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Co-existence of ants and termites in *Cecropia pachystachya* Trécul (Urticaceae)

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ABSTRACT

Individuals of *Cecropia pachystachya* Trécul (Urticaceae) host *Azteca* (Hymenoptera: Formicidae) colonies in their hollow internodes and feed them with glycogen bodies produced in modified petiole bases (trichilia). In turn, ants keep trees free from herbivores and lianas. Here, we report for the first time the association of nests of *Nasutitermes ephratae* Rambur (Isoptera: Termitidae) with these trees, in South-Pantanal (Brazil). We aimed to describe the *Cecropia*-ant-termite relationship and to investigate how their coexistence is made possible. We hypothesize that: 1) The frequency of termite nests in *C. pachystachya* is lower than in neighbor trees; 2) Termite nests occur in trees with lower density of foraging ants; 3) The time that ants take to find and remove live termite baits in *C. pachystachya* trees is lower in leaves (close to trichilia) than in trunks; 4) Termite nests are fixed preferentially in the smallest and less branched trees; and 5) Termite nests are fixed preferentially distant from the canopies. Unexpectedly, termitaria occurred in *C. pachystachya* at the same frequency as in other tree species; there was no relationship between ant patrol activity and the occurrence of termite nests in *C. pachystachya*; and they occurred mainly in the tallest and more branched trees. However, termite nests generally were fixed in the trunk, fork or basal branches, where there is better physical support and ant patrol is more modest. The segregation of termite and ant life-areas may represent a escape strategy of termites in relation to ants inhabiting *C. pachystachya*, specially during nest establishment. The isolation of termites in fibrous nests and galleries may complete their defense strategy.

Introduction

The neotropical genus *Cecropia* (Urticaceae) includes 60-70 species, 80% of them are trees inhabited by obligatory symbiotic ants of at least four subfamilies: Dolichoderinae, Formicinae, Myrmicinae e Ponerinae (Davidson & Fisher 1991, Davidson & McKey 1993, Folgarait *et al.* 1994). The relationship between *Cecropia* spp. and *Azteca* spp. (Hymenoptera: Formicidae) – one of the most conspicuous and well studied mirmecophilic interactions – is considered a symbiotic relationship because ants live only in the large hollow internodes of some species, feeding on Müllerian bodies produced in modified petiole bases (trichilia) (Wheeler 1942, Janzen 1969, Dejean *et al.* 2009). These food bodies are rich in carbohydrates, lipids, proteins and primarily glycogen, which remarkably is the principal storage carbohydrate found in animals and is

extremely rare in plants (Rickson 1971, Rico-Gray & Oliveira 2007). *Azteca* ants supplement their diet with invasive insects, which they aggressively attack (Dejean *et al.* 2009). There is strong evidence that ants provide nutrients to *Cecropia* individuals (Putz & Holbrook 1988, Sagers *et al.* 2000) and keep them free from herbivores and vines, thus acting as allelopathic agents and increasing tree competitive ability (Janzen 1966, Downhower 1975, Schupp 1986, Vasconcelos & Casimiro 1997).

Ants involved in obligate mutualisms reduce their foraging area to plant's surface and develop specialized behaviors to protect food resources, becoming extremely aggressive (Carroll & Janzen 1973). They are able to detect physical disturbances and chemical signals, such as volatile substances from leaves, responding with rapid recruitment of numerous soldiers (Agrawal *et al.* 1998, 1999, Dejean *et al.* 2009). Some studies show that



herbivores prefer *Cecropia* trees unoccupied by *Azteca* individuals, including trees smaller than 2 m tall, which are usually not inhabited by ants or that present a smaller ant patrol activity (Downhower 1975, Schupp 1986, Vasconcelos & Casimiro 1997). However, some insects escape from predation even in trees occupied by ants. Ant genus such as *Cephalotes*, *Crematogaster* and *Pseudomyrmex*, were found foraging on *Cecropia pachystachya* Trécul (Urticaceae) branches (Vieira *et al.* 2010) and *Camponotus*, *Solenopsis* and *Procrystocerus* were found in *Cecropia insignis* (Liebm.) inhabited by *Azteca* ants (Longino 1991). Herbivore larvae such as *Ophtalmoborus* (Coleoptera: Curculionidae) are usually present in the spikes of *Cecropia* pistillate inflorescences (Berg *et al.* 2005). Schupp (1986) showed that the leaf damage made by chewer beetles was lower in ant-occupied *Cecropia obtusifolia* Bertol. than in unoccupied individuals. On the other hand, according to the same author, gall flies (Diptera) and phloem-feeding homoptera (Hemiptera) activity was not affected by presence of ants in these plants. He attributed ant ineffectiveness to gall flies small size and rapid oviposition, and to the motionless feeding pattern of homoptera that must be contacted by patrolling ants, while beetles are detectable from a distance due to leaf vibration caused by chewing and body movements. Also, when contacted, homoptera ‘explode’ off the leaf and alight undetected elsewhere on the plant.

Ants are the main predators of termites (Hölldobler & Wilson 1990). There are at least six ant genera specialized in feeding on such insects, and arboreal termitaria are negatively influenced by predator ants (Wilson 1971, Gonçalves *et al.* 2005). Termites are often attacked during mating flights or after the accidental breakage of nests and galleries (Weber 1964, Shepp 1970, Carroll & Janzen 1973). Some ant colonies, such as *Solenopsis*, *Carebara*, *Centromyrmex* and *Hypoconer*, invade termite nests and attack their eggs, nymphs and adults (Lemaire *et al.* 1986, Delabie 1995, Dejean & Feneron 1999). However, early in the 20th century about 200 ant species were described living in pacific association with termites (Wheeler 1936), including the mutualism between *Amitermes laurensis* Mjoeberg (Hymenoptera: Termitidae) and two ant species of the genus *Camponotus*, which inhabit termite mounds and protect them from attack by the “meat ant” *Iridomyrmex sanguineus* Forel (Hymenoptera: Formicidae) (Higashi & Ito 1989). Little is known about the opposite situation, i. e., the occupation of ant colonies by termites (Quinet *et al.* 2005).

Nasutitermes ephratae Rambur (Hymenoptera: Termitidae) and other arboreal termite species are often found in Southern-Pantanal. The presence of this termite species in *Cecropia pachystachya* is remarkable because such trees host entire colonies of aggressive ants, mainly of the genus *Azteca*, which do not establish peaceful association with termites. Thus, the objective of this study was to describe the *Cecropia*-ant-termite relationship and to investigate how their coexistence is possible.

We hypothesize that: 1) The frequency of termite nests

in *C. pachystachya* is lower than in neighbor trees; 2) Termite nests occur in trees with lower density of foraging ants; 3) The time that ants take to find and remove live termite baits in *C. pachystachya* trees is lower in leaves than in trunks; 4) Termite nests are fixed preferentially in the smallest and more branched trees; and 5) Termite nests are fixed preferentially distant from the canopies (where trichilia are concentrated).

Material and Methods

Study area

The Pantanal is a seasonal floodplain in tropical South America, located in the upper Paraguay River basin. It occupies an area of 147.572 km², between 80 and 150 m above sea level (Alho & Gonçalves, 2005). There is a rainy season from November to March corresponding to 72% of the total annual rainfall (1,182.5 mm) and a dry season from April to October. The average annual temperature is 25.5 °C, but the absolute maximum exceeds 40° C and the minimum is close to 0° C. The average relative humidity is 82% (Soriano *et al.* 1997). Annual floods occur during summer (February to May), although there are also multi-annual floods, which produce long periods of pronounced dry and wet seasons. Flooding results mainly from drainage difficulties caused by the low declivity of the terrain, which varies from 3 to 5 cm/km (east-west), and from 1 to 30 cm/km (north-south) (Alho & Gonçalves, 2005).

Sampling was done along the highway MS-184 (Park Road), between the coordinates 19°38’56.4’’S, 057°01’37.6’’W and 19°22’20.28’’S, 57°02’32.40’’W, in the municipality of Corumbá, Mato Grosso do Sul state, Brazil. The tree community along the road was dominated by *C. pachystachya*, *Vitex cymosa* (Verbenaceae), *Copernicia alba* (Arecaceae), *Enterolobium contortisiliquum* (Fabaceae) and *Tabebuia* spp (Bignoniaceae).

Study species

Cecropia pachystachya occurs throughout the Pantanal, where it is common in riparian flooded areas and non flooded forested patches (“capões” and “cordilheiras”) (Pott & Pott 1994). Their large-hollow internodes provide nesting space for ants, and the thin spots in their upper wall (prostomata) allow ants to circulate from inside to outside the tree (Berg *et al.* 2005). They also present trichilia formed by patches of dense indumentum abaxially at the base of the petiole of adult leaves, which produce food corpuscles called Müllerian bodies (Berg *et al.* 2005).

In the study area, *C. pachystachya* are inhabited by *Azteca ovaticeps* Forel, *A. isthmica* Wheeler and *A. alfari* Emery (Vieira *et al.* 2010). *Azteca* are territorial ants that feed on Müllerian bodies and form dense colonies in *Cecropia*. During foraging activity, workers move randomly through the

tree until they find any invader. They recruit soldiers by alarm pheromones and aggressively attack the invader (even when it is dead), killing and throwing it from the tree, and eventually feeding on it (Carroll & Janzen 1973, Quinet *et al.* 2005, Dejean *et al.* 2009).

Nasutitermes ephratae is a Neotropical termite that feeds on plant-debris and inhabits lowland areas (Thorne 1980, Vasconcellos & Moura 2009). It builds arboreal, spherical or ellipsoidal, carton nests in trunks or branches, with internal or external galleries spreading from nests toward food sources (Thorne 1980, Thorne & Haverty 2000). There are records of aggressive encounters between *Nasutitermes* individuals and *Azteca* ants (Brackman *et al.* 1983; Noirot & Darlington 2000, Quinet *et al.* 2005). Although these termites feed mainly in litter wood, they are usually found, attacked and removed by ants that inhabit *Cecropia* trees when used as baits (e. g. Oliveira *et al.* 1987, Dejean *et al.* 2009). *Nasutitermes* soldiers defend themselves throwing a viscous secretion produced by frontal glands (see Eisner *et al.* 1976).

Sampling methods

To compare the frequency of termitaria between *C. pachystachya* and its neighbor trees, we covered a path of ~ 30 km of a dirt road counting trees from several species, with and without nests. We sampled only trees whose trunks and crowns were fully visible (not hidden by other trees or vines), a total of 140 individuals of *C. pachystachya* and 78 from other tree species.

To verify whether ant patrol activity differed between *Cecropia* trees with or without termitaria, we counted the number of ants that crossed an area of 5 x 2 cm², defined by a carton frame disposed in the tip of a branch and in a leaf (near petiole insertion). The count was done after a soft tap in the branch. The procedure lasted for two minutes and was done between 8 am and 11 am, in 17 trees without termite nests and in eight trees with termite nests.

To test how long ants took to find and remove live termite baits in different parts of the trees, we used white school glue to adhere *N. ephratae* soldiers on leaves (in the abaxial surface), petioles (next to trichilia) and trunks. We repeated this procedure in 20 *C. pachystachya* individuals and observed for up to seven minutes.

To characterize the architecture of *C. pachystachya* individuals with and without termitaria, we estimated the height of trees (H), we counted the number of branches per tree (N) and calculated the ratio branches: tree height (N/H) as an indicator of canopy density, in 90 trees, 22 of which had termitaria. Histograms of H and N/H of trees were made, highlighting the occurrence of termite nests in the population of *C. pachystachya*.

In order to have an indication of termitarium distance from the canopy, we estimated the height (h) of 27 nests and then calculated the ratio nest height: tree height (h/H) and

separated the results into four categories. Thus, the closer the ratio h/H was to zero, the nearest to ground the nest was. We also determined the tree structure in which 18 nests were fixed (trunk, fork, lower or upper branches).

Data analysis

We compared the frequency of termite nests between *C. pachystachya* and its neighbour tree species with the chi-square test. Ant patrol activity in leaves and branches were compared between *C. pachystachya* individuals with and without termitaria using the Student's t test.

Results and Discussion

In the study area, termitaria were composed by a carton nest with rigid galleries made of dirty and fibrous material, spreading toward branches (Fig 1).

While ants were present in all the *Cecropia pachystachya* trees with which we had direct contact, termite nests were present in 42.9% of the *C. pachystachya* individuals and in 36.8% of the other tree species, with no statistical difference between them ($\chi^2 = 0.105$, $p = 0.74$, $n = 218$).

Ants crossed the defined 10 cm² area in *C. pachystachya* individuals with and without termite nests, respective-



Fig 1: *Cecropia pachystachya* Trécul (Urticaceae) in South-Pantanal, Brazil, with a nest of *Nasutitermes ephratae* Rambur (Termitidae). Note the galleries spreading in trunk and branches.

ly, 70.75 ± 27.12 and 56.47 ± 18.16 times in branches, and 3.63 ± 2.56 and 10.94 ± 3.80 in leaves (average $\pm$ standard error of mean). Ant patrol activity was similar between trees with and without termite nests in branches ($t = -0.44$, $p = 0.60$, $df = 23$, $n = 25$) and in leaves ($t = 1.25$, $p = 0.22$, $df = 23$, $n = 25$).

Thirty five per cent of termites used as baits were found and attacked by ants. In some cases, especially in trunks, they were found but were not attacked. Attacks occurred in 65% of 20 trials in petioles, 25% in leaves and 15% in trunks. The time elapsed for attacks were 112.54 ± 32.53 seconds ($n = 13$) in petioles, 151.40 ± 56.94 s ($n = 5$) in leaves and 67.77 ± 28.26 s ($n = 3$) in trunks. It was not possible to compare statistically the time of ant attack due to the small size of samples. We also observed that the galleries spreading from nests were not examined or attacked by ants.

In the sampled population ($n = 90$), *C. pachystachya* individuals varied from 3-12 m tall, but termitaria ($n = 22$) occurred only in trees to 7-11 m tall, with a modal class of frequency in 8 m that coincided with the population mode (Fig 2).

The number of branches per height varied from 0.20 – 6.86. Termitaria occurred in trees with one to 6.86 branches per meter. Again, the modal classes of trees with termitarium coincided with the modal class of branching in the population, i. e. 1.51 – 2.50 branches per meter (Fig 3).

Almost fifteen percent (14.8%) of termite nests were fixed in the lower one-quarter of trees, 63% in the second, 18,5% in the third and only 2.7% in the fourth one-quarter (from bottom to up). Most of them were located at the base of the lower branches (60%), followed by the fork and upper branches (15% each), and finally the trunk (10%).

Opposite to our hypothesis' predictions, *Nasutitermes ephratae* termitaria occur in *Cecropia pachystachya* individuals in the same frequency than in non-mirmecophyte trees, as well as in *C. pachystachya* individuals with intense or modest

ant patrol activity. Although it is an unexpected result, considering the mirmecophilic life story of *Cecropia*, we suggest that physical mechanisms mediate the relationship between *N. ephratae* and ants of the genus *Azteca*, namely the occupation of distinct parts of the tree by termites and ants, and the physical isolation of termitaria (nests and galleries) by fibrous structures.

Although the distribution of *C. pachystachya* individuals with termitarium have the same modal class than the population as a whole (regarding tree height and number of branches per height), termite nests did not occur randomly. Termite nests were found only in a restricted range of tree height within the population studied. By their turn, ants are expected to occur in *C. pachystachya* trees taller than 2 m after Downhower (1975) and Schupp (1986).

One might expect that termites fixed their nests preferentially on small trees, which are not inhabited by ants or

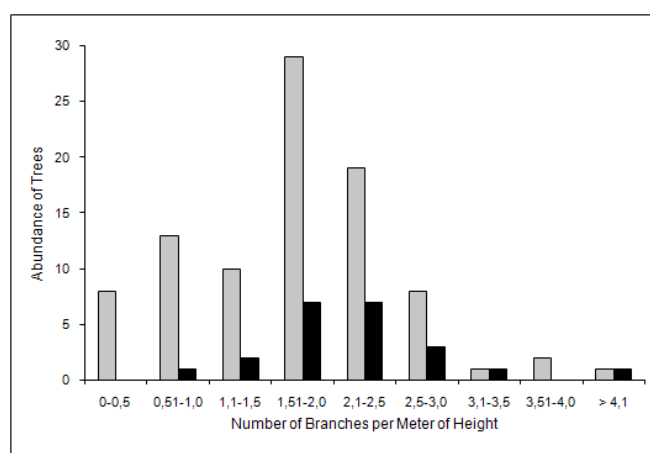


Fig 3: Abundance of individuals of *Cecropia pachystachya* Trécul (Urticaceae) in Pantanal Sul, Brazil, regarding their ratio branches: height of the trees. Black bars: trees with termitarium of *Nasutitermes ephratae* Rambur (Termitidae); gray bars: trees without termitarium.

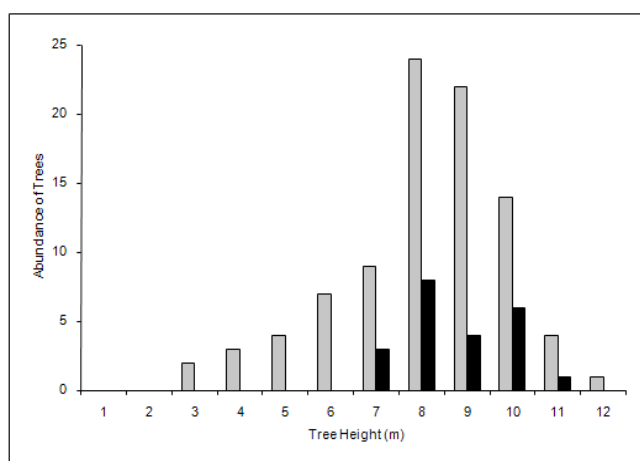


Fig 2. Abundance of individuals of *Cecropia pachystachya* Trécul (Urticaceae) in Pantanal Sul, Brazil, regarding their height. Black bars: trees with termitarium of *Nasutitermes ephratae* Rambur (Termitidae); gray bars: trees without termitarium.

present a smaller ant patrol activity, being preferred by herbivores (Downhower 1975, Schupp 1986). However, besides the scape of predation, physical support must be a determinant of termitaria establishment, as it is suggested by the absence of termite nests in *C. pachystachya* individuals smaller than 7 m and its scarcity in trees with less than 1.51 branches per meter of height. In fact, Cunha (2000) found that *Constrictotermes cyphergaster* Silvestri (Isoptera: Termitidae) usually fixed their nests in trees with intermediate trunk circumference.

Although termite nests predominated in trees with 1.51 to 2.5 branches per height (the modal class of branch density in the population), they were disproportionally under-represented in the smaller classes. Termitaria predominance in more branched trees once more indicates that its occurrence is not random. Densely branched individuals may provide more opportunity for nesting and better support conditions, and although they have more dense canopies, it does not necessarily imply in larger density of trichilia and therefore greater

patrol by ants, since the lower branches often had no leaves or ants. In other species of mirmecophyte *Cecropia* it was observed that ant patrol differed between leaves in different portions of the canopy, as well as herbivory. In *Cecropia peltata* Linnaeus, 53.9 % of ants were located in leaves in the upper canopy and only 11.2 % in the leaves of basal branches, resulting in proportional rates of herbivory (Downhower 1975). In *C. pachystachya* termite nests were more frequent in the lower half of the trees and in lower branches, i. e. distant from young-active trichilia in the top canopy, where ant patrol may be more intense. This suggests that there is a displacement of the location of termites and ants, avoiding overlap. This finding is corroborated by the fact that termites are rarely attacked by ants in trunks, but they are attacked and removed when experimentally placed in leaves or petioles, which are close to trichilia.

One hypothesis to explain the coexistence of *Azteca* sp. and *N. ephrateae* in *C. pachystachya* is that they do not engage in agonistic encounters. However termites were readily attacked and removed from leaves and petioles, and sometimes from trunks when experimentally introduced. Ant's attacks to termite would probably be more frequent, especially in branches, if they did not construct galleries with fibrous and dust material.

We suggest that, after a period of large vulnerability during the establishment of termitaria, nest and galleries built with rigid material contribute to the coexistence of these groups of insects, allowing termites to move protected inside them, even in the canopy. This strategy is consistent with the one adopted by other termite species that coexist with ants without predation. In cases that ants colonize termitaria, these insects often dwell distinct portions. For example, *Crematogaster rochai* Forel (Hymenoptera: Formicidae) inhabit termite nests of *N. ephrateae* and *Nasutitermes corniger* Motschulsky (Hymenoptera: Termitidae) and maintains a physical separation with its hosts by plugging the cells that they inhabit with fibrous material (Quinet *et al.* 2005).

The observed trend of tree occupation is also in agreement with the distribution of vines in *Cecropia*, that, as well as herbivores, are cut and removed by ants (Janzen 1969, Downhower 1975, Vasconcelos & Casimir 1997). Vines are often found on the stem and the lower parts of the lower branches, but not higher up (Berg *et al.* 2005). This was attributed to the pattern of branches' growth and loss – lower branches depart from the trunk in angles of 45 degrees and lower leaves are continuously lost –, thus affecting the growth of vines (Berg *et al.* 2005). We suppose that in mirmecophyte *Cecropia* it may also be attributed to the pattern of tree occupation by ants and their vine cutting activity.

In conclusion, this study shows that *N. ephrateae* nests occur at the same frequency in *Cecropia* individuals than in non mirmecophyte trees, as well in *Cecropia* individuals with intense or modest ant foraging activity. The determinants of nest occurrence are probably the mechanical support offered by trees and nest distance from trichillia, i. e. from the area

more intensively patrolled by ants, that may influence specially the colonization time. After that, isolation of termites inside fibrous nests and galleries may contribute to their coexistence with ants. So, our results indicate that the coexistence between termites and ants in *C. pachystachya* may be possible due to spatial segregation of their colonies, avoiding agonistic interactions.

To the best of our knowledge, this is the first report of the occurrence of termites on *Cecropia* trees, although this is a common association in the study area. Further research on the interaction between these insects would help to understand how their coexistence is made possible, as well as the influence of the flood pulse in the Pantanal in the evolution of this ecological relationship.

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