LEAFCUTTER ANT (*ATTA SEXDENS*) (HYMENOPTERA: FORMICIDAE) NEST DISTRIBUTION RESPONDS TO CANOPY REMOVAL AND CHANGES IN MICRO-CLIMATE IN THE SOUTHERN COLOMBIAN AMAZON.

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Abstract

At regional scales, leafcutter ant nest distribution is regulated by environmental factors such as vegetation, predators, soil and climate. This study investigated the effect of micro-climate on *Atta sexdens* (L.) nest distribution. It was carried out on a farm located on the Colombian Amazon River shore, where an extension of secondary forest was felled. Prior to felling, we located 20 *A. sexdens* nests and monitored them over the course of one year. Ten of the nests became exposed to the sun as a result of tree felling, and ten nests, located in neighboring unlogged forest, remained unaffected. Within six weeks, five of the exposed nests had moved to the cover of nearby vegetation patches and the remaining five nests had died. The ten unexposed nests remained active at the same location. In comparison with relocated nests, exposed nests experienced significantly higher air and soil temp, and lower soil moisture. The results of this study suggest that changes in micro-climate may trigger nest relocation and therefore play an important role in local *A. sexdens* nest distribution.

Key Words: disturbance, nest relocation, soil moisture, tree felling, temp

Resumen

A nivel regional, la distribución de los nidos de la hormiga arriera es regulada por factores ambientales así como la vegetación, los depredadores, el suelo y el clima. Este estudio investigó el efecto del micro-clima sobre la distribución de los nidos de *Atta sexdens* (L.). El estudio se llevó a cabo en una finca en la orilla colombiana del Río Amazonas, donde se taló una extensión de bosque secundario. Anterior a la tala, ubicamos 20 nidos de *A. sexdens* y los monitoreamos sobre el transcurso de un año. Diez de ellos se expusieron al sol como resultado de la tala, y diez, ubicados en el bosque vecino no talado, quedaron sin afectar. En seis semanas, cinco de los nidos expuestos se habían reubicado hacia la cobertura del dosel de la vegetación cercana y los otros cinco se habían muerto. Los diez nidos no expuestos quedaron activos en el mismo sitio. En comparación con los nidos reubicados, los nidos expuestos experimentaron temperaturas significativamente más altas del aire y del suelo, y humedad más baja del suelo. Los resultados de este estudio sugieren que los cambios microclimáticos pueden inducir la reubicación del nido y por lo tanto juegan un papel importante en la distribución local de los nidos de *A. sexdens.*

Palabras Clave: disturbio, humedad del suelo, reubicación del nido, tala de árboles, temperatura

Leafcutter ants (*Atta* and *Acromyrmex* spp.) are considered important ecosystem engineers in the Neotropics (Fowler et al. 1989). They are also of great relevance as key herbivores during successional processes (Vasconcelos & Cherrett 1997; Vasconcelos 1997), and as pest species in planted forests (e.g., agroforestry, restoration programs) and agricultural lands (e.g., permanent agriculture) (Della-Lucia 2003). Their cutting, carrying and digging activities can drastically affect forest structure and composition, seedling establishment as well as soil and micro-climatic conditions (Alvarado et al. 1981; Vasconcelos & Cherrett 1997; Garrettson et al. 1998; Hull-Sanders & Howard 2003; Moutinho et al. 2003; Wirth et al. 2003; Farji-Brener 2005; Silva et al. 2007; Corrêa et al. 2010). However, the underlying mechanisms that determine leafcutter ant nest distribution and densities are poorly understood.

Multiple biotic and abiotic environmental factors control leafcutter ant demography top-down (i.e., natural enemy driven) or bottom-up (i.e., resource driven). Higher natural enemy pressure can reduce nest densities in forest fragments (Rao 2000). The greater availability of palatable forage (i.e., pioneer plant species in particular) in secondary, disturbed and fragmented forests favors *Atta* colony development and leads to higher nest densities, whereas

lower nest densities are found in mature forests (Vasconcelos & Cherrett 1995; Farji-Brener 2001; Wirth et al. 2003; Urbas et al. 2007; Wirth et al. 2007; Meyer et al. 2009). Colony founding success, and therefore nest distribution and density, also seem to be affected by soil conditions (Bento et al. 1991; Perfecto & Vandermeer 1993; Diehl-Fleig & Rocha 1998; Araújo et al. 2003) and micro-climate (Vasconcelos et al. 2006; Bollazzi et al. 2008; Mintzer 2009; Vieira-Neto & Vasconcelos 2010). A suitable micro-climate is particularly crucial for the development of *Leucoagaricus gongylophorus* (Homobasidiomycetes: Agaricomycetidae), the fungus cultivated by leafcutter ants for nutrition (Quinlan & Cherrett 1978; Powell & Stradling 1986; Roces & Kleineidam 2000; Bollazzi & Roces 2002).

Leafcutter ants trade off temp to maintain high humidity levels, probably to prevent dehydration of fungus and brood (Bollazzi & Roces 2010a, b). Therefore, air temp may be the most critical microclimatic variable for nest development. RH in nest chambers of this ant species in the field is consistently over 90% (Stahel & Geijskes 1940). Air temp is also crucial for leafcutter ant nest functioning (Bollazzi & Roces 2002; Bollazzi et al. 2008) and seems to govern geographic distribution patterns and nest design on the American continent (Schoereder 1998; Bollazzi et al. 2008). Within nest chambers, air temp is regulated by ventilation (Kleineidam & Roces 2000; Kleineidam et al. 2001; Bollazzi & Roces 2010b). For example, *A. sexdens* maintains nest temps at 25 ± 0.4 °C (Eidmann 1936), which is the optimum temp for fungus and brood (Quinlan & Cherrett 1978; Powell & Stradling 1986; Roces & Kleineidam 2000).

Atta sexdens (L.) is found in a wide range of Neotropical habitat types (Fowler et al. 1989). In a mosaic of habitat types in the Colombian Amazon, active nests were located in habitat types with relatively high percentages of canopy cover, but active nests were absent from those with minimal levels of canopy cover (van Gils et al. 2010; van Gils et al. 2011). Moreover, canopy cover at each active *A. sexdens* nest was significantly higher than measured at approximately 15 m from the nest (van Gils 2012). This could suggest the need for specific (i.e., relatively cooler and moister) (Fetcher 1985) micro-climatic circumstances. To date, no field studies have measured micro-climatic variables and related these to local leafcutter ant nest distribution. The objective of this study was to evaluate how micro-climatic changes (soil and air temp and soil moisture) because of canopy cover removal affect *A. sexdens* nest distribution.

Materials and Methods

Study Area and *Atta sexdens* Nests

This study was carried out on the private farm "Versalles" on the Colombian shore of the Amazon River (S 3° 49' 51.2' W 70° 14' 26.9'). Before the experiment, the farm had been covered with 15-yr old secondary tropical forest. Dominant plant genera in these forests were *Warszewiczia* (Gentianales: Rubiaceae), *Chomelia* (Gentianales: Rubiaceae), *Euterpe* (Aricales: Arecaceae), *Astrocaryum* (Aricales: Arecaceae), *Iriartea* (Aricales: Arecaceae), *Ryania* (Malpighiales: Salicaceae) and *Perebea* (Rosales: Moraceae) species (van Gils 2011). In the study region, mean annual rainfall is 3,200 mm. There is a dry season between Jun and Sep, and a wet season between Oct and May. Mean RH is approximately 86% and air temp oscillates around 26 °C all year round (Riaño 2003).

In Nov 2007, a plot of approximately 30 ha of forest was felled. Immediately prior to felling, 20 *A. sexdens* nests in this field were selected, which had been active at the same site for at least 5 yr according to local residents. Ten nests were located in the forest to be felled and were exposed to the sun after felling. The distance between any of the exposed nests and the intact adjacent secondary forest was at least 100 m. Ten other nests were located within this intact forest and at least 30 m from any forest disturbance. In the felled area, several randomly located patches of secondary forest (maximum 15 m^2) were intentionally left untouched, because they consisted of useful tree and palm species for the farm owner. Nests were monitored twice a week (Mon and Thu) for 1 yr to observe responses to canopy cover elimination.

Canopy Cover

Felling took place in Nov 2007. One mo before (Oct 2007) and 3 mo after (Feb 2008) the forest had been felled, we measured canopy cover at the 20 nests and at 4 equally spaced locations at 15 m distance from any outermost nest mound using a Robert E. Lemmon densiometer (Englund et al. 2000). The edges of these mounds were clearly identifiable by the characteristic fresh clumps (Ø 2-3 mm) of damp soil (consisting of ± 38% clay and ± 40% silt; van Gils et al. 2010) recently deposited by the ants. At the nest and at each of the 4 measuring locations per nest, a reading was taken to the north, south, east, and west. The mean of these 4 readings was calculated and multiplied by 1.04 to establish percent canopy cover per nest and each of the 4 distant locations. During the experiment, casual observations were made to see whether the ants cut leaves from vegetation surrounding the nests.

Soil and Air Temperature

Approximately 3 mo after tree felling, and over the course of 3 sunny d between 0630 and

1730 h, the following hourly measurements were taken at each of the 10 nests within the logged area: (i) soil temp at 25 cm depth at 2 locations on the most central nest mound; (ii) soil temp at 25 cm depth at 2 equally spaced locations, 1 m from any outermost nest mound, and (iii) air temp immediately above the most central nest mound. The 2 soil temp measurements of the nest mound and at 1 m distance were taken with analog Weksler 2" Dial Size Bi-Metal thermometers and averaged to establish hourly soil temp per nest per day. Air temp was measured with an analog maximum-minimum mercury thermometer.

Soil Moisture

Also approximately 3 mo after tree felling, percent soil moisture near the 10 nests within the logged area was measured as follows. At each nest soil cores of 100 cm^3 were taken at 20-25 cm depth at 4 equally spaced locations, 1 m from any outermost nest mound. The cores were sealed in a plastic bag and weighed on the same d, and re-weighed after 14 d of air drying to determine gravimetric soil moisture percent (gr water / gr dry soil × 100). The 4 soil moisture percentages per nest were averaged to establish soil moisture percent per nest.

Statistical Analysis

We carried out all statistical analyses with the spss software package version 15.0.1 (Spss Inc. 2006). A two-way repeated measures anova was carried out to compare percent canopy cover (after e^{x+1} transformation) before and after tree felling (fixed factors: nest reference - unexposed, exposed and relocated - and measurement location - nest, north, east, south and west -; repeated measure: canopy cover - before and after tree felling -). To compare canopy cover on nests after tree felling, we used a Kruskal-Wallis test. Separate two-way repeated measures anova were applied to compare nest mound soil temp, soil temp at 1 m from the outermost nest mound and air temp (after e^{x} transformation) between nests (fixed factors: measurement day -1, 2, 3- and hour -1 to 12-; repeated measure: temp at the 2 nest references -exposed and relocated-). Before each repeated measures anova, the Mauchly's test of sphericity was carried automatically out to confirm if the variances of the differences between all combinations of the groups were equal. If this test results in $P < 0.05$, the F-ratios produced must be interpreted with caution as it can result in an increase in the Type I error rate of the repeated measures anova. In this case, a Greenhouse-Geisser correction was applied to alter the degrees of freedom and produce an F-ratio where the Type I error rate is reduced. A Mann-Whitney U test was used to compare soil moisture differences between nests.

Results

Atta sexdens Nests

Nests located in the intact secondary forest adjacent to the felled area remained apparently unaltered during the monitoring year (these are hereafter designated: "unexposed nests"). In the 2 wk after tree felling, worker ants from the 10 nests within the felled area deposited relatively large quantities of little clumps of damp soil over the nest mounds. After the fourth visit, soil had deposition decreased drastically. Ants had only deposited tiny quantities of soil around only 3 to 4 entrances per nest. Meanwhile, the previously deposited clumps had already started to merge into each other to form a firm layer of soil. At the seventh visit, soil deposition had ceased completely (i.e., no new clumps appeared) at 3 nests and at the eighth visit, it had also stopped at the other seven. Five of these nests (designated "exposed nests") located further than 50 m from remnant patches of secondary forest did not show any further activity during the monitoring yr and we assumed that these colonies had died. The February 2008 temp and soil moisture measurements for these 5 nests were taken at the exposed nest locations.

During this study, we concluded that the 5 other nests (designated "relocated nests) had relocated to the remnant patches of secondary forest at 5, 16, 18, 22 and 45 m from the nests because at each of these patches *A. sexdens* colonies started to make new mounds of fresh soil exactly between 4 and 6 wk after tree felling and between 0 and 2 wk after the nests in the felled area had become inactive. There had been no recent mating flight and there are no literature records of ways to establish a new nest other than by a queen after the her mating flight or by relocation. Also, and the growth rate of these 5 new nest mounds was much faster than that of a newly established nest. By Feb 2008 the new nest mounds were visually estimated to be comparable in size with those of the original nests prior to exposure by tree felling. The Feb 2008 temp and soil moisture measurements for these 5 nests were taken at the new nest locations.

The remnant vegetation patches to which nests relocated were principally comprised of *Oenocarpus bacaba* Mart. (Arecaceae), *Matisia cordata* Bonpl. (Bombacaceae), *Cedrela odorata* L. (Meliaceae) and some low herbs. According to local residents, the leaves of none of these species are utilized by *A. sexdens* for fungus cultivation. Indeed, during our monitoring year we never observed leaf damage or leafcutter ants carrying leaves or fruits from any of them, whereas ants from unexposed nests cut leaves from various (unidentified) plant species in their surroundings.

Canopy Cover

After tree felling, little canopy cover remained at the exposed nests and their surroundings (Fig. 1a). Canopy cover at relocated nests was lower at their new location than at their original location before tree felling, but much higher than at the locations 15 m away (Fig. 1b). Even though no vegetation was removed at nests located in the adjacent intact secondary forest, mean percent canopy cover at and near these nests was also reduced (Fig. 1c). The two-way repeated measures anova confirmed that overall canopy cover had been reduced significantly after tree felling (Mauchly's test of sphericity P < 0.05; Greenhouse-Geisser corrected $F_{1,4}$ = 294.89; P < 0.01). The Kruskal-Wallis test showed that canopy cover over the nests after tree felling was significantly different between the 3 nest references (H (2, n = 20) = 12.96; P < 0.01).

Soil and Air Temperature

Mean temp of exposed nests mounds was consistently higher than for relocated nest mounds (Fig. 2a). Maximum exposed mound temp reached 28.0 °C at 1730 h, whereas relocated mound temp only reached 24.8 °C at 1430 h. Mean soil temp at 1 m from exposed nests followed a similar pattern (Fig. 2b). Mean air temp near the soil surface at exposed nests was mostly much higher than at relocated nest (Fig. 2c) and even reached a maximum of 38.6 °C at 1230 h, which was 10 °C warmer than at relocated nests. The separate two-way repeated measures anova per temp confirmed that after tree felling temp were significantly higher at exposed nests than at the relocated ones (for nest mound soil temp: Mauchly's test of sphericity P > 0.05; assumed sphericity $F_{1,2}$ = 52.56; P < 0.05, for soil temp at 1 m distance from the outermost nest mound: Mauchly's test of sphericity P > 0.05; assumed sphericity $F_{1,2}$ = 20.08; P < 0.05 and for air temp: Mauchly's test of sphericity P > 0.05; assumed sphericity $F_{1,2}$ = 13.17; P < 0.05).

Soil Moisture

The Mann-Whitney U test showed that gravimetric soil moisture at 25 cm depth near exposed nests (32.6 ± 1.41%) (n = 5) was significantly lower than near relocated nests (45.3 ± 1.76%) (n = 5) (Z = -2.611; P < 0.05).

Discussion

The results of this study strongly suggest that micro-climatic changes caused by canopy cover removal play an important role in the bottom-up determination of local *A. sexdens* nest distribution. The combination of higher soil and air temp as well as lower soil moisture, as a result of tree felling, seemed to result in exposed colonies seek-

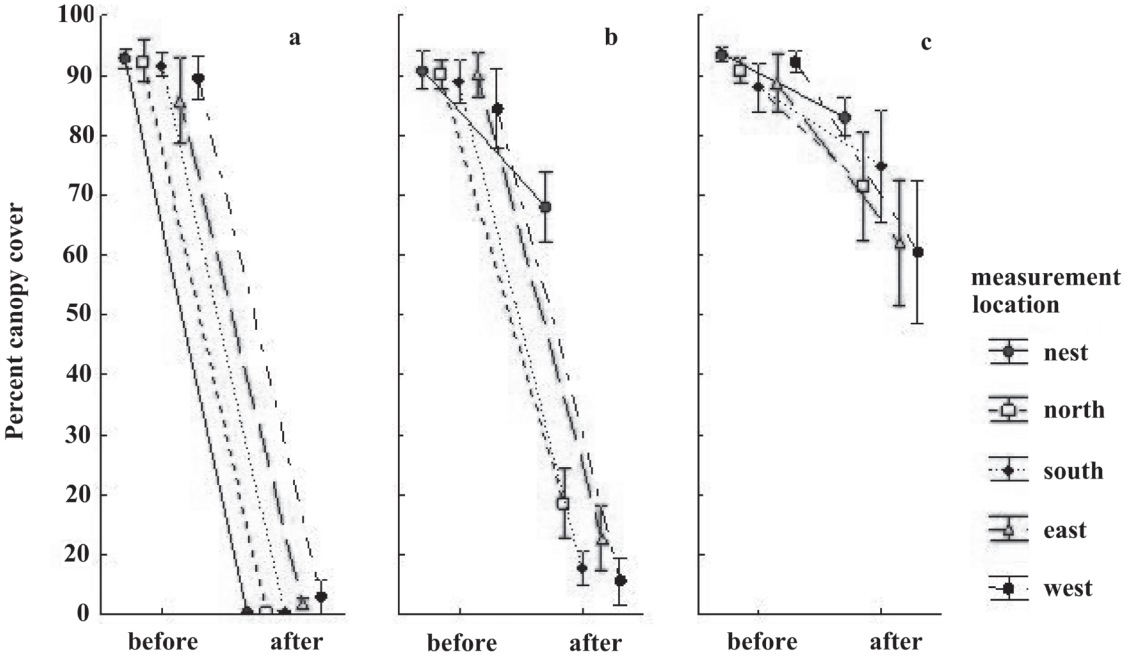


Fig. 1. Percent canopy cover (mean + SE) of *Atta sexdens* nests at and near (15 m north, east, south and west); (a) exposed nests, (b) relocated nests, and (c) unexposed nests. Measurements made before and after tree felling, Oct 2007 and Feb 2008, respectively.

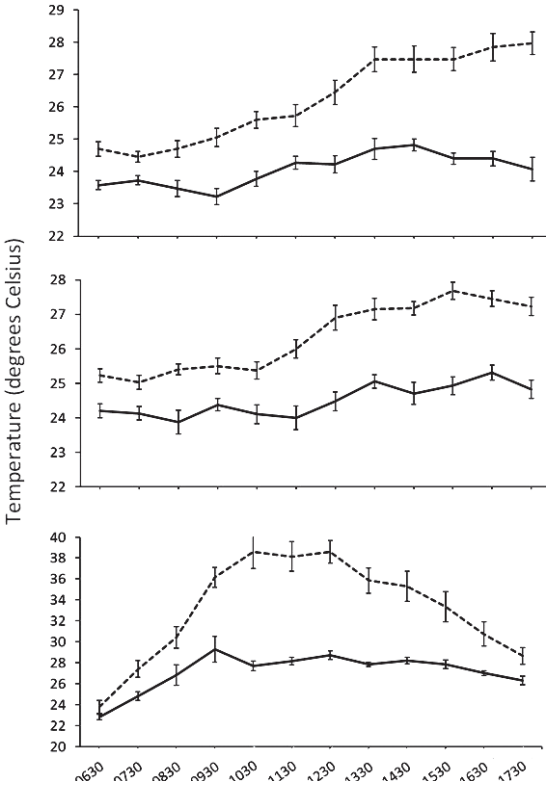


Fig. 2. Mean hourly temperatures (°C + SE) affecting *Atta sexdens* nests. Dotted line: exposed nests and solid line: relocated nests. Trees were felled and the canopy was removed in Nov 2007 and 3 mo later in Feb 2008 temperatures were measured: (a) soil temperature at the nest mound at 25 cm depth, (b) soil temperature at 1 m from the nest mound and at 25 cm depth and (c) air temperature near the soil surface.

ing to relocate to sites with greater canopy cover. When these were not available nearby, colony death occurred. On the other hand, nests which maintained their canopy cover, and presumably experienced lower soil and air temp and higher soil moisture percentages in comparison with exposed nests or even relocated nests, remained unaffected.

Canopy cover reduction may imply a lack of suitable forage for leafcutter ant colonies, and thus resulting in colony death. However, forage deficiency was not likely to have caused exposed nest relocation or death in this study. *Atta* worker ants travel distances of over 200 m to reach suitable forage (Eidmann 1932; Cherrett 1968; Hölldobler & Wilson 1996). Nests within the felled area were located little more than 100 m from the intact adjacent secondary forest. The characteristic underground tunnels constructed by *A. sexdens* (Eidmann 1932) assure that leaf harvesting can continue even when above ground temp are too high for foraging (Viana et al. 2004). Additionally, the remnant vegetation patches to which nests relocated did not contain suitable forage either. Relocation away from the exposed locations, therefore, did not favor food resource availability to these nests. Even though an unfavorable microclimate is thought to have been the cause of nest relocation in this study, exposed nests may also have suffered an increased exposure to predators or parasites. This factor should not be discarded as another possible cause for nest relocation.

Canopy cover removal led to significantly higher soil and air temp at exposed *A. sexdens* nests than at relocated nests. The warmer air on the exposed soil surface enters the nest through ventilation (Kleineidam & Roces 2000; Kleineidam et al. 2001). While this air will cool as it is conducted through the nest tunnels (Kleineidam & Roces 2000), we expect that it may still result in a substantially higher air temp in the brood and fungal chambers. When provided an experimental temp gradient of 10-37 °C, the leafcutter ant, *Acromyrmex heyeri* Forel, moved fungus and brood to locations where the temp was between 20 and 25 °C (Bollazzi & Roces 2002). Leafcutter ant colonies in the field also locate fungus and brood tin nest chambers with temp in this range (Lapointe et al. 1998; Moser 2006). When these are not available, the ants are triggered to start digging (Bollazzi et al. 2008). *L. gongylophorus* cannot survive in air temp that exceed 30 °C and growth rates are significantly reduced when temp fall to 10 °C (Quinlan & Cherrett 1978; Powell & Stradling 1986).

The measured higher soil temp may prevent incoming air from losing warmth immediately upon entering the nest tunnels and thus maintain its higher temp for a larger distance. In addition, higher soil and air temp may elevate CO_2 production by leafcutter ants, and possibly by the fungus (Hebling-Beraldo & Mendes 1982; Hebling et al. 1992; Kleineidam & Roces 2000). This may result in a need for increased ventilation activity and therefore even more warm air could enter the nest. Thus, a vicious cycle could be created which progressively warms the nest, to the detriment of the fungus culture and brood.

The observed low soil moisture levels near exposed nests and the expected relatively lower moisture levels of incoming warmer air may both reduce RH within the nest chambers, and represent another threat to the fungus culture and the brood (Stahel & Geijskes 1940; Roces & Kleineidam 2000; Bollazzi & Roces 2007). In response to 4 RH temp options between 33 and 98%, *Atta sexdens* locate fungus cultures and brood to the most humid sites (Roces & Kleineidam 2000). A climate change in the Sonoran desert resulting in dryer soil is also thought to have caused the death of many *A texana* nests and to have limited the establishment of new nests over a course of 20 yr (Mintzer 2009). Increased mortality of incipient

A. laevigata nests during a period of low rainfall may indicate the susceptibility of these nests to low RH in comparison with older nests (Hernández et al. 1999).

Mean canopy cover on successfully relocated nests was 68%. Although this was lower than at their original location prior to tree felling, it was still much higher than at 15 m of the new location, where average canopy cover was only 11%. It is possible that a minimum level of canopy cover is required at the immediate *A. sexdens* nest location to guarantee an adequate micro-climate, whereas lower or even minimal canopy cover over surrounding areas may not be detrimental to colony survival. Nonetheless, only an experiment offering a continuum of different canopy covers to many nests would confirm such a requirement.

Nest abandonment and relocation after severe nest disturbance has been documented before (Autuori 1941; Wilson 1971 in Rockwood 1973; Haines pers. com. in Rockwood 1973; Fowler 1981; H. Herz pers. com. in Farji-Brener & Illes 2000). However, it was always assumed this phenomenon is uncommon for *Atta* and likely to kill the nest (Rockwood 1973). Only *Atta colombica* was documented to undertake relatively frequent colony relocations and to do so over distances up to 258 m (Wirth et al. 2003). The cause of this relocation remained unknown (micro-climate was explicitly discarded as a possible cause). In our study, any nest located at 45 m or less from canopy cover seemed able to relocate, whereas those located at more than 50 meters did not seem to be able to survive at their original location or to successfully relocate to a more favorable one. Perhaps, relocation ability also depends on factors not identified in this study, such as soil consistency, colony or worker ant size. The results of this study suggest that in forest environments experiencing frequent anthropic changes in canopy cover, *A. sexdens* colony relocation and death due to local micro-climatic conditions may be quite common.

In sub-tropical open forests in eastern Australia, tree felling resulted in the decline of the shade tolerant green-headed metallic pony ant, *Rhytidoponera metallica* (Smith), which was replaced by sun-loving *Iridomyrmex rufoniger* (Lowne 1865 (Vanderwoude et al. 2000). In this case, one species is replaced by another. In our study and Vasconcelos' (1990), tree felling resulted in a local reduction of the range of *A. sexdens,* a key herbivore and ecosystem engineer (Farji-Brener & Illes 2000; Wirth et al. 2003, 2007; Corrêa et al. 2010). At *Atta* nest sites, soil is disturbed (Alvarado et al. 1981; Perfecto & Vandermeer 1993) and soil penetrability improved (Moutinho et al. 2003). The year-long organic waste disposal enriches the soil with nutrients (Haines 1978; Moutinho et al. 2003; Sternberg et al. 2007). Changed soil properties, in addition to selective harvesting, the accumulation of seeds and the modification of micro-climatic conditions, alter vegetation structure and composition at nest sites (Garrettson et al. 1998; Hull-Sanders & Howard 2003; Silva et al. 2007; Corrêa et al. 2010). The disappearance of leafcutter ant nests from any area may significantly decrease its soil and vegetation heterogeneity. Therefore, we argue that the bottom-up impact of micro-climate on *A. sexdens* nest distribution, and subsequently on ecosystem engineering, should not be underestimated.

Contrary to many other *Atta* species, intrinsic factors allow *A. sexdens* to adapt to a broader range of environmental conditions and colonize a larger variety of non-forested habitat types in which it may even replace other leafcutter ant species (Fowler 1995; Vasconcelos & Cherrett 1995; Fowler et al. 1996). *A. sexdens* is even favored by human-induced disturbance, which usually involves reduced canopy cover (Vasconcelos 1990; Corrêa et al. 2005; Wirth et al. 2007). However, it seems that this species is unable to survive in completely deforested habitat types despite forage availability. In this scenario, other *Atta* or *Acromyrmex* species may benefit from this absence and augment their own distribution.

The effect of micro-climate on leafcutter ant nest distribution may differ with ant species, nest size, soil type, habitat type or other factors. Further studies may also elucidate the effect of micro-climate on nest foundation and early development; a subject that has only been touched upon recently (Bollazzi & Roces 2007; Bollazzi et al. 2008; Mintzer 2009; Vieira-Neto & Vasconcelos 2010).

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