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Terrestrial arthropods colonizing an abandoned termite nest in a floodplain forest of the Amazon River during the flood

Abstract

Terrestrial arthropods were identified as secondary colonizers of an abandoned termite nest (*Nasutitermes tatarendae*) at the beginning of the inundation period in a floodplain forest influenced by whitewater in central Amazonia. About 50 individuals of non-termite meso- and macrofauna were recorded per liter of nest volume, mainly terrestrial Arachnida, Isopoda, Diplopoda, Blattodea, Staphylinidae, and Formicidae. Apparently, abandoned termite nests could be important for the survival of the soil-fauna which migrates to the canopy during the flood period.

Kurzfassung

Terrestrische Arthropoden als Besiedler eines verlassenen Termitennests in einem Überschwemmungswald während der Überflutungsphase

In einem várzea-Wald Zentralamazoniens wurden zu Beginn der Überschwemmungsphase terrestrische Arthropoden als Sekundärbesiedler eines verlassenen Termitennestes (*Nasutitermes tatarendae*) identifiziert. Etwa 50 Individuen der Meso- und Makrofauna (keine Termiten) wurden pro Liter Nestvolumen registriert, überwiegend terrestrische Arachnida, Isopoda, Diplopoda, Blattodea, Staphylinidae und Formicidae. Verlassene Termitennester können offensichtlich für das Überleben der Bodenfauna, die während der Flutphase in die Baumkronen wandert, wichtig sein.

Resumo

Colonização por artrópodos terrestres de um ninho abandonado de cupim no início do período da enchente numa floresta de várzea

Artrópodos terrestres foram identificados como colonizadores secundários de um ninho abandonado de cupim (*Nasutitermes tatarendae*) no início do período da enchente numa floresta de várzea da Amazônia Central. Aproximadamente 50 indivíduos de meso- e macrofauna (não cupins) foram achados no volume de um litro de ninho, sobretudo Arachnida, Isopoda, Diplopoda, Blattodea, Staphylinidae, e Formicidae. Evidentemente ninhos abandonados de cupins podem ser importantes para a sobrevivência da fauna de solo que migra ao dossel da floresta durante a inundação.

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Introduction

Survival strategies of soil arthropods in the periodically inundated floodplain forests (várzea) along the Solimões-Amazon River have long been in the focus of research (IRMLER 1981, ADIS 1992). Migration to tree canopies is one possibility for soil species to survive flooding. Termites represent a considerable part of the várzea fauna (MARTIUS 1989), and a great part of their arboreal nests is abandoned (MARTIUS 1994). However, the question whether these nests are „refugia“ for the migrating soil fauna has never been analysed.

To get an insight into this problem we present here some data gathered during field studies on termite colonization (MARTIUS 1989) of Ilha de Marchantaria, an island in the river Amazon near Manaus, Brazil (fig. 1), and a typical várzea (= white water floodplain forest fig. 2) site (JUNK 1984).

The fauna of an abandoned termite nest of *Nasutitermes tatarendae* was determined. The nest was located on a tree which base had been flooded the day before sampling. Its lower half (with a volume of more than 80 liters) was cut from the tree with a chain saw, then transported in an aluminium container to the laboratory, split into small fractions of approx. 5-10 dm³ each, and extracted by heat in a Tullgren Funnel. Specimens were separated to orders, stored in alcohol, and identified. Additionally, nine abandoned arboreal *Nasutitermes* nests (mostly *N. corniger*) which were found on the forest floor during the low-water period were screened for associated fauna.

Secondary colonizers of the abandoned nest of *Nasutitermes tatarendae*

Table 1 shows the arthropods which we found in the abandoned termite nest of *Nasutitermes tatarendae*. No termites, not even of other species, were found in this nest. Due to the sampling procedure, the small mesofauna (usually <1mm, e.g. Acari and Collembola) has not been quantitatively assessed, and its presence is only assigned with an „x“ in table 1. Animals of size classes usually ≥1 mm (larger meso- and macrofauna) have been quantitatively assessed. At least 77 different arthropod taxa were registered in this single abandoned nest. With a total of 4054 individuals of the fauna with a size of ≥1 mm the nest contained a high density of arthropods (corresponding to about 50 individuals per liter of nest volume). We clas-



Figure 1. Aerial view of Ilha de Marchantaria during high water level; Photo: J. ADIS.

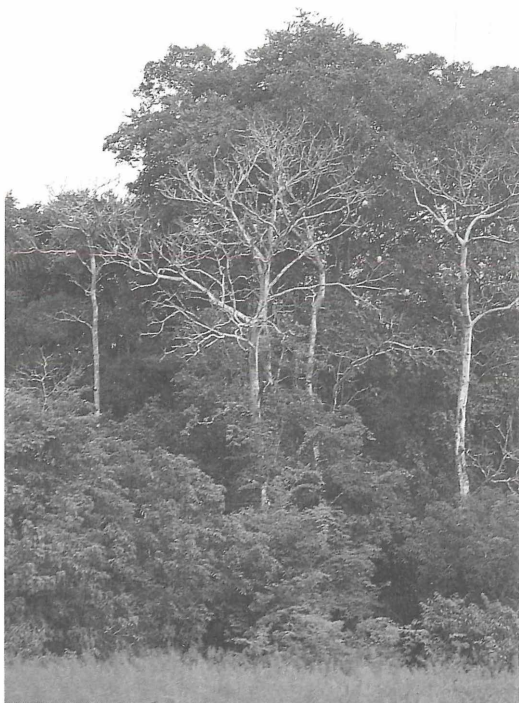


Figure 2. Edge of the study site in the várzea forest on Ilha de Marchantaria, where the termite nest has been found; Photo: H. Höfer.

Table 1. Arthropods found in an abandoned nest of *Nasutitermes tatarendae*. x = no quantitative assessment; n = not determined.

Taxa	Number of Individuals	Number of Species
Chelicerata - Arachnida		
Araneae	156	11
Pseudoscorpiones	1	1
Opiliones		
sp. 1 ad.	22	1
sp. 2 ad.	17	1
sp. 3 ad.	18	1
juv.	412	
Acari	x	?
Crustacea, Chilopoda, Diplopoda		
Isopoda		
<i>Dubioniscus</i> sp. (Eubelidae)	159	1
<i>Prosekia</i> sp. (Philosciidae)	158	1
Chilopoda - Scolopendromorpha	72	n
Diplopoda - Polydesmida (juv. & adults)	185	2
Insecta		
Collembola	x	?
Orthoptera - Blattodea	104	n
Dermaptera	2	n
Homoptera - Stenorrhyncha	8	n
Coleoptera		
unident. larvae	7	n
Carabidae	26	10
Elateridae	3	n
Staphylinidae	370	n
Pselaphidae	3	n
Tenebrionidae	27	3
Scarabaeidae	x	n
Scolytidae	7	n
Colydiidae	16	1
Histeridae sp. 1	5	1
sp. 2	12	1
sp. 3	1	1
Scydmaenidae	13	1
Scaphidiidae sp. 1	3	1
sp. 2	3	1
sp. 3	1	1
Leptodiridae	1	1
others (small mesofauna)	64	7
Hymenoptera		
Formicidae (det. M.VERHAAGH)		
Ponerinae	782	1
<i>Pachycondyla constricta</i>		
workers (735)		
alates (13)		
pupae (34)		
Myrmicinae	86	4
<i>Solenopsis (Diplorophthrum)</i> sp.		
<i>Cyphomyrmex rimosus</i>		
<i>Pheidole</i> sp.		

<i>Crematogaster</i> sp. (<i>limata</i> -group)		
Formicinae	1291	2
<i>Paratrechina</i> sp.		
<i>Camponotus</i> sp.		
Dolichoderinae	1	1
<i>Tapinoma melanocephalum</i>		
Bethyilidae	7	4
unident. Hymenoptera	8	4
sum	>4054	>77

sify them mostly as opportunistic users of the nest structure (facultative „termitariophiles“; ARAUJO 1970). It was particularly striking how many large scolopenders were extracted. This shows the extension of the internal surface area of the chambers in termite nests (cf. MARTIUS 1994).

Spider species are listed in table 2. All spider species, collected in the abandoned termite nest, have already been collected in the same várzea forest during an ecological survey of the spider fauna (HÖFER unpubl.). Most of them can be considered ground living species. The oonopid species, *Anapistula* sp. and *Theotima* cf. *minutissima* (PETRUNKEVITCH), are tiny spiders dominant in leaf litter samples, pitfall traps and ground-photoeclectors taken in blackwater and whitewater inundation forests during the non-inundated period (HÖFER 1990). When these forests are being flooded (February-April) these spiders migrate into the trunk region, where they have been collected in arboreal funnel traps. The same is true for *Tricongius amazonicus* PLATNICK & HÖFER, 1990, a small sized (≈3 mm) gnaphosid species. The juveniles migrate to the trunks, where they become adult. Adult spiders return to the ground when the water has receded from the forest (September) and reproduce there (PLATNICK & HÖFER 1990). Thereafter the spiderlings of the new generation spread out on the newly emerged ground.

Orthobula sp. and *Diestus* sp. are medium sized spiders which were only rarely captured in traps during our studies in inundation forests. It seems possible that they live permanently in higher strata.

Ctenus spp. are the most conspicuous large ground living spiders (>10 mm) in all central Amazon forests. In inundation forests they avoid being flooded by vertical or horizontal movements away from the rising water. Consequently they also appear in arboreal funnel traps during inundation.

A wide variety of beetles was found in the nest, many of them very small. Although Staphylinidae are among the most abundant groups (tab. 1), no termitophilous species (KISTNER 1969) were present among them, probably because these species only live in inhabited termite colonies.

Among the ants the ponerine *Pachycondyla* (= *Mesoponera*) *constricta* (MAYR, 1883) was present with wor-

Table 2. Spiders (Arachnida) collected in the abandoned nest of *Nasutitermes tatarendae* in the várzea forest (det. H. HÖFER).

Family	Genus/Species	Number of Individuals
Spiders <2 mm body length:		
Oonopidae		
Gamasomorphinae		3
Oonopinae		2
		116 juv.
Symphytognathidae	<i>Anapistula</i> sp.	2
Ochyroceratidae	<i>Theotima cf. minutissima</i>	2 juv.
Salticidae		1 juv.
Spiders >2 mm body length:		
Gnaphosidae	<i>Tricongius amazonicus</i>	15 juv.
Corinnidae	<i>Orthobula</i> sp.	2
Corinnidae	<i>Diestus</i> sp.	2
Ctenidae	<i>Ctenus</i> sp. 1	3 juv.
	<i>Ctenus</i> sp. 2	7 juv.
n. det.		1 juv.
Total number of individuals		156
Total number of species		11

kers, sexual castes and brood. During an ant survey in Amazonian Peru (VERHAAGH unpubl.), *P. constricta* nests were normally found in soil or rotting wood of advanced state, and in one case in the earth mound of a soil living termite species. The ant (≈ 8 mm) lives in different forest types as well as in open, man – made habitats, and the nests may contain several hundred up to probably more than thousand workers. Activity is mostly on the ground, and partly hypogeic in litter and soil cavities. We therefore conclude that a whole colony of *P. constricta* moved from the ground into the termite nest, carrying the pupae to the refuge, and possibly other brood as well, which died during the extraction process.

The little (≈ 3 mm) attine (leafcutting ants and other fungus growers) *Cyphomyrmex rimosus* (SPINOLA, 1853) does not cut leaves but cultivates its fungi on different organic material, mainly insect feces and parts of insect corpses. It can be found active on the

ground and in the vegetation, and nests are located in soil, or rotting wood, sometimes high on trees (VERHAAGH, unpubl.). Therefore, workers from the termite nest did not necessarily come from the ground. We did not find any brood, but there might have been brood together with more workers in the upper part of the termite nest which was not examined. The same is true for the the myrmicine ants *Solenopsis* (*Diplorophthrum*) sp. and *Pheidole* sp., and the formicine *Camponotus* sp. In all these genera, species exist which nest on the ground as well as on trees, in dead wood or epiphyte humus.

The only dolichoderine species, *Tapinoma melanocephalum* (FABRICIUS, 1793), is a tramp species ($\approx 1,5$ mm) with a wide distribution in the neotropics and other tropical regions (KEMPF 1972). It nests in small cavities of any types in all vegetation strata and the single worker certainly did not belong to a nest on the ground; the same we conclude for the single worker of the arboricolous *Crematogaster* sp. (*limata* group).

Most ants found in the termite nest were workers of the formicine *Paratrechina* sp. ($\approx 2,5$ mm). 1285 of 1291 formicine ants belonged to this species. *Paratrechina* species in Amazonia nest e.g. in rotten wood, in plant cavities, and in detritus nests which they construct on undersides of leaves (VERHAAGH unpubl.). In general, they are very mobile ants ready to leave their nests at the slightest disturbance. This makes it probable that the workers caught are part of a colony that fled the rising water.

Only one arboricolous pseudoscorpion was found in this mound, but additional species (all arboricolous; MAHNERT & ADIS 1985) were found in other abandoned termite nests, and in dead wood colonized by termites (tab. 3).

Abandoned nests on the ground

Typical secondary colonizers found in abandoned termite nests on the ground are mostly terricolous spiders, harvestmen, isopods, cockroaches, and ants (tab. 4). Generally, the nests contained only few specimens of these groups, and were thus much less populated than the *N. tatarendae* nest described before.

Table 3. Pseudoscorpions collected in association with termites in the várzea forest (det. V. MAHNERT); P, D, T = Proto-, Deuto-, Tritonymphe.

Date	Termite Species	Pseudoscorpion Species & Numbers	
22.04.86	<i>Nasutitermes tatarendae</i>	<i>Dolichowithius</i> (?) sp.	1P
10.12.85	<i>N. macrocephalus</i>	<i>Parawithius</i> sp.	1D
11.03.86	<i>Nasutitermes corniger</i>	<i>Lustrochernes intermedius</i>	1
28.01.87	<i>Anoplotermes</i> sp. A(?)	<i>Pachychernes baileyi</i>	1T
14.02.85	termites in dead wood	<i>Lustrochernes intermedius</i>	1

Table 4. Presence of secondary fauna in dead arboreal termite nests (mostly of *Nasutitermes corniger*) fallen to the ground. 1= Araneae; 2= Opiliones; 3= Isopoda; 4= Blattodea; 5= Formicidae.

Nest No.	Date	Conditions	1	2	3	4	5	Others
75-1	1.4.86	dry	X	X	X	X	X	
98-13		moist	X	X	X	X		
118-6		fresh, dry			X	X		
197-5		++ dry						
197-7		++ dry						
109-15	2.4.86		X	X	X			
242-2			X	X				
52-4	10.3.86	moist, fungus	X	X	X	X	X	X*
206-9	22.3.86	moist, fungus	X	X	X	X	X	X**

*= Oligochaeta, Pseudoscorpiones (cf. tab. 3), Chilopoda, Coleoptera; **= Acari, Staphylinidae

Abandoned termite nests on the ground generally show a higher moisture content than those which are still attached to the trees. Secondary colonization is compartmentalized, which means that some nest parts are occupied and others are not. This is in part due to stochastic processes (who comes first occupies the place and defends it against other immigrants), and in part related to differences in moisture which determine suitability of the nest parts for the different species (the top region of the nests is dry and hard, and the side which is in contact with the ground is moist and rot). In some nests, the activity of the decomposers (mainly isopods) results in a complete filling of the former nest chambers with detritus (for example feces of digested termite nests), which makes further colonization by larger faunal elements almost impossible.

Conclusion

Termitaria in general offer a suitable habitat for a wide variety of arthropods (ARAUJO 1970, WILSON 1971). They seem to be important hiding places for many of the principally nocturnal spider species even in non-inundated forests (MARTIUS & HÖFER pers. obs.). Ants, too, have often been recorded from inhabited or abandoned termitaria all over the tropics (WHEELER 1936) but in most cases their relationships to the termites and the significance of the termitarium as nesting habitat remained obscure.

In the case of the reported nest, the base of the tree on which this nest was located was flooded the day before it was sampled. Therefore we conclude that the arthropods recorded in that nest belong in large part to the soil fauna which was driven up the trunk by the flood. In fact, the abandoned termite nests on the ground contained much less animals.

Survival strategies of the soil fauna in the floodplains include migration to the trunk and canopy of trees due to the rising water (ADIS 1992). The high number of ar-

thropods found indicates that abandoned termite nests on tree trunks above the highest water level are important temporal refuges for the survival of soil arthropods during the flood period in inundation forests. Although the internal surface of termite nests is small in relation to the surface existing in the tree canopy (MARTIUS 1994), abandoned termite nests could be highly attractive to the soil fauna due to their elevated moisture and many small cavities.

Alternatively, the high catches can be explained by a „trap“ effect of the nest: Arthropods on their way into the upper trunk region which would hide under loose bark, in fresh water sponges on the trunk or disperse into the canopy, are gathered in the nest and will disperse into the canopy only during the following days. Due to the presence of many predators (e.g. most of the ants, the spiders and the centipeds), a considerable mutual predation pressure is likely to be exerted within the nest. In this scenario, the nest „catalyzes“ predatorial interactions between the fauna which is only „accidentally“ agglomerated in the nest. Thus, the nest could lower the density of the migrating fauna instead of enhancing survival. Probably, both processes will occur.

Further comparative studies of the migration processes in relation to the colonization of termite nests by arthropods in the várzea are necessary for a better understanding of the function of abandoned termite nests for migrating soil fauna.

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