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CHRISTOPHER MARTIUS

Termite nests as structural elements of the Amazon floodplain forest

Abstract

In periodically flooded várzea forests of the Amazon River the most dominant termite constructions were arboreal nests of 5 wood-feeding *Nasutitermes* spp. with densities of 37-68 nests per hectare and nests of the geophagous *Anoplotermes* sp. A (Apicotermitinae) with 3-333 nests per hectare. A bark-feeding species, *Anoplotermes* sp. C, which covers tree trunks with soil coatings, showed densities of up to 389 „covered trees" per hectare.

Of all *Nasutitermes* nests in one of the investigated plots, 73% were „living" nests inhabited by termites (2/3 „juvenile" and „adult", 1/3 „senile" nests), and 27% were abandoned („dead") nests. The decaying nests or nest parts („dead" and „senile" nests together; 51%) represent a spatial resource which can be used by secondary colonizers. *Nasutitermes corniger* nests accounted for 69-86% of the *Nasutitermes* nests and for 31-70% of the total nest volume. The surface of the chambers in all dead nests on trees of *N. corniger* was calculated to 197-408 m^2 ha^{-1} (up to 1/25 ha per ha of forest; 0.43 ± 0.06 m^2 per liter of nest volume). One ant species, *Dolichoderus bispinosus*, occupied 62% of the living and 69% of the dead nests of *N. corniger*.

The nests of *Anoplotermes* sp. A are built in the soil during the dry season. At the beginning of the flood season, the termites erect voluminous epigeic nest extensions which reach beyond the future flood level and where the colonies survive the flood. Colonies of *Coptotermes, Rhinotermes,* and *Anoplotermes* sp. D, and other arthropods as well, use these constructions for survival of the flood, too. The submerged parts of the *Anoplotermes* sp. A nests are colonized by Oligochaeta which accelerate the decomposition of the flooded nest parts. This results in an almost complete turnover of the nest constructions every year, and almost no dead nests are left for potential invaders.

Anoplotermes sp. C builds 0.5-0.8 cm thick soil coatings which cover the tree trunks. The species affected 23% of all trees >3 cm Ø and extended the soil coatings up to a height of 12-14 m on the trunks. These „covered feeding places" probably allow the survival of these bark-feeding termites and other soil arthropods during the flood.

Kurzfassung

Termitennester als strukturelle Elemente im amazonischen Überschwemmungswald

In periodisch überschwemmten Várzea-Wäldern des Amazonas waren die Baumnester von 5 holzverzehrenden *Nasutitermes*-Arten mit Dichten von 37-68 Nestern pro Hektar und die Nester der geophagen Art *Anoplotermes* sp. A (Apicotermitinae) mit 3-333 Nester pro Hektar die häufigsten Termitenbauten. Eine rindenfressende Art, *Anoplotermes* sp. C, die die Baumstämme mit Schichten aus Erdmaterial überzieht, wies Dichten von bis zu 389 „überdeckten Stämmen" pro Hektar auf.

Von allen *Nasutitermes*-Nestern auf einer der Untersuchungsflächen waren 73% „lebende" Nester (von Termiten bewohnt; 2/3 „juvenile" und „adulte", 1/3 „senile" Nester), und 27% waren verlassene („tote") Nester. Die verfallenden Nester oder Nestteile („tote" und „senile" Nester zusammen; 51%) stellen eine Raumnische dar, die von sekundären Besiedlern genutzt werden kann. Der Anteil der Nester von *Nasutitermes corniger* betrug 69-86% aller *Nasutitermes*-Nester und 31-70% des Gesamt-Nestvolumens. Die innere Oberfläche der Nestkammern in allen toten Nestern von *N. corniger* auf Bäumen wurde auf 197-408 m^2 ha^{-1} berechnet (= bis zu 1/25 ha pro Hektar Wald; 0.43 ± 0.06 m^2 pro Liter Nestvolumen). Eine Ameisenart, *Dolichoderus bispinosus*, besetzte 62% der lebenden und 69% der toten Nester von *N. corniger*.

Die Nester von *Anoplotermes* sp. A werden während der Trockenzeit im Boden errichtet. Zu Beginn der Überschwemmungsperiode bauen die Termiten voluminöse Anbauten, die über den kommenden Hochwasserspiegel herausragen, und wo die Termiten die Überschwemmung überdauern. Kolonien von *Coptotermes, Rhinotermes,* und *Anoplotermes* sp. D sowie andere Arthropoden überdauern ebenfalls die Flut in diesen Bauten. Die gefluteten Teile der Nester von *Anoplotermes* sp. A werden von Oligochaeten besiedelt, die den Abbau dieser Nestteile beschleunigen. Das Resultat ist ein fast vollständiger Umsatz aller Nestkonstruktionen in jedem Jahr, so daß für potentielle sekundäre Besiedler kaum tote Nester übrigbleiben.

Anoplotermes sp. C überzieht die Stämme der lebenden Bäume mit 0.5-0.8 cm dicken Schichten aus Bodenmaterial. Diese fanden sich auf 23% aller Bäume >3 cm Ø und reichten bis zu einer Höhe von 12-14 m auf den Stämmen. Diese „überdachten Fraßplätze" erlauben vermutlich das Überleben dieser rindenfressenden Termiten und anderer Bodenarthropoden während der Überschwemmungsperiode.

Resumo

Ninhos de térmitas como elementos estruturais em florestas inundadas da Amazônia

As construções de térmitas mais dominantes em florestas de várzea periódicamente inundadas do río Amazonas foram ninhos arbóreos de 5 espécies xilófagas de *Nasutitermes* spp. com densidades de 37-68 ninhos por hectare, e ninhos da espécie geófaga *Anoplotermes* sp. A (Apicotermitinae) com 3-333 ninhos pro hectare. *Anoplotermes* sp. C, uma espécie que se alimenta de casca e cobre os troncos das árvores com coberturas de material de solo, ocorreu em densidades de até 389 „árvores cobertas" pro hectare.

De todos os ninhos de *Nasutitermes* numa das áreas em investigação, 73% foram ninhos „vivos" inabitados por cupins (2/3 dos ninhos „juvenis" e „adultos", 1/3 „senis"), e 27% foram ninhos abandonados („mortos"). Os ninhos ou partes de ninhos em decadência (ninhos „mortos" e „senis" juntos; 51%) representam um espaço que pode ser usado por colonizadores secundários. Ninhos de *Nasutitermes corniger* representaram 69-86% dos ninhos de *Nasutitermes* e 31-70% do volume total dos ninhos. A área calculada da superfície de todas as câmaras em todos os ninhos mortos de *N. corniger* foi de 197-408 m^2 ha^{-1} (até 1/25 ha por hectare de floresta; 0.43 ±

0.06 m^2 por cada litro de volume de ninho). Uma espécie de formiga, *Dolichoderus bispinosus*, ocupou 62% dos ninhos vivos e 69% dos ninhos mortos de *N. corniger*.

Os ninhos de *Anoplotermes* sp. A são construídos no solo durante a estação seca. No início da enchente, estes cupins constroem extensões epígeas dos seus ninhos que são mais altos que o futuro nível da enchente, e onde as colônias sobrevivem a inundação. Colônias de *Coptotermes, Rhinotermes,* e *Anoplotermes* sp. D além de outros artrópodos usam estas construções para sobreviver a enchente. As partes submersas dos ninhos de *Anoplotermes* sp. A são colonizadas por Oligochaeta que aceleram a decomposição das partes inundadas dos ninhos. Isto resulta numa reciclagem quase total de todos os ninhos em cada ano, e quase não sobram ninhos mortos desta espécies para possíveis invasores.

Os cupins de *Anoplotermes* sp. C constroem camadas de solo sobre troncos de árvores, de uma grossura de 0.5-0.8 cm. Estas construções afetaram 23% de todas as árvores >3 cm Ø e extenderam até uma altura de 12-14 m nos troncos. Estes „lugares de forageio cobertos“ provávelmente permitem a sobrevivência desta espécie e de outros artrópodos de solo durante a inundação.

Author

Dr. Christopher Martius, II. Zoologisches Institut der Universität Göttingen, Abteilung Ökologie, Berliner Str. 28, D-37073 Göttingen, Germany.

1. Introduction

Termites are important decomposers in tropical ecosystems. Their social life requires the construction of nests which provide isolation from climatic factors and from predators. This building behaviour puts termites among the few animals which accomplish work in the physical sense of the word (Brafield & Llewellyn 1982). Termitaria, made from degraded organic matter, feces, and saliva, are generally solid structures, which often persist for a long time even after the death of the colony. These structures are important and frequently determining characteristics of many landscapes, particularly of savannas („Termitensavannen“: Troll 1936; also Lee & Wood 1971, Grassé 1984, 1986, Sattaur 1991). Wood & Sands (1978) recognized several aspects of the „role“ of termites in ecosystems:

- physical and chemical change of soil characteristics, particularly the disturbance of soil profiles and re-allocation of organic matter;
- modification of the vegetation: either damage (due to feeding on plant seedlings, roots, leaves or due to ring barking), or benefits (from changed soil structure or enhanced fertility);
- the building of more or less persistent constructions which often considerably modify and structure the environment, and to which other fauna can adapt. In the German literature these structures are referred to as „Biochorion“, which is translated as „minor habitat“ (Schaefer & Tischler 1983).

The first two aspects are matter of many studies (to mention only a few: Lee & Wood 1971, Wielemaker 1984; Spain et al. 1985, César et al. 1986, Lal 1987, Lobry De Bruyn & Conacher 1990). Regarding the third aspect, there exists much information about the fauna associated with termites (termitophiles: Kistner 1969, 1990, Wilson 1971, Fontes 1977, 1978, Jacobson & Pasteels 1992, Costa-Leonardo & Soares 1993) and their nests (termitariophiles: Berg 1900).

Araujo (1970), for example, provided extensive lists of mostly non-obligatory associations between termites and non-termite fauna in the neotropics. The amazing behavioural adaptations shown by some termitariophilous bees have been described in detail by Kerr et al. (1967) and Camargo (1970, 1984). Redford (1984) identified *Cornitermes cumulans* as a „keystone species“ in Brazilian savannas („cerrado“), because it is the dominant mound builder whose constructions are an important structural element used by many other arthropods. Bandeira (1983) found, on average, 320-1180 non-termite cohabitants per dm^3 nest volume in *Cornitermes ovatus* and *Nasutitermes minimus* in eastern Amazonia, mostly Acari (92.2-92.7%), Collembola (1.8-4.2%), and ants (0.2-4.8%). Apolinário (1993) identified various groups of Plathelmintes, Mollusca, Annelida, Arthropoda, and Vertebrata associated with termite nests in terra firme rain forest. And Martius et al. (1994) recorded the fauna associated with abandoned termite nests in floodplain forests.

Peculiar earth mounds (murundus) in southern Brazilian savannas are sometimes the result of termite activity (Oliveira 1992); although in other cases these landscape patterns seem to be produced by erosion processes (Furley 1986, Haridasan 1990). In closed forests, termite constructions are not so conspicuous as in savannas, but their high density (Bandeira 1978, 1979, 1983, 1989, Martius in press) suggests that they are also important features here. The present paper is an attempt to establish an inventory of structures and spaces offered by termite nests in floodplain forests (várzea = white water floodplains; Sioli 1956, Prance 1980). In this ecosystem, characterized by periodic floodings (Junk 1984, 1989, Junk et al. 1989), and which covers about 150.000 km^2 of Amazonia (Sippel et al. 1992), the termite density is high (Martius 1989, in press), and their population structure is simple and relatively easy to study.

In the following, the terms „nest“, „mound“ or „termitarium“ are used as synonyms for the constructions of the termites, whereas „colony“ refers to the socially organized group of termites living in one or several of such nests. (Some colonies extend over various nests; cf. Martius 1989; this is neglected here). Nests in the várzea are either arboreal (on trees, being connected to the ground only by galleries) or „intermediate“ between arboreal and soil nests (a term introduced by

Apolinário (1993), which refers to nests attached to trees but still in broad contact with the ground, and normally made of soil). Nests can also be completely confined to dead wood. „Galleries" are the covered runways built by termites to cover the trails which lead to their feeding places.

A termite colony („living" nest) passes through various life stages (Noirot 1969):

1. the juvenile phase, with a high percentage of larvae in the colony, when the nest grows according to the size requirements of the colony;
2. the adult phase, marked by the formation of sexual reproductives (alates) and the nuptial flight(s), which represent a severe loss of living biomass to the colony (Wood & Sands 1978);
3. the senile phase, with reduced or declining individual numbers. Abandoned peripheral nest chambers become subject to erosion; nest walls break down and the open chambers represent a spatial niche which is soon invaded by animals of other taxa.

A natural population comprises colonies in all these phases plus the „dead" nests which have been abandoned by their colonies, generally due to the death of the termites. Dead nests are completely, and senile nests at least partially accessible for secondary invaders.

2. Material and Methods

Locality

The study was carried out on 3 sites on Ilha de Marchantaria, an island in the River Amazon („Solimões"; i.e. the Amazon above its confluence with Rio Negro), near Manaus, Brazil (see Worbes 1986, and Martius 1989, for a site description). Site P (an area of 1.465 ha) was a forest stand in the early secondary stage („lightwood association"; Worbes et al. 1992) which had been deforested 20 years ago. The second site (Z = 0,601 ha), about 80 years old, corresponds to the late secondary stage of Worbes et al. (1992). Site C, similar and near to site Z, was established to study a population of *Anoplotermes* sp. A.

Only the higher areas of the floodplains, which are flooded for shorter periods, are covered by forest. Many of the more accessible sites are frequently logged for wood, and secondary forest evolves which seems to be able to support higher termite densities than the later successional stages (Martius 1989 and unpubl.).

Material

The *Nasutitermes* spp. were determined by Dr. S. Bacchus, then Natural History Museum, London (U.K.), and Dr. Luis R. Fontes, then Universidade de São Paulo, São Paulo (Brazil). The species belonging to the subfamily of Apicotermitinae were grouped into morphospecies and placed into the genus *Anoplotermes*; however, they do not agree with any description given by Fontes (1985, 1986) for the 5 existing genera of Apicotermitinae. *Anoplotermes* sp. A is a new species and probably a new genus (Fontes in litt. 1992).

The ant *Dolichoderus bispinosus* (Olivier, 1791) (formerly *Monacis bispinosa*, cf. Martius 1989) was determined by comparison with specimens from the Entomological Collection of the INPA, Manaus.

Oligochaeta found in termite nests were identified by Dr. G. Righi, Universidade de São Paulo.

Methods

The termite nests in the plots were marked and mapped; maximum height and circumference were measured in *Nasutitermes* nests, and maximum height and diameter in nests of *Anoplotermes* sp. A. In *Anoplotermes* sp. C, maximum height of the constructions on the tree stems was recorded only. Termites were sampled from nests or connected galleries. Nests with termites were considered as „living" independently of how many individuals were found. Nests without termites were recorded as „abandoned" (they are free of termites, but can be inhabited by „secondary" colonizers, mostly arthropods). Ant colonies associated with termite nests were recorded without regarding their colony size.

For Nasutitermitinae, the nest volume V_{Nest} was calculated on the basis of a simplified geometrical model of the nest shape (a cylinder combined with two half spheres), using nest height H_N and maximum circumference U_N as follows:

$$V_{Nest} = \pi r^2(H_N-2r)+4/3\pi(U_N/2\pi)^3 \text{ with } r = U_N/2\pi$$

I neglected the generally small volume of the tree trunk around which the nest was built.

The external surface of the *Nasutitermes* nests was calculated according to:

$$O_{Nest} = U_N(H_N+U_N/\pi)$$

The volume of *Anoplotermes* sp. A nests was calculated from their height H_N and maximum diameter D_N (= distance from nest surface to tree surface) using as basic shape a half cylinder (in which $D_N = r_{Cylinder}$), according to:

$$V_{Nest} = \pi D_N^2 H_N/2$$

and the nest surface was calculated from:

$$O_{Nest} = \pi D_N(D_N+H_N)$$

The real area of the inner surface of the chambers in a termite nest is difficult to assess. The „idealized internal surface" of *Nasutitermes* nests was determined from transverse and radial slices which were cautiously cut from a nest of *N. corniger*. On the surfaces exposed by the cut, areas of 4 x 4 cm were chosen at random, from which all nest walls which crossed the cutting plane were copied to a transparent sheet. The length of the lines on the sheet was then determined with the help of a map measurer (a device used in determining distances on maps). Each single area (n = 8) was measured 5 times, and the average calculated. This procedure gave a value of the total length of all nest walls crossing the cut. If the cutting plane is seen as one side of a block, 4 x 4 cm large and wide, and 0.5 cm deep (= 8 cm^3), the total internal surface of this block can be calculated by multiplying the average extension of the nest walls in the block by 0.5, and then by 2 (each wall has two sides). The total internal surface of one liter nest volume is then calculated by multiplying the block surface by 125. Due to the breaking of nest parts during cutting, this method probably underestimates the inner surface (at an estimated rate of 10%) of the nests of *N. corniger*. The nests of *N. macrocephalus* and *N. surinamensis* were not measured, but the individuals of these species are larger and produce wider nest chambers, and probably therefore the internal area of the nests of these species is smaller.

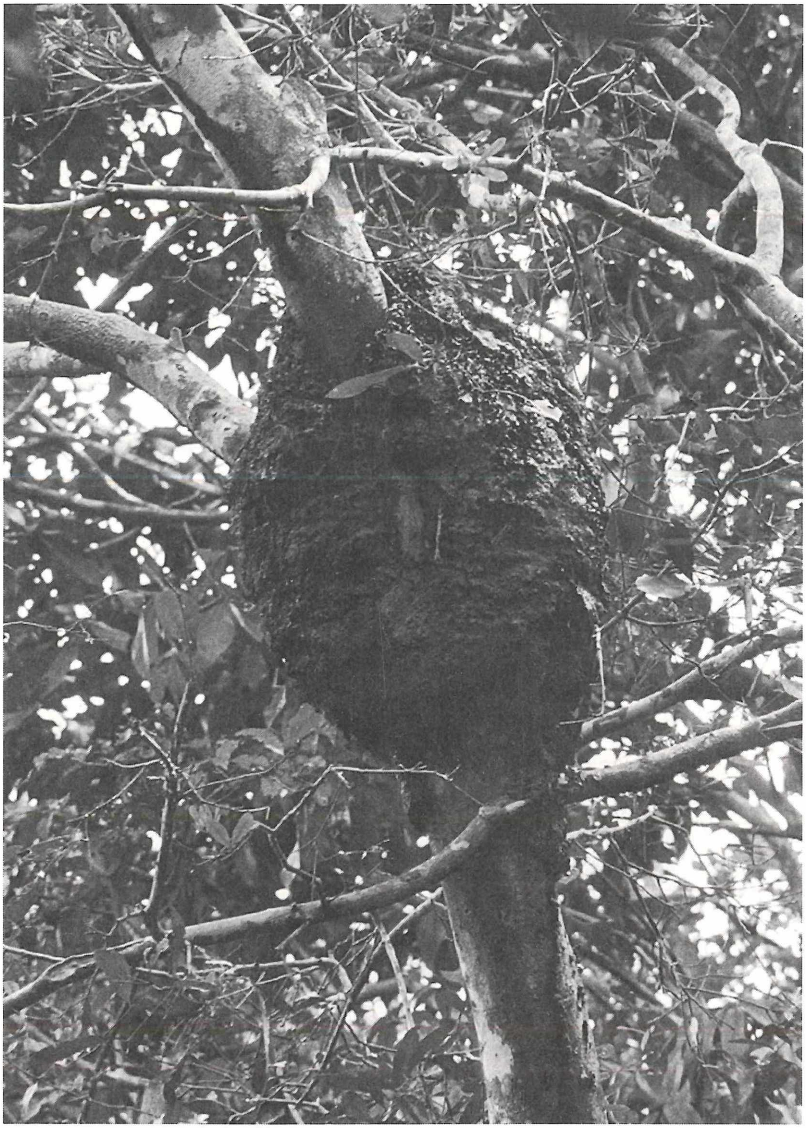

Figure 1. View of a nest of *Nasutitermes surinamensis* on the tree species *Crataeva benthamii* in várzea forest, Ilha de Marchantaria. Nest height approx. 0.9 m, nest above ground approx. 6.5 m. Note the eroding nest parts on the upper right side of the nest.

The *Nasutitermes* nests on site P were surveyed in monthly intervals between 17.6.1985 and 8.4.1986 (due to technical reasons, the annual cycle could not be completed); the number of living and dead nests (on trees and on the ground), and the dates of the death of old nests and advent of new nests, as well, were recorded.

Tree trunks (>3 cm diameter) and the occurrence of used and abandoned *Nasutitermes* galleries on the trunks were counted within an area of 900 m^2 (12 plots of 5 x 15 m; Tab. 5) on site P (>1 gallery of the same termite species per tree was counted as one case). The idealized trunk surface from the ground to a height of 10 m was calculated from these data using the dbh (diameter at breast height) of the trees.

3. Results and Discussion

Thirteen termite species were found in the várzea (Martius 1989) (tab. 1). From a structural viewpoint, the most abundant species among them divide into 3 groups according to their nest types: 5 wood-feeding *Nasutitermes* species with arboreal nests, the geophagous *Anoplotermes* sp. A living in intermediate nests, and the bark-feeding *Anoplotermes* sp. C with intermediate constructions, too.

Among the less frequent species, *Termes medioculatus* and *Microcerotermes* build arboreal nests from

Table 1. Termites species, nest types and feeding biology in várzea floodplain forest (Ilha de Marchantaria and * Ilha do Careiro).

Wood feeders	
Tree nest builders	*Nasutitermes corniger* *Nasutitermes tatarendae* *Nasutitermes macrocephalus* *Nasutitermes surinamensis* *Nasutitermes ephratae* *Microcerotermes* sp.*
Nests in dead wood	*Rhinotermes marginalis* *Rhinotermes* sp. 1 *Coptotermes* sp. 1
Soil feeders	
Intermediate nests (epigeic/arboreal)	*Anoplotermes* sp. A *Anoplotermes* sp. C
Arboreal nests	*Termes medioculatus*
Inquilines (in nests of other species)	*Anoplotermes* sp. D

earth and carton laterally on tree trunks. *Coptotermes* and *Rhinotermes* species generally establish their nests within decaying moist wood. Considerable numbers of Kalotermitidae colonies must exist in the várzea (REBELLO & MARTIUS in press), but their habits are very cryptic and they were never recorded in termite nest assessments (MARTIUS 1989, CONSTANTINO 1992).

3.1 Nest types

Arboreal *Nasutitermes* nests

These more or less rounded nests, made from carton material (= digested cellulosic material), are attached to trees in varying heights (2-15 m) (fig. 1-2). Although the nests of the 5 *Nasutitermes* species are all very similar in their general features, they differ in characteristical, species-specific manners which allow to distinguish the species in the field, even after the death of the colony (MARTIUS 1989, cf. also THORNE 1980).

Intermediate nests

Anoplotermes sp. A termitaria are long soil „columns" attached to the sides of tree trunks, from the ground up to a height of 4.8 meters on average (MARTIUS 1990, and unpubl. data) (fig. 3-5). The nests of *Anoplotermes* sp. C are thin soil coatings which extend irregularly over the tree trunks up to a maximum height of 14 m (fig. 6). Some of the tree trunks in their lower parts are completely covered by these crusts which are not thicker than 0.5-0.8 cm.

Table 2. Average nest volume and surface for 5 *Nasutitermes* species of the várzea floodplain (average ± standard deviation).

Species		Nest volume [liter/nest]	Nest surface [dm^2/nest]
N. corniger	92	35.36 ± 41.40	48.7 ± 37.1
N. ephratae	6	118.59 ± 89.97	127.2 ± 74.7
N. macrocephalus	6	350.80 ± 121.52	257.3 ± 69.4
N. surinamensis	5	405.41 ± 323.92	279.4 ± 191.3
N. tatarendae	21	46.34 ± 67.85	61.0 ± 60.3

3.2 Termitarium inventories

3.2.1 Arboreal *Nasutitermes* nests and galleries

Nests

The largest nests were those of *Nasutitermes surinamensis* and *N. macrocephalus* (tab. 2); their volume was, on average, 6-11 times higher than in *N. corniger* and *N. tatarendae*, and their external surface about 4-6 times. However, due to the different size of young and old nests the intraspecific nest size variation was high.

Table 3 shows the number, total volume and total surface of the *Nasutitermes* nests on the two várzea plots. The nest density (n/ha) on site P was about 2 times higher than on site Z, the total nest volume was 2.7 times, and the total nest surface 2.4 times higher. For all nests, total volume amounted to 2.0-5.3 m^3 ha^{-1}, and total surface to 2.2-5.3 m^2 ha^{-1}, respectively, for site Z and P.

Nasutitermes corniger had the highest nest density and volume of all species. It accounted for 69.1% of the nest number and for 31.4% of the total nest volume on plot P, and for 86.3% of the nests and 69.5% of the nest volume on plot Z. Approximately 3/4 of all *N. corniger* nests on trees on site P were „living" nests (juvenile, adult, and senile), and 1/4 were „dead" (fig. 7). Dead and senile nests together amounted to half of the nest number. Figure 7 shows the composition of the nests as a snap shot, but table 4 shows that the proportion of living and dead nests remained almost stable in the course of a year.

The idealized inner surface of nests of *N. corniger* was determined to 0.43±0.06 m^2 per l of nest volume (fig. 2), which for all living *N. corniger* nests on site P (cf. tab. 3) gave a total internal surface area of 716 m^2 ha^{-1} (1/14 ha per hectare of forest). The internal surface area of all dead nests amounted to 265 m^2 ha^{-1} I estimate that dead parts of senile nests accounted for approximately 20% of the total nest volume. Corrected by this figure, the internal surface area in inhabited and abandoned nests of this site amounted to 573 and 408 m^2 ha^{-1}, respectively (1/17 and 1/25 ha per ha forest). On site Z a calculated internal surface of 384 and 197 m^2 ha^{-1} was available in living and dead *N. corniger* nests (using the same assumption for senile nests).

Figure 2. A tangential view of the internal structure of *Nasutitermes corniger* nest. Same size as in Figure 4.

Nests of senile colonies often fall from the tree when the attachment of the nest loosens. A few nests are knocked down by falling trees or branches. About half (8 of 15) of the dead nests on the ground registered in 1986 (tab. 4) were living nests which fell to the ground while the colony was dying. The other half (7 of 15) were nests which had died on the tree and fallen later.

Roughly 80% of the dead nests remained longer than 7 months on the tree (n=18), 17% longer than 10 months (fig. 8a). Dead nests on the ground vanished faster (fig. 8b). There, the higher humidity (particularly after the flood) and increased abundance of decomposers on the ground are likely to accelerate the decay of the nests. Nests on the ground are not protected from flooding and can only temporarily be used by secondary colonizers.

The total number and volume of dead nests on the ground is given in table 3. Their external surface was broken and therefore not assessed. Their internal surface area amounted to 88-231 m^2 ha^{-1} (using the average size of 35.36 l per nest from table 2; they were mostly nests of *N. corniger*).

It is mainly the internal surface of the dead and eroding nests which is interesting in the context of this paper. The numbers seem relatively high; however, the calculated surface of only the lower parts of the tree trunks (between 0 and 10 m from the ground) amounted to 12 650 m^2 ha^{-1} in plot P. In comparison to this value, the deserted *Nasutitermes* nests certainly represent only a very small area to be occupied by secondary fauna. (The trunk surface is a roughly calculated value, not the real surface which includes spaces in fissures of the bark, hollow branches etc.; in addition the surface of the branches, twigs, and leaves in the crown has been neglected.) However, tree trunks and termite nests are only in part comparable, as termite nest matter is more soil-like, more malleable and as such represents a substrate probably preferred by many (soil) arthropods. In fact, dead termite nests are poorly inhabited by other fauna, except for ants (cf. 3.3.2) and for the periods when the ground is flooded (Martius et al. 1994).

Galleries

Total gallery lengths of 45-150 m were recorded for 5 nests of *Nasutitermes macrocephalus*. Termites abandon galleries when new feeding places are found, and when nests die. The gallery walls break up, and other arthropods, e.g. small ants and springtails, invade them. Sometimes, other termite colonies of the same or different species „reactivate“ such unoccupied runways. I found that abandoned galleries remained for several years on the tree trunks. They persisted even flooding and were only destroyed by mechanical impact (falling branches, climbing animals). A count of used and deserted galleries on trunks (tab. 5) shows that, on average, 19.3% of all trunks (emergent and understorey trees) had at least one abandoned gallery (333 galleries per ha). On the assumption of an average tree height of 20 m and only one gallery running linearly from the base to the top of the tree I calculated a total gallery length of 5.7 km per hectare. This does not take into account the galleries within the litter layer, but their contribution to space for secondary colonizers in the litter is certainly insignificant.

3.2.2 Intermediate nests I: *Anoplotermes* sp. A

Living nests

Anoplotermes sp. A seems to be particularly adapted to the periodical floodings (Martius in press). The colony starts with a soil nest, which later is transformed into an epigeic nest extending in height beyond the water level of the coming flood, which allows the survival of the colony (fig. 3). Contrary to the nests of *Nasutitermes*, the nests of this species consist of thick layers of soil containing only small tunnels or nest chambers (fig. 4). The internal surface area was not determined.

The density of this species varied between 3 (site Z) and 219 (site P) nests per ha, due to differences in

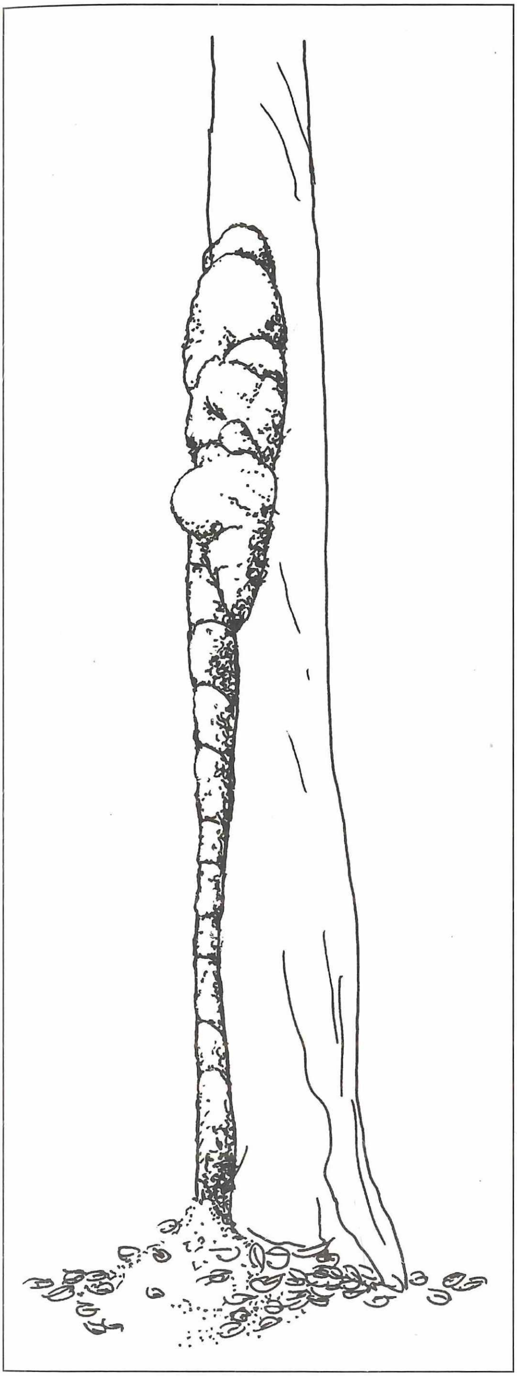

Figure 3. Epigeic nest parts of *Anoplotermes* sp. A in várzea forest, Ilha de Marchantaria. Nest height approx. 4 m from ground to top Note the heap of old nest matter at the foot of the tree. Drawn from a photograph by the author.

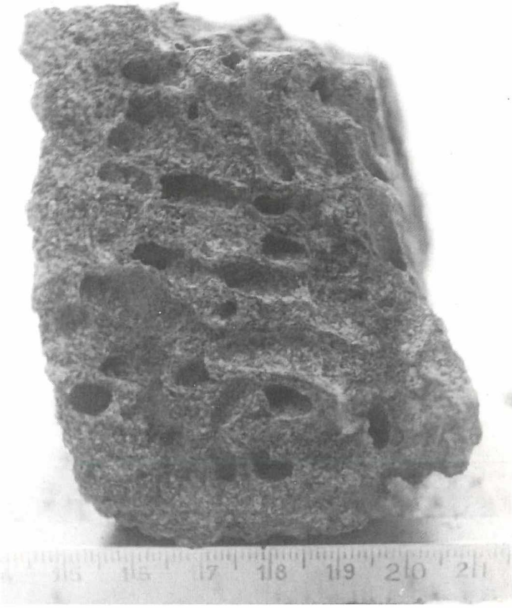

Figure 4: Radial view of the internal structure of a nest of *Anoplotermes* sp. A. Compare the thickness of the walls with Figure 2. The right side is the one which was attached to the tree.

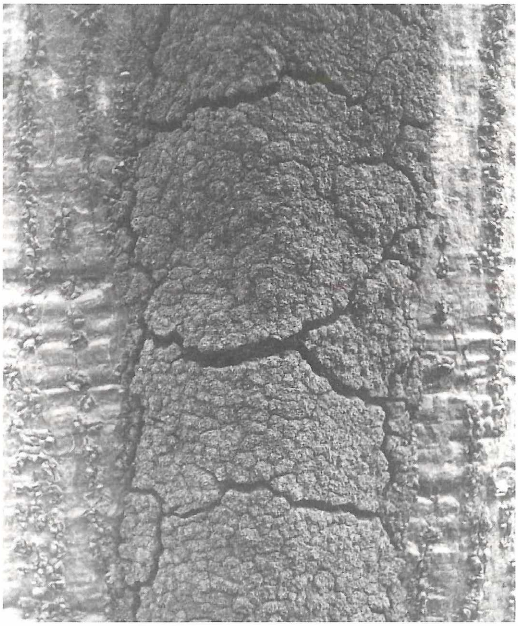

Figure 5. External view of a nest of *Anoplotermes* sp. A on the tree *Pseudobombax munguba*. Note the cracks which appear after the nest dries.

Figure 6. View of the „covered feeding places" of *Anoplotermes* sp. C, várzea forest, Ilha de Marchantaria.

flood duration and soil particle size at the different sites, and the total volume of the nests varied accordingly between 0.3 and 16.4 m^3 ha^{-1} (tab. 6).

Dead nests

Due to the peculiar life cycle and the activity of earthworms which invade the drowned nest parts (cf. 3.3.2), almost no dead nests of *Anoplotermes* sp. A remained for longer than one year on the plot. If nests died naturally, they soon fell from the tree. The only remnants were the „heaps" (fig. 3) of accumulated old nest material found at the base of the trees. Their size varied according to how many cycles (years) had been fulfilled by the colony at the site. As these heaps were very persistent through time, their number in a given area was 4-6 times higher than the number of the active nests (tab. 6). This means that 0.7-50.9% of the trees are provided with a heap (tab. 5, 6). The chemical and physical soil parameters of the heap material are likely to influence tree growth (MARTIUS 1990).

3.2.3 Intermediate nests II: *Anoplotermes* sp. C

Anoplotermes sp. C covers the tree trunks with a thin soil layer, probably in order to graze on the bark or on the lichens and mosses growing on the tree trunks (similar „covered feeding places" have been found in other termite species in India and Java: BECKER 1972, GRASSÉ 1984: 487). As neither alates nor larvae or eggs have ever been found in these constructions I think that the proper nest must be in the soil. Probably the colony uses these constructions for flood survival as in *Anoplotermes* sp. A.

As much as 23% of all trees >3 cm Ø were covered by these soil sheaths (tab. 5). Soily nest matter rich in or-

Table 3. Volume and external surface of nests of *Nasutitermes* spp. in the várzea forest, Ilha de Marchantaria.

	Site P = 1.465 ha			Site Z = 0.601 ha		
Species	n/ ha	Nest volume [liter/ha]	External nest surface [dm²/ha]	n/ ha	Nest volume [liter/ha]	External nest surface [dm²/ha]
Living nests						
N. corniger	47.1	1665.5	2293.8	31.6	1117.4	1538.9
N. ephratae	2.7	320.2	343.4	0	0	0
N. macrocephalus	4.1	1438.3	1054.7	0	0	0
N. surinamensis	3.4	1378.4	950.0	1.7	689.2	475.0
N. tatarendae	10.9	505.1	664.7	3.3	152.9	201.2
Total	68.2	5307.4	5306.5	36.6	1959.5	2215.1
Dead nests						
On trees	16.4	579.9	n.d.	6.6	233.4	n.d.
On the ground	14.3	505.6	n.d.	5.8[1]	205.1	n.d.
Total	30.7	1085.5		12.4	438.5	

(1 calculated form the proportion of dead nests on ground to dead nests on trees on site P.

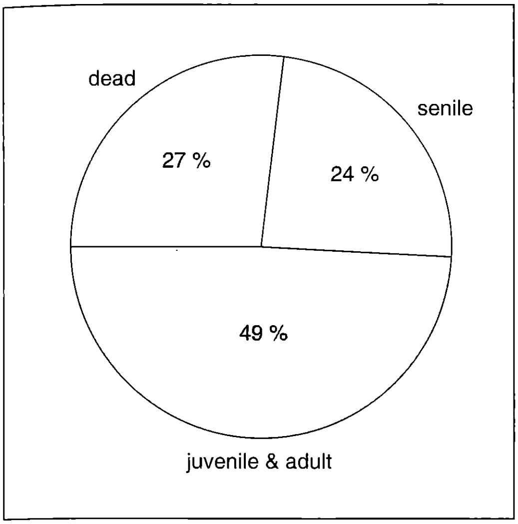

Figure 7 Proportion of juvenile, adult, senile and dead nests on trees in a population of *Nasutitermes corniger* on Ilha de Marchantaria (site P).

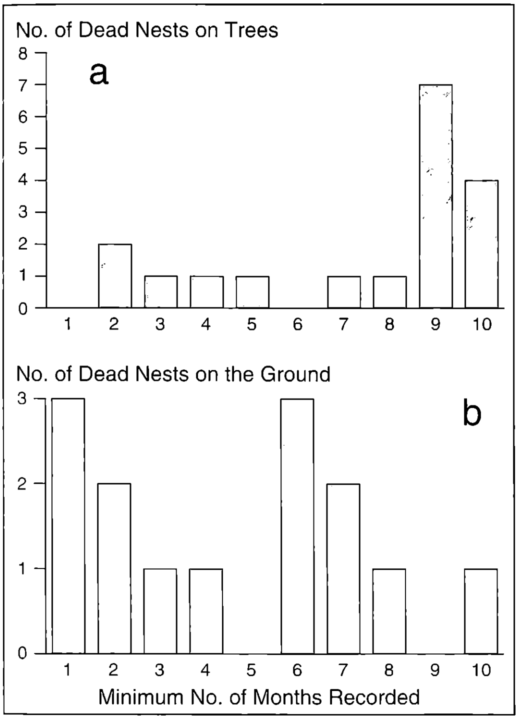

Figure 8. Persistence of dead nests in a population of *Nasutitermes corniger* in a várzea forest (site P, Ilha de Marchantaria). a) Number of dead nests on trees observed for 1 to 10 months during the nest population survey. b) Number of dead nests on the ground observed for 1 to 10 months.

Table 4. Survey of *Nasutitermes* nests on part of site P, Ilha de Marchantaria; month 1 = 17.6.1985, month 10 = 8.4.1986.

Month	Living nests	Dead nests	
		on trees	on ground
Nasutitermes (5 species)			
1	71	17	n.d.
10	72	19	15
N. corniger			
1	40	15	n.d.
10	42	15	10

ganic compounds which erodes from these constructions will concentrate near the tree base, with possible consequences for tree growth, very much like in *Anoplotermes* sp. A, however to a much lesser extent.

3.3 Non-termite organisms associated with termite nests

External and internal surfaces of living nests of all termite species are colonized by microorganisms, for example methanotrophic (HEYER 1990, ROULAND et al. 1992), and probably nitrogen-fixing as well as decomposing bacteria (HEYER & BERGER unpubl.).

3.3.1 Fauna in termite-inhabited nests

Unfortunately, termitophiles have never been studied in the várzea. Some termitariophiles which use the spaces offered in *Nasutitermes* nests in this ecosystem during the flood are listed in MARTIUS et al. (1994). Additional qualitative information follows here.

Termites are generally not active during the day on their nest surface, and all kinds of other arthropods can run freely around. Spider webs are often found on termite-inhabited nests. Some termitariophilous meliponid bees (CAMARGO 1970, 1984) are observed in the várzea. Local farmers know that parrots frequently construct their nests within *Nasutitermes* termitaria. Use of termite nests by breeding birds is also known from other parts of Amazonia (KOEPCKE 1972).

In the flood-safe parts of inhabited, vigorous nests of *Anoplotermes* sp. A other termite species (*Coptotermes, Rhinotermes, Anoplotermes* sp. D) could sometimes be found. The latter species was exclusively recorded here and seems to be an „inquiline“ species which never builds a nest of its own. *Coptotermes* and *Rhinotermes* are colonizers of dead wood, and when this is flooded some colonies manage to invade nearby nests of *Anoplotermes* sp. A. Consequently, the nests of *Anoplotermes* sp. A can be seen as a key structure which positively influences the survival of other termite species in the várzea.

3.3.2 Fauna in senile and dead nests

Nasutitermes-nests

The composition of the colonizer fauna of eroding nest areas and totally dead nests of *Nasutitermes* species is probably identical. Major differences depend on the season (MARTIUS et al. 1994). During the dry season, particularly ants use abandoned parts of termite nests to settle their own colonies, but abandoned termite nests are also frequently recolonized by other colonies of the same or different species.

Dolichoderus bispinosus (OLIVIER, 1791), a widely distributed neotropical ant of the subfamily Dolichoderinae, has a close affinity to *N. corniger* nests (tab. 7). Of the studied set of nests, 70.9% were inhabited by termites, and 63.6% by ants. Ants were found in 61.5% of all nests inhabited by termites, and 68.8% of the „dead“ nests were occupied by ants. The ants stayed permanently in the termite nests over the course of the

Table 5. An assessment of *Nasutitermes* galleries and constructions („covered feeding places“) of *Anoplotermes* sp. C in várzea forest; site P, Ilha de Marchantaria; gall. = galleries, aband. gall. = abandoned galleries, constr. = constructions.

			Nasutitermes spp.			*Anoplotermes* sp.C	
1	2	3	4	5	6	7	8
Subplot Nº	N trees >3cm Ø	Used gall.	% of gall. (3) per trees(2)	Aband. gall.	% of aband. gall.(5) per trees (2)	N constr. per subplot	% of constr. (7) per trees (2)
1	11	4	36	6	54	3	27
2	11	2	18	0	0	3	27
3	7	3	43	0	0	1	14
4	17	2	12	3	18	4	24
5	25	6	24	2	8	4	16
6	21	1	5	5	24	0	0
7	16	2	13	6	38	0	0
8	9	0	0	1	11	3	33
9	5	2	40	0	0	0	0
10	10	4	40	3	30	4	40
11	11	1	9	3	27	7	64
12	12	2	17	1	8	6	50
sum	155	29	19	30	19	35	23
ha^{-1}	1722.2	322.2		333.3		388.9	

Table 6. Density, volume, and weight of nests and heaps of *Anoplotermes* sp. A, várzea forest, Ilha de Marchantaria. Total nest weight calculated from nest volume and physical density of nest/heap matter (0.6 g cm^3; MARTIUS 1990). Plot C was investigated before flood, Plot P and Z during the flood, therefore heap numbers in sites Pand Z were calculated from nest-to-heap-ratio in site C.

Plot	Area studied [m^2]	Density of nests or heaps [ha^{-1}]	Total nest volume [m^3/ha]	Total nest weight [t/ha]
Nests				
C before flood	6000	30-50	2.3-3.8	1.4-2.3
P	1050	219	16.4	9.8
Z	6013	3	0.3	0.2
Heaps				
C before flood	6000	200	26.7-35.6	16.0-21.4
P		876-1445		
Z		12-20		

Table 7 Ants and termites: *Dolichoderus bispinosus* in nests of *Nasutitermes corniger*, site P, Ilha de Marchantaria

	Number of nests on subplot	Number of nests [%]
Total	55	100.00
Only inhabited by *N. corniger*	15	27.27
Only inhabited by *D. bispinosus*	11	20.20
Termites and ants in one nest	24	43.64
Nest without ants or termites	5	9.09
Total nests with termites	39	70.91
Total nests with ants	35	63.64

year. In nest parts hold by the ants no termites were found; often both colonies were separated only by a thin nest wall. The ants preyed heavily on the much smaller termites when the isolating walls were destroyed experimentally. However, if fights were carried out in the open, the ants clearly avoided encounters with nasute soldiers, probably in consequence of their chemical defense (EISNER et al. 1976, MILL 1982a, b). It is also likely that *N. corniger* soldiers are in advantage in the narrow nest chambers, which could explain why termites and ants could coexist over more than a year in some cases. Although *D. bispinosus* seems to colonize termite nests mainly for reasons of space, the ants were the observed mortality factor in 5 of 9 nests of *N. corniger* during the observation period.

On the other hand the termite colonies probably take advantage from the reaction of the ants to disturbances: Knocking on the trunk of the nesting tree provokes the ants to emerge immediately from the nest, rushing all over it and up and down the tree. The nest surface is virtually transformed into a whirling mass of ants which exhale a strong smell (alarm pheromone?) and bite every living being in their way. Many ants fall to the ground. All these reactions practically impede any approximation to the nest.

D. bispinous has also been reported as a colonizer of living and dead termite nests in Panama (WHEELER 1936). Termite nests are also important for nesting ants in other parts of Amazonia (cf. BANDEIRA 1978 MILL 1984, M. VERHAAGH, Karlsruhe, pers. comm.), and in other ecosystems (savanna: REDFORD 1984, OKWAKOL 1991). *D. bispinosus*, however, is not exclusively termitariophilous, as it can also be found in hollow dead trees, in accumulations of litter trapped in the canopy and similar places.

Anoplotermes sp. A nests

Nest parts which emerge from the water often show holes made by termite-preying birds (particularly in older nests). Arthropods like myriapods, spiders, ants (*Crematogaster* sp. and others) and even small vertebrates (frogs, lizards) can often be found in abandoned parts of decaying nests. They sometimes dig their way into the nest like into soil, although the very hard nest walls normally impede this.

Various Oligochaeta were found in submerged nest parts of *Anoplotermes* sp. A (juveniles of *Drilocrius* sp., family Almidae, and juveniles and adults of *Glossodrilus* sp., Fam. Glossoscolecidae). They seem to be the only responsibles for transforming all the nest matter, which is very hard, into heap material. During the rising of the flood, these heaps are the last islands of soil emerging above the water level, and many arthropods can then be found here, an easy prey for birds which are attracted to these places.

Anoplotermes sp. C nests

Many small arthropods are found in abandoned parts of the constructions of this species. These soil layers on trees are likely to extend the activity radius of the more mobile elements of the soil fauna onto the trunks and may play an important role in the survival of these animals during the flood. However, this relationship has never been investigated (e.g. IRMLER 1979, ADIS 1992).

3.3.3 Termite-plant interactions

It is not the purpose of this paper to discuss the termite-plant interactions in the várzea, but some ideas should be mentioned. Future research should be directed to this important area. One major accomplishment of the *Anoplotermes* species is the concentration of organic-rich soil in „heaps“ near the base of the trees. The activity of the nest-burrowing annelids results in one of the highest turnover rates of termite nest material found in the world (MARTIUS 1990). Almost 1/10 of the nutrient rich upper soil of the várzea is concentrated in the heaps. The possible consequences for tree growth are still to be analyzed.

Trees might possibly be destroyed by bark-feeding *Anoplotermes* sp. C, but I could not observe any damage beyond superficial bark scraping. On the other hand, the trees might be protected from attack by bark-beetles and other wood-attacking organisms by the soil cover which these termites build around the trunks, but this also remains to be studied.

It should be mentioned that the outer surface of living *Nasutitermes* nests is often colonized by mosses, algae, lichens, and sometimes small ferns, in the same manner as tree trunks.

4. Conclusion

Living *Nasutitermes*-nests contain an astonishing large volume and internal surface area. This huge space is fiercely defended by the termites. Only those animals can have access to the nest which are able to overcome the defense and recognition barriers of the termites. These animals must either eliminate the termites in a war-like encounter like ants do, or they have to use some „tricks" to „smuggle" themselves into the termite colony. These tricks are the amazing adaptations of the termitophiles and some termitariophiles (e.g. the meliponine bees). An aggressive strategy generally ends with the retreat or death of the termites and allows the appropriation of whole nests or at least parts of them by a large number of secondary users, whereas the infiltration tactics allow only a small number of termitophiles to survive in a termite colony. Termitophile biomass has been assessed to be <1% of that of the termites (BANDEIRA 1983). With an average termite colony of 111 000 individuals (BANDEIRA & TORRES 1985) and an average termite biomass of 1 mg per individual (MARTIUS in press) this makes ideally 111 g of termites per nest and about 1 g of termitophiles per nest, or 35-70 g ha^{-1} of termitophiles (tab. 3), which is 0.03-0.07% of the soil arthropod mass (10.5 $g \cdot m^{-2}$ without termites; ADIS & RIBEIRO 1989). In spite of their insignificant biomass, termitophiles are important elements of the genetic information of the ecosystem, and attention should be directed to the study of termitophiles in Amazonia, with particular focus on the differences between várzea and terra firme forest.

Dead *Nasutitermes* nests together with senile parts of inhabited nests have a minor total volume than the living nests, however, they are the only structures which are totally accessible to secondary colonizers. The occupation of dead nests is particularly high when ants are present (cf. 3.3.2) or during the flood when soil fauna migrates onto trees with termite nests (cf. MARTIUS et al. 1994).

Inhabited nests of *Anoplotermes* sp. A are temporary resources which provide flood-survival not only for the constructing species itself but also for other termite species. The constructions of *Anoplotermes* sp. C are likely to have a similar function for the builders themselves and for the soil fauna as well.

The study presented here was carried out in secondary floodplain forests which seem to have higher termite densities than older stands. The question remains open whether the lack of termite nests in late successional stages is compensated for in other ways. We observed also partially deforested várzea areas with much higher termite nest densities (mainly *Nasutitermes corniger* and *N. ephratae*; MARTIUS & HURTADO unpubl.), where, due to the reduced number of trees, abandoned nests might be much more important for the survival of other fauna.

In non-flooded terra firme forest there is no need for flood survival (unless in water-logged depressions). The termite community in terra firme forest is generally much more diversified in terms of species and nest types. We recently started to sample fauna from conspicuous termite nests in rain forest (MARTIUS & HANNE in press).

The present study on purpose concentrated on a look at the ecosystem structure in the Amazon floodplains in order to show that termites, although they are not as conspicuous as in other ecosystems, generally occur in high densities and are significantly structuring this ecosystem. There is good reason to believe that termites and their nests are important key elements of várzea forests, which affect and determine the performance and diversity of other organisms including animals and plants.

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Artikel/Article: Termite nests as structural elements of the Amazon floodplain forest 137-150