rainy, springs wet, and summers hot (Carnevali 1994). The mean annual temperature is 19.7 °C (maximum 26 °C and minimum 13.7 °C), and mean annual precipitation is 1323 mm. Frosts occur on average three times per year (Fernández et al. 1993). Soils have developed on Triassic basalt and sandstone, with a large contribution of Pliocene fluvial clays. This has led to the existence of primarily Brunizem hydromorphic soils (Purnell & Hein 1969). Climax plant communities in the region are natural grasslands dominated by *Andropogon lateralis* (Carnevali 1994).

The region has been intensively exploited for timber and intensively grazed (by cattle and sheep) for more than a century (Carnevali 1994). Recently, agricultural activities have increased in the region. Large farms commonly cultivate rice, while most farms have enlarged their grazing area by sowing pastures with *Setaria* (*Setaria sphacelata*) or *Pangola* (*Digitaria decumbens*). Our study plots were located at two farms. At one of the farms we compared a seven-year old *Setaria* cultivated plot with a natural grassland plot. Plots were separated by a wire fence. At the second farm (available only in the summer), we compared a seven-year old *Pangola* cultivated plot with a natural grassland plot that were separated by a narrow road.

Sampling design

We evaluated ant activity by using 24-hour baits, and pitfall traps. The baits were put out on three days, each day in a different season, and the pitfalls were put out for one week during the summer. Both, baits (Tennant 1994; Bestelmeyer 1997; Hollway 1998) and pitfall traps (Romero & Jaffe 1989; Andersen 1991; Jusino-Atresino & Phillips 1994; Bestelmeyer & Wiens 1996) are commonly used methods for evaluating ant activity and biodiversity. Baits and pitfall traps were set up at sampling stations along transects in the sown pastures and natural grasslands. Climatic data were

obtained from the meteorological station located at the Experimental Station of INTA at Mercedes, Corrientes.

We took advantage of an existing sampling protocol that had been used previously to gather *C. punctulatus* demography and behavioural data in relation to food preferences. On two transects per land use type (150 x 6 m each, one oriented north–south and the other east–west), 12 anthills of *C. punctulatus* were randomly chosen along each transect. Each anthill was marked, and its distance and location, in relation to the prior and the next anthill was recorded. Each anthill constituted a sampling station. In the natural grassland plot (NG1), where the anthills had very little density, we repeated the sampling design for each transect independently of where the sampling stations fell (anthills or not). We used the same sampling design for the Pangola plot and its paired natural grassland (NG2). Both pastures had similar density of anthills (~180.0 anthills/ha).

Here we report data from two different baits: tuna fish and sugar solution (50% water : 50% sugar). These particular baits attract a large spectrum of ants with different diet (Stradling 1987; Tennant 1994), and exhibited the greatest recruitment and richness in our system (PJ Folgarait, unpubl. data). Baits were set in *Setaria* and NG1 plots for one day in the fall (March), winter (July), and summer (December) in order to have replicated measures of ant activity. The Pangola-sown pasture NG2 plot were sampled only in December (summer). The tuna bait was placed in plastic petri dishes (9 cm diameter x 1 cm height), while the sugar solution was offered in plastic tubes (5 ml volume) plugged with cotton. Both types of bait were left directly on the ground at each station (if stations were anthills, baits were placed 20–30 cm from each mound); positions representing randomly the four bearings. Baits were replaced regularly, if necessary, in order to provide food ad libitum. Measurements were taken every 2–3 h (time required to sample both plots) during a period of 24 h to include diurnal and nocturnal ant activity. Number of individuals per species and number of occupied baits were recorded during each observation. Ant species were identified in the field to genus or species level, and un-

known species were collected at the end of the 24 h period and preserved in alcohol (70%) for later identification.

To obtain an independent measure of the competitive ability of ant species at food resources, we set up pitfalls during one week in the summer. We used plastic pitfall traps (30 ml volume and 3 cm diameter) buried in the ground and filled with 70% ethylene glycol in ethanol. This liquid is neither attractive nor repellent to ants (Greenlade & Greenlade 1971). At the east–west transects, pitfall traps were located as baits at 12 *C. punctulatus* anthills chosen haphazardly in the sown pastures, or located at equivalent positions in the natural grasslands (repeating the design used above for baits). Along the north–south transects, twelve pitfall traps were set at 10 m distances from each other, irrespectively of anthills, in the sown pastures as well as in the natural grassland plots. The north–south sampling was set up differently to compare with the east–west transect in order to test if closeness to anthills could affect our measurements of ant activity/diversity.

Species diversity was estimated through species (morphospecies) richness, and ant activity through hourly/daily changes in ant abundance (Longino & Colwell 1997; Hollway 1998). Ant community organisation was examined by constructing abundance-rank plots from pitfall data, in which the species were arranged on the horizontal axis ranked from most to least abundant, and the number of individuals for each species was plotted on the vertical axis (Longino 1994).

Statistical analysis

We used non-parametric statistics because the data were not normally distributed and did not show homoscedasticity. Ant richness and abundance were calculated per site, bait, and pitfall. We use the Mann–Whitney U-test to compare data between sites, the Kolmogorov–Smirnov test to compare the distributions of foraging activity, and Spearman correlations to analyze changes in foraging activity with temperatures (Statistix Analytical Software, FL, USA). When the same data set was compared more than once, we used a Bonferroni correction to maintain an experimentwise error of $P = 0.05$ (Neter et al. 1985).

RESULTS

We recorded at baits a total of 4507 ants in *Setaria* and 23318 ants in NG1 across the three sampling days. Ant activity at *Setaria* baits was restricted to *C. punctulatus* ants. Therefore, the *Setaria* plot exhibited the lowest values of diversity, whereas in NG1 the number of baited species per site changed through sampling days from 4 in the winter-24 h cycle, 8 in the autumn-24 h cycle, to 10 in the summer-24 h cycle. The abundance of ants per plot changed accordingly from 1446 and 3243 in winter, to 2909 and 13473 in the fall, and to 7152 and 6602 in the summer, for the *Setaria* plot and its NG1, respectively. At baits, ant species richness, but not ant abundance, were significantly lower ($P < 0.01$ and $P > 0.05$, respectively, for each case) in the *Setaria* sown pasture when compared to NG1. Only *C. punctulatus* was recorded at *Setaria*, while up to 3 species were observed at any single bait at the natural grassland; in NG1 the three species most frequently found at baits ($n = 144$) were: *Solenopsis* sp. (56 baits), *C. punctulatus* (50 baits), *Pheidole* sp3 (31 baits). Non systematic records of baits located at random in *Setaria* have shown the presence of *C. punctulatus* exclusively. The same pattern was found in the Pangola–NG2 comparison: only *C. punctulatus* was found at the baits in Pangola, whereas in NG2 we found up to 3 species foraging per bait ($P < 0.001$). These species were ($n = 48$ baits): *Pheidole* sp3 (35 baits), *C. punctulatus* (24 baits), and *Solenopsis* sp. (11 baits); no differences in ant abundance per bait were found between plots ($P < 0.173$; 4602 ants in Pangola and 5739 ants in NG2).

Ant foraging activity differed significantly between each sown pasture and its paired natural grassland (for each sampling day and for averages across dates; all distributions $P < 0.0001$). Ants were observed throughout all the hours across dates (Figure 1). Temperature seemed to be the main environmental factor associated with differences in foraging activity at the baits, only if each sampling day was analysed separately. Foraging activity was negatively correlated with temperatures during the summer-day, for the natural grassland as well as for *Setaria* (Spearman rank correlation: $\rho = -0.845$, $P < 0.001$, median and 25–75% quartiles of ants at baits = 309.0 and 245.0–345.7, respectively, for *Setaria*;

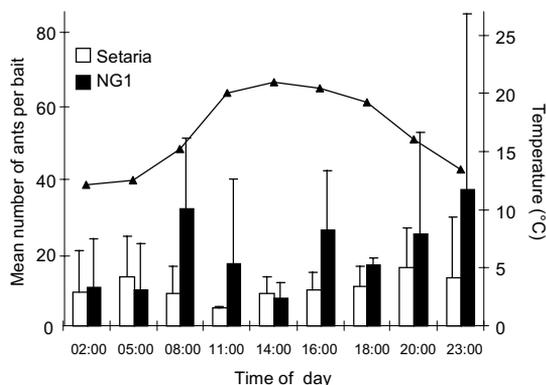


Figure 1. Average (\pm SD) number of ants collected at the baits throughout the day in the *Setaria* sown pasture and in the paired natural grassland (NG1). Note that data were gathered every 2 or 4 h at each site throughout three-24 h periods (6 paired measurements were gathered in the autumn, 8 in winter and 10 in the summer). Triangles show the average temperature recorded for each sampling hour for the three sampling days.

Figure 1. Número promedio (\pm DE) de hormigas colectadas a lo largo del día en los cebos en la pastura implantada *Setaria* y en el pastizal natural NG1. Los datos fueron tomados cada 2 o 4 h en cada sitio a lo largo de tres períodos de 24 h (se tomaron 6 mediciones pareadas en otoño, 8 en invierno y 10 en verano). Los triángulos muestran la temperatura promedio registrada en cada hora de muestreo para los tres días de muestreo.

$\rho = -0.927$, $P < 0.001$, median and quartiles = 239.0 and 144.2–358.2, for NG1). In contrast, in the winter-day, foraging activity was positively correlated with temperatures ($\rho = 0.649$, $P < 0.005$, median and quartiles = 56.5 and 33.5–84.5 for *Setaria*; $\rho = 0.667$, $P < 0.005$, median and quartiles = 39.0 and 0.25–242.0 for NG1). During the autumn-day, however, we found no relationship between hourly ant activity and temperature ($\rho = -0.028$, $P > 0.05$, median and quartiles = 109 and 76.7–164.0 for *Setaria*; $\rho = -0.543$, $P > 0.05$, median and quartiles = 206.5 and 69.7–975.5 for NG1). In the autumn-day (March) and summer-day (December), we found opposite trends in foraging activity between *C. punctulatus* and the other ant species in the natural grasslands, where more than one species occurred at the baits (Figure 2).

We counted 1216 ant individuals in the pitfall traps. We did not find differences in the

number of ant species (median of 2 species/pitfall; $P > 0.90$) nor in ant abundance (median ranges between 5–17 individuals/pitfall; $P > 0.17$) between Setaria and NG1 plot. However, we found a significantly greater number of *C. punctulatus* individuals than of ants from other species in Setaria ($P < 0.0001$), whereas the opposite pattern of ant abundance was found at NG1 ($P < 0.0015$). For the Pangola–NG2 comparison, we found the same pattern: no differences in ant species richness ($P > 0.68$) from the pitfall traps but a significantly greater relative abundance of *C. punctulatus* in the pitfalls in Pangola than in NG2 ($P < 0.0001$). The number of individuals from other ant species remained unchanged between sites ($P > 0.105$).

The number of *C. punctulatus* ants found in pitfall traps was not related to closeness of traps to anthills of *C. punctulatus*. In Setaria and Pangola, there were no differences between transects in the number of *C. punctulatus* ants ($P > 0.10$ and $P > 0.14$, respectively) nor in the number of individuals of other ant species ($P > 0.40$ and $P > 0.83$, respectively). Moreover, no differences were found in ant species richness or overall ant abundance calculated per pitfall trap when comparisons were made between transects at each plot (all $P > 0.05$).

Land use history, in this case sown pastures, appeared to change the ant community structure, mainly by changing the dominant ant species, as *C. punctulatus* was the most numerous ant in the sown pastures, while *Pheidole* sp. 3 dominated the NG1 and NG2 plots (Figure 3). According to pitfall trap data, at both sown pastures we found one dominant species, two or three co-dominants with intermediate abundance (>20 individuals/pitfall) and some rare species. A similar ant community structure to sown pastures was found for NG2, although with lower numbers, and with *C. punctulatus* representing only 4% of the total ant abundance. However, at NG1 there were no dominant species, there were three co-dominants and few rare species. In this case, *C. punctulatus* represented 7% of the total ant abundance (Figure 3). The composition of the ant communities differed most, because of the rare species found at a single site. It has been noted that singletons continue to appear indefinitely with increasing sampling effort in ant communities (Longino & Colwell 1997). Each sown pasture shared with its natural grassland between 43% and 55% of ant spe-

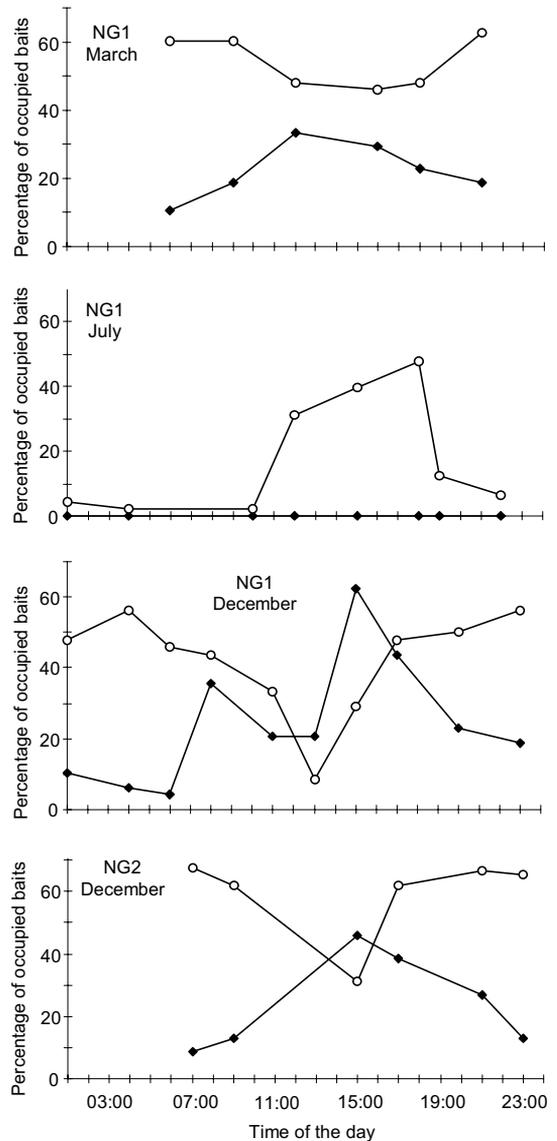


Figure 2. Percentage of occupied baits by *Camponotus punctulatus* (black rhombi) and other ant species (open circles) throughout a 24 h sampling day in March, July, and December at the natural grassland sites, NG1 and NG2. Data were gathered every 2 or 4 h.

Figura 2. Porcentaje de cebos ocupados por *Camponotus punctulatus* (rombos negros) y por otras especies de hormigas (círculos blancos) a lo largo de un día de muestreo en marzo, julio y diciembre en los pastizales naturales NG1 y NG2. Los datos fueron tomados cada 2 o 4 h.

cies (for Setaria–NG1 and Pangola–NG2, respectively), both natural grasslands shared 43% of ant species, while the sown pastures shared 62% of ant species. Although there were more ant species in Setaria and NG1, in

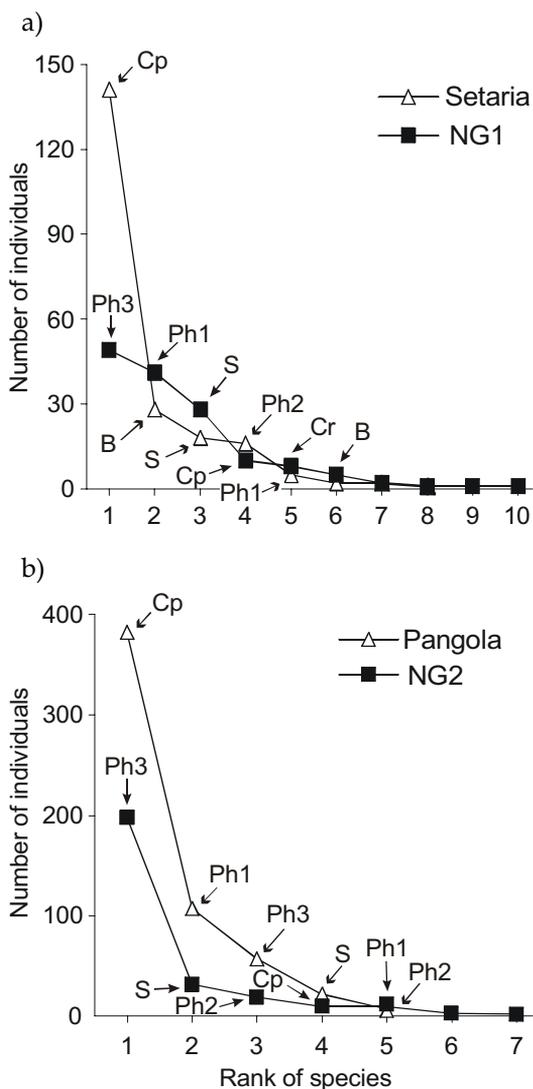


Figure 3. Species abundance-rank curves, obtained with data from all pitfall traps. Comparisons are (a) between Setaria and NG1 plot, and (b) for Pangola and NG2 plot. Note that axis scales differ in each figure. Ant species names are indicated for the most abundant species (>10 ants in all pitfall traps), with short arrows for sown pastures and with long arrows for natural grasslands. B: *Brachymyrmex* sp., Cp: *Camponotus punctulatus*, Cr: *Crematogaster* sp., Ph1: *Pheidole* sp1, Ph2: *Pheidole* sp2, Ph3: *Pheidole* sp3, S: *Solenopsis macdonaghi*.

Figure 3. Curvas de rango-abundancia obtenidas con datos de todas las trampas de caída. Las comparaciones son (a) entre Setaria y la parcela NG1 y (b) entre Pangola y la parcela NG2. Las escalas de los ejes son diferentes en cada figura. Se indican los nombres de las especies de hormigas más abundantes (>10 hormigas en todas las trampas de caída), con flechas cortas para las pasturas implantadas y con flechas largas para los pastizales. Ver la clave de los nombres de especies arriba.

comparison to Pangola and NG2 (Figure 3), ant abundance was greater in Pangola ($n = 575$) and NG2 ($n = 280$) than in Setaria ($n = 215$) and NG1 ($n = 146$).

DISCUSSION

C. punctulatus was the dominant ant species in the sown pastures, whereas in the natural grasslands this species had much lower abundances. The greater dominance of *C. punctulatus* in Setaria and Pangola-sown plots was indicated mainly by its greater abundance shown in pitfalls. In the natural grasslands, on the contrary, two or three species were co-dominants, but *C. punctulatus* was never one of them. These data suggest that agricultural activities (i.e., sown pastures) favoured the demographic explosion of *C. punctulatus*. Data from baits also support this conclusion. Although we cannot rule out a bias on the single presence of *C. punctulatus* at the sown pastures because of the proximity of the baits to their nests, baits from the natural grasslands showed that this species has a great ability to find food resources as it is one of the three species most frequently found. The latter occurred despite the much lower *C. punctulatus* nest density and abundance (from pitfalls) and despite the fact that baits of transects did not fall close by *C. punctulatus* nests in the natural grasslands. Moreover, two other studies performed by the authors (unpublished) at other systems where *C. punctulatus* attains very high densities have shown that this ant species monopolizes most of the regularly spaced baits along a transect. Therefore, we believe that if baits would have been regularly placed along the transect in the pastures we would have observed the same level of dominance of *C. punctulatus* simply due to its greater abundance. It is a known pattern that ant species that become abundant monopolize the baits (Andersen & McKaige 1987; Hölldobler & Wilson 1990; Suarez et al. 1998).

Why then did only *C. punctulatus* achieve such dominance? There are many possible explanations. One just discussed is related to *C. punctulatus* dominance at baits. It seems that this ant species is very good at gathering food despite its abundance, and other experiments demonstrate that it is the fastest species at finding food in natural grasslands (unpubl.

data), therefore, both traits may give this species a competitive edge during the invasion of agricultural fields. Additionally, after soil disturbance, *C. punctulatus* could have been the first species able to invade and/or able to build its nests on compact soils, imposing a priority effect on occupation of space. Another reason could have been cattle trampling, an effect more prominent in sown pastures. Trampling could have impeded the successful establishment of hypogeous ant species. Also, the removal of the original flora in the sown pasture could have lead to the local extinction of a natural enemy (parasitoid, pathogen, predator), which in the natural grassland regulated the abundance of *C. punctulatus*. Finally, although the pastures were seven years old, it is possible that we were still looking at the initial stages of the succession of the ant community, in which *C. punctulatus* behaved as the first pioneer species.

Ant foraging activity increased with temperature if ants were sampled on a winter-day, or decreased with temperature, if it was recorded on a summer-day, irrespectively of whether the community was in the sown pasture or natural grassland. This is a common pattern for ants (Hölldobler & Wilson 1990). However, foraging patterns of both ant communities were different; ants from the natural grassland exhibited a few peaks of activity throughout the day, whereas those from pastures (i.e., *C. punctulatus*) seemed to have a more constant pattern of activity (Figure 1). It is possible that different physiological tolerances by ant species could be responsible for the differences in daily activities, as well as for the opposite foraging patterns observed between *C. punctulatus* and the rest of the ant community in natural grasslands (Figure 2). However, in the latter case, it could also reflect a temporal partitioning due to past competition (Fellers 1987; Savolainen & Vepsäläinen 1988). Records about interspecific interactions at the baits could shed some light on the observed patterns.

Since other walking arthropods besides ants had fallen in our pitfalls, since we found a greater number of *C. punctulatus* on *Setaria* pitfalls than on natural grassland ones, and since other studies have shown variable changes in arthropod soil diversity at sown pastures in comparison to control areas (Hutchinson & King 1970; King et al. 1976;

Paoletti et al. 1991; Decaëns et al. 1994; Lavelle et al. 1994), we were interested to find out if there were correlated differences in other arthropods (besides ants) between sown pastures and natural grasslands. In general, we found no differences in arthropod diversity (identified by trained entomologists as recognizable taxonomic units or morphospecies, Oliver & Beattie 1996, within the following groups: Acarina, Aranae, Collembola, Coleoptera, Diptera, Formicidae, Homoptera, and Others as those comprising less than 5% of the total abundance) between sown pastures and natural grasslands (each comparison $P > 0.05$). The exceptions were the greater richness and abundance of arthropods per pitfall ($P < 0.02$ in each case) in Pangola compared to NG2. Taxonomic groups of arthropods with greatest richness at the four sites were the Coleoptera, followed by Formicidae, Acarina or Aranae. Both natural grasslands shared 23% of the total 83 morphospecies (52 morphospecies were registered in NG1 and 51 in NG2). Both sown pastures shared 34% of the total 87 morphospecies (58 morphospecies were found in *Setaria* and 56 in Pangola). Closeness to anthills did not affect either the total number of individuals found in pitfall traps or the richness (comparisons between north-south and east-west transects for each plot; all $P > 0.05$). Therefore, although *C. punctulatus* seemed to reduce the relative abundance of other ant species at the sown pastures, this effect was not observed for the rest of the arthropod community. Although we have set pitfalls only in the summer, we found the same pattern of activity at baits in *Setaria* vs. NG1 in the summer, as well as at other times of the year. We therefore predict that the same relationship between *C. punctulatus* and other ants should be found at pitfalls for other seasons.

It is worth pointing out that, in this study, we were not able to disentangle the effect of *C. punctulatus* from the direct effect of agriculture because we could not find sown pastures with comparable histories but without anthills. However, ongoing experiments which include records of *C. punctulatus* interactions with other members of the ant community during the invasion, immediately after agricultural disturbance, will allow us to test some of the hypotheses, predictions, and patterns discussed in this study.

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