

Effects of Fire on Termite Generic Richness in a Savanna-like Ecosystem ('Cerrado') of Central Brazil

by

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ABSTRACT

Fire can affect ecological communities by direct elimination of organisms or through changes in resource availability, leading to diminished, increased, or unchanged richness. Termite generic richness (= number of genera) as well as termite abundance (= number of records per genus) are shown to not change following fire in a savanna-like ecosystem ('Cerrado') in central Brazil. Since fire is a natural recurrent event (i.e., predictable) in this ecosystem, it seems plausible that termites would have evolved mechanisms to cope with such a disturbance. Such mechanisms would include (i) inhabiting hard, protective, clay nests; (ii) temporary migration into adjacent less affected nearby, satellite, mounds; and (iii) absence of strict dietary specialization, coupled with low levels of competition, allowing niche overlap thereby minimizing adverse effects due to temporary reduction in food availability.

Keywords: Isoptera, fire, cerrado, Brazilian savanna.

INTRODUCTION

Fire is an important event among several factors affecting ecological communities in savanna-like ecosystems. In Brazilian Cerrado, an ecosystem physiognomically similar to savannas, fire is a recurrent event, resulting from natural and man-induced processes, whose frequency is mostly annual (Eiten 1972). The Cerrado flora is known to have evolved effective adaptations to fire: some plants, for instance, keep tunics which protect their living parts during burning events (Edwards 1956). In contrast, little is known about the effects of fire on the Cerrado fauna, especially invertebrates. However, given the abundance of adaptations to fire presented by the Cerrado flora, it seems reasonable to assume that similar adaptations would help the Cerrado fauna to cope with fire.

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Termites are an important component of the Cerrado fauna presenting effects as diverse as being (allegedly) responsible for the origin of floodplain earthmounds ('murundus', Oliveira-Filho 1992); or being intrinsically related to the small mammal community structure and composition (Mares *et al.* 1986).

While studies on fire effects on termites in Cerrado are virtually nonexistent, for regions other than the Cerrado such studies are scarce. Benzie (1986) has shown strong evidence of a limitation of termite numbers in guinea savanna by fire. Abensperg-Traun & Milewski (1995) report that harvester termites in the semi-arid southwest of Western Australia appear unaffected by high-intensity fire. An opposite result was reported subsequently by Abensperg-Traun *et al.* (1996) who showed that *Drepanotermes tamminensis* (Hill) is markedly affected by fire in the same region

The present study examines the effects of fire upon termite generic richness in the Cerrado of central Brazil. We focus on genera rather than species because termite identification to species level is not always feasible, specially for samples lacking soldiers. In fact, analyzing ecological relationships with higher taxa is being advocated as a valid alternative, specially when species data is of doubtful quality (Gaston & Williams 1993). In addition, termite genera richness is highly correlated to species richness, which allows the assumption that ecological and even historical relationships are mirrored by this higher taxon (Eggleton *et al.* 1994). Many studies circumvent this by restricting themselves to the epigeous mound building termite species, but that has the drawback of delaying our understanding of the ecology of whole termite communities. This paper aims to contribute to the necessary initial steps towards reversing such a delay. We explore the hypothesis that termite generic richness does not change following fire in Cerrado, since fire is a natural and roughly predictable disturbance event in this ecosystem. First, a theoretical framework of pathways leading to changes in richness following fire events is discussed. Then our results are superimposed onto this framework, and the likely pathways and mechanisms are discussed in the light of termite biology and ecology.

Theoretical effects of fire upon richness of ecological communities

Fire affects richness of ecological communities by direct elimination of organisms or through changes in resource availability. Two pathways are likely to happen when fire eliminates organisms directly (Fig. 1A, B, C, and downward arrows): either (i) all individuals are affected equally, irrespective of their identity and function; or (ii) only individu-

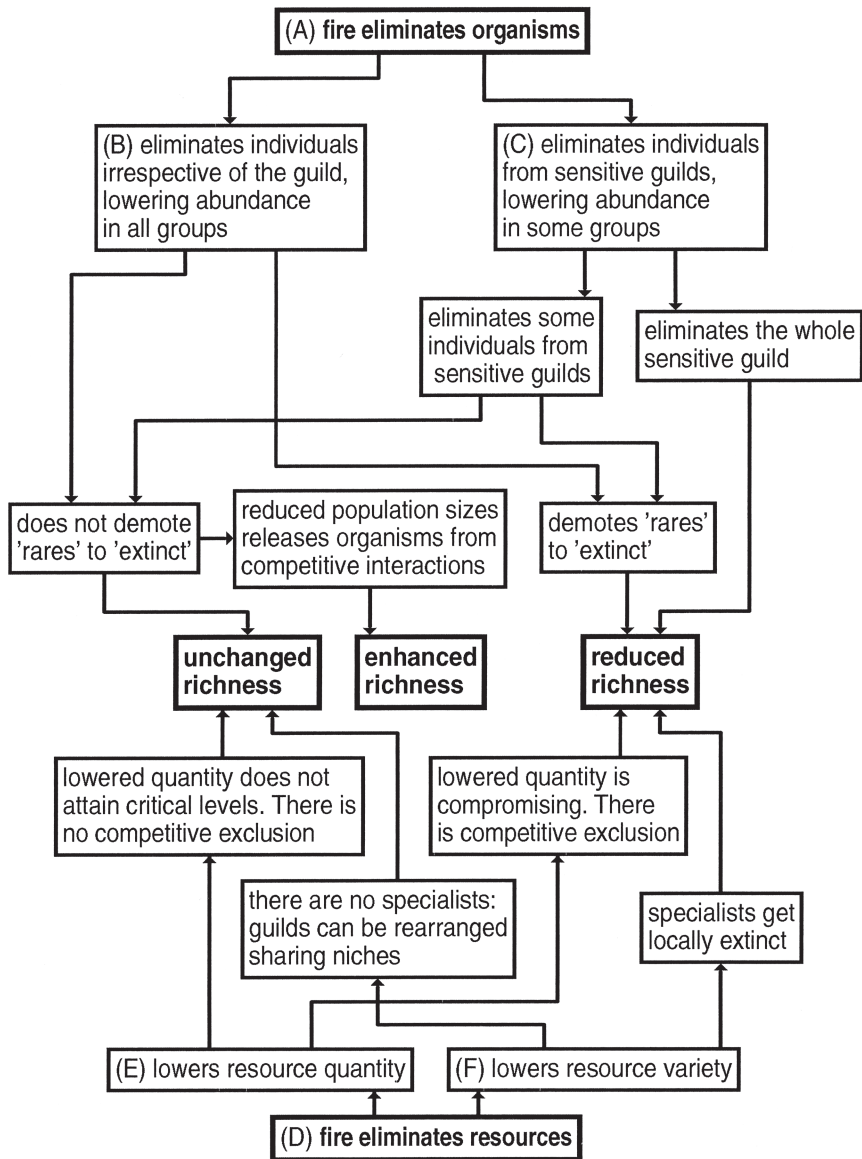


Fig. 1. Theoretical pathways leading to changes in community richness following a fire event. Arrows from top to bottom show likely pathways when fire eliminates individuals; arrows from bottom to top show likely pathways when fire eliminates resources.

als belonging to guilds sensitive to fire are affected.

If fire reduces abundance of all groups, some populations may be lowered below their minimum critical size, entering extinction vortex (Tracy & George 1992), thereby decreasing site richness. If the disturbance is not drastic enough to demote 'rare' groups to the status of 'locally extinct', then, richness may remain unchanged. Alternatively, richness may be increased following disturbance, providing reduced population sizes releases organisms from competitive interactions, thereby easing species coexistence (Christensen 1985). If sensitiveness varies among groups, whole guilds can be eliminated by fire, reducing site richness. However, if sensity **sensitivity ?** varies among organisms within groups, (i) killed individuals might not compromise persistence of rare groups, which would keep original richness; (ii) population densities might be reduced to levels that favor stochastic extinction, with a consequential diminishment of richness in the site; or (iii) again, richness may be enhanced providing that reduced population sizes releases individuals from competitive interactions. Similar results would occur where organisms resemble each other in terms of sensitivity to fire, but the burning event occurs patchily over the area.

Fire may also eliminate resources, rather than organisms, thereby lowering the quantity or the variety of food in the area (Fig. 1D, E, F, and upward arrows). If lowered quantity is not critical, community parameters can remain unchanged. However, richness may be reduced if lowered resource quantity is drastic enough to promote competitive exclusion. Like organisms, resources may also be affected differentially by fire. Depending on the fire type and intensity, some resources may get burnt whereas others do not, which reduces resource variety in burnt sites. As a consequence, specialists species might go locally extinct, lowering richness of the community. In the absence of specialists species, resource utilization may be rearranged, providing the community tolerates high levels of niche overlap. As a consequence, fire may have no effect on richness. Alternatively, in 'interactive communities' (sensu Cornell & Lawton 1992), reduction of resource variety could lower richness in burnt sites, because competitive interactions would prevent rearrangement of resource utilization patterns, thereby provoking local extinction of inferior competitors.

In summary, fire may reduce richness of ecological communities by (i) eliminating individuals, thereby demoting populations from the status of 'rare' to 'extinct'; (ii) eliminating whole fire-sensitive groups; (iii) reducing resource quantity to a level where competitive exclusion is important; or (iv) reducing resource variety, thereby promoting local extinction of specialists and/or inferior competitors. Richness will not

respond to fire where: (i) population reduction is not drastic enough to drive groups to extinction vortices; (ii) lowered resource quantity is not critical enough to enhance competitive exclusion; and (iii) there are no specialists to suffer extinction following reduction in variety of resources. Fire may enhance richness in cases where reduced population sizes release groups from competitive interactions.

METHODS

Collections of termites were undertaken in sites of the Cerrado vegetation, an ecosystem physiognomically but not floristically similar to savannas, occurring in central Brazil. The Cerrado is a strict upland vegetation, occurring on deep, infertile soils, usually Latosols ('Oxisols'). Despite its xeromorphic aspect, the region may present annual rainfall values as high as 2000 mm. In this ecosystem, fire is a recurrent event, resulting from natural and man-induced processes, happening as frequently as annually in most cases (Eiten 1972).

Three geographically distinct localities were chosen within a radius of 300 km in this region: (i) Campo Grande (20 26'34"S×54 38'47"W), altitude 532 m a.s.l.; (ii) Chapada dos Guimarães (15 17'25"S×55 48'W), altitude 840 m a.s.l.; (iii) Primavera do Leste, (15 33'45"S×54 17'42"W), altitude 636 m a.s.l. Annual mean rainfall is, respectively, 1793 mm, 1750–2000 mm, and 1560 mm. Fire occurred, respectively, 12, four, and seven months prior to data collection.

In each of these localities, a pair of burnt and unburned sites was selected. One 100 × 2 m transect was marked within each of the sites. The transects were divided into subplots, 2 m (width of transect) × 5 m. Sampling was performed within one subplot at a time, by two people instructed to avoid overlap in space, until 20 min had elapsed. A third person took the relevant notes simultaneously. This arrangement of transect dimension and sampling effort was selected since it provided a satisfactory number of samples in preliminary studies. However, it carries the drawback of lacking soldiers in most samples, because the collector has to adjust time usage to cover the whole sampling surface, not being able to insist in waiting for soldiers to come out. The absence of soldiers make termite identification to species level not always feasible.

Sampling was undertaken with the aid of a spade and forceps, in rotting logs (diameter >5 cm) and the soil underneath (up to 5 cm deep), bases of living trees (diameter at base of tree >10 cm), epigeous (soil surface) termitaria. In addition, litter was scanned to improve chance of finding termites. Colonies/galleries overlapping two subplots were recorded only once. Sampling was performed from 02 to 12 November

1995, at daylight, from 0800 h, avoiding heavy rain periods.

Specimens were preserved in 80% alcohol, labeled, and subsequently identified to genus. Since most of the samples collected did not contain soldiers, identification did not proceed to species level. Mandibular and gut patterns of workers were used for identifications, following Ahmad (1950), Mathews (1977), Johnson (1979), Fontes (1986), Constantino (1999). Identifications were confirmed using the collection of the Entomological Museum of the Universidade Federal de Viçosa, where voucher specimens were deposited.

Termite variables described generic richness (= number of genera) and abundance (= number of records per genus). This measure of abundance refers to the number of colonies, rather than its classical approach, which refers to the number of individuals. That is, since we avoided sampling colonies and galleries twice, termites recorded in a collection point would denounce the existence of a single colony, regardless the number of individuals being found. We acknowledge that some uncertainty is involved here, as two foraging parties could belong to the same colony, and this is not always obvious in the field.

Generalized linear modelling (glm) with Poisson errors, was used to check for effects of fire on the number of genera (y-var) present in burnt and unburned sites (x-var). Linear mixed effects modeling (lme) was used to check for effects of fire on the number of records per genera. This last procedure was needed due to the nested structure of data ('genera' within 'fire' within 'site'). Variance was estimated using restricted maximum likelihood (REML) method. Inspection of residuals dictated the use of log-transformed y-var from 'number of records' to \ln ('number of records'+ 0.0001). All analyses were performed using R statistical system (Ihaka & Gentleman 1996), with nlme package and lme function, freely available at <http://termix.ufv.br/CRAN>.

RESULTS

We collected a total of 181 samples, which comprised two families, four subfamilies and 13 genera (Table 1). The vast majority of the genera collected have been already recorded, at least in the Neotropics, inhabiting clay nests ('epigeous termitaria') or below ground (Table 1). The number of termite genera present in the sites, was not affected by the occurrence of fire ($F[1,4] = 0.22$; $P = 0.64$). Accordingly, termite abundance (=number of records per genus) differed among genera, but these differences, however, were not due to the occurrence of fire (Table 2).

Table 1. Nesting habits of termite genera recorded in burnt and unburnt sites of Cerrado in central Brazil. "Clay walls": living in mounds with clay walls (either as its builder, or as inquiline); "below ground": living within soil matrix; "within wood": living within logs. A "x" means that at least one species in that genus is known to present such an habit.

	Nesting habit			Authority
	clay walls	below ground	within wood	
RHINOTERMITIDAE: Heterotermitinae				
<i>Heterotermes</i> Froggatt	-	x	x	Mathews 1977
TERMITIDAE: Apicotermitinae				
<i>Anoplotermes</i> Fr. Müller	x	x	-	Mathews 1977
<i>Aparatermes</i> Fontes	-	x	-	Fontes 1986
<i>Grigiotermes</i> Mathews	x	-	-	Mathews 1977
TERMITIDAE: Nasutitermitinae				
<i>Armitermes</i> Wasmann	x	-	-	Grassé 1984
<i>Cornitermites</i> Wasmann	x	-	-	Grassé 1984
<i>Diversitermes</i> Holmgren	x	-	-	Mathews 1977
<i>Nasutitermes</i> Dudley	x	x	x	Mathews 1977
<i>Procornitermes</i> Emerson	x	x	-	Emerson 1952
<i>Velocitermes</i> Holmgren	x	-	-	Mathews 1977
TERMITIDAE: Termitinae				
<i>Dihoplotermes</i> Araujo	x	-	-	Araujo 1961
<i>Termes</i> Linnaeus	x	-	-	Mathews 1977
Unidentified	?	?	?	-

Table 2. Analysis of Variance table for the effects of fire, taxonomic identity ("genus"), and their interaction, on the number of termite records in Cerrado region, central Brazil. Geographical location ("site") treated as a blocking factor. Linear Mixed Model with REML variance estimation.

	Effect	Effect Df	Residual Df	F-value	p-value
Site (block)	2	2	6.2026	0.1388	
Genus	12	48	7.9407	<0.0001	
Fire	1	2	0.8717	0.4490	
Genera: Fire	12	48	0.7827	0.6650	

THIS IS NOT THE TABLE THAT WAS MAILED WITH THE MANUSCRIPT, ALSO WHY IS THERE AN EXTRA COLUMN WITHOUT NUMBERS?

DISCUSSION

Effects of fire on termite generic richness in the Cerrado Generic richness of termite communities did not change following fire in the Cerrado stands. Absence of changes in generic richness may occur simply because such a taxonomic category would present higher persistence than its composing species (i.e., one species can disappear

without compromising genera presence in the area). This mechanism, however, seems to not play an important role in the system reported here, since the termite community studied here is not characterized by species-rich genera (more than a half of the identified genera comprises two or less species in Cerrado region). Furthermore, upon the local extinction of one species, a diminishment in abundance of the community would be observed, unless extant species would respond to this extinction by increasing their own abundance, thereby recomposing the original numbers. Termite genera abundance (= number of records per genus), however, did not change significantly according to fire (Table 2), which suggests that either termite populations were not lowered by fire or that possible reductions have been quickly recomposed in the time lag between the fire event and data collection.

Termite populations may escape reductions following fire by inhabiting hard clay mounds (Abensperg-Traun & Milewski 1995). This should be even more effective in environments such as the Cerrado, where fire is normally of moderate intensity. During a burning event in the Cerrado, soil surface temperatures attain a maximum of 74° C, last for a few minutes only and return to normal values within one hour. Temperatures in soil layers 1, 2 and 5 cm deep reach values even lower than that of the surface (Coutinho 1978). Therefore, not only builders of hard clay mounds seem to be able to survive, but also those inhabiting nests within the soil matrix. Among the genera studied here, the majority build clay nests, either above or below ground (Table 1). Exceptions would include *Heterotermes*, which can live in diffuse nests within wood and *Nasutitermes*, which exhibits a variety of nesting habits. Notwithstanding those exceptions, the fire in our Cerrado study was not intense enough to cause reductions on termite populations, at least not enough to cause changes in generic richness, which make pathways A, B, C of Fig. 1 not applicable here.

Resilience, or the ability of populations to return to pre-disturbance levels, could also help termites to cope with fire (Abensperg-Traun *et al.* 1996). One of the traits favoring high resilience in termites is the ability to build a single colony composed by several satellite, spatially spread nests ('polycaly', 'polycalism' or 'polycalicity', see Emerson 1952). Upon a fire event, termites could migrate temporarily into less affected adjacent nests (Abensperg-Traun *et al.* 1996). It is still unknown how many termite species present polycalic nests. However, among the genera studied here, at least *Procornitermes* has one species for which polycaly has already been recorded (Emerson 1952). Thus, polycaly could have been one of the mechanisms helping termites to cope with fire. Even without detectable changes in total abundance, fire may

affect richness through changes in resource availability. As seen before, termite generic richness did not change according to fire in the Cerrado, which could have resulted from two possibilities. First, lowered resource quantity did not attain critical levels so as to promote competitive exclusion (Fig. 1F). Absence of strong competitive asymmetry in termites is possible at least in theory, since, as detritivores, they do not affect directly the availability nor the regeneration of their resource. That is, the amount of resource needed by one species does not depend directly on resource consumption by another coexisting detritivore species (see DeSouza & Brown 1994). If this seems plausible at species level, so it would be for genera, where competitive interactions are, per definition, comparatively weaker. Secondly, termite generic richness might not have been affected by the fire because lowered resource variety did not promote local extinctions, which is likely when there are no strict specialists and guilds are flexible enough to support strong niche overlap (Fig. 1E). Although frequently associated with a certain food type, termite genera often are not strict specialists (Abensperg-Traun 1992). *Heterotermes*, for instance, is commonly cited as a wood feeder (Mathews 1977), but is the main termite pest feeding on sugarcane (Constantino 2002). Therefore, even if the fire event would have acted selectively, destroying only certain resource types, termites could have survived by rearranging their dietary requirements.

Concluding, termite genera in burnt stands of the Cerrado escape local extinction because (i) fire in the Cerrado may not be intense enough to kill colonies housed within soil or behind protective clay walls; (ii) populations may be able to recover quickly; and (iii) absence of strict dietary specialization, coupled with low levels of competitive interactions, may allow niche overlap, minimizing effects of reductions in food resource.

ACKNOWLEDGMENTS

The authors are grateful to M. Abensperg-Traun, L. Kirton, R. Constantino and C.F. Sperber, whose critical comments significantly improved the manuscript. ODS is grateful to the staff and students of Pós-graduação em Ecologia e Conservação da Biodiversidade, Univ. Fed. Mato Grosso, for all support during the academic visit from which this paper has arisen. ODS is supported by a CNPq Research Fellowship. CAPES and CNPq provided graduate studentships. This manuscript was entirely produced using free software (Linux, LaTeX2e, Xemacs, BibTeX, and R).

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