UNIVERSIDADE DE BRASÍLIA

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

Run to the Hills: Cupinzeiros como abrigo contra o fogo para a herpetofauna do Cerrado

Luis Felipe Carvalho de Lima

Brasília

Setembro/2024

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Dissertação de Mestrado apresentada ao Programa de Pós-graduação em Zoologia, Instituto de Ciências Biológicas, da Universidade de Brasília, como parte dos requisitos necessários à obtenção do título de Mestre em Zoologia.

Orientador(a): Reuber Albuqueque Brandão

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“Pois quem dorme, sonha. Quem vive, realiza.”

Luiz Fernando Correia da Silva, Tribo da Periferia.

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RESUMO

Run to the Hills: Cupinzeiros como abrigo contra o fogo para a herpetofauna do Cerrado

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Resumo da Dissertação de Mestrado apresentada ao Programa de Pós-graduação em Zoologia, Instituto de Ciências Biológicas, da Universidade de Brasília, como parte dos requisitos necessários à obtenção do título de Mestre em Zoologia.

No Cerrado, os incêndios são fenômenos naturais sazonais que moldam a biodiversidade do bioma, com um histórico de ocorrências que contribuiu para a adaptação da fauna local. Embora os incêndios naturais sejam um componente crucial para a manutenção de certas espécies, a intensificação dos eventos provocados por atividades humanas pode desestabilizar o equilíbrio ecológico, afetando negativamente a sobrevivência e a regeneração das populações. Os cupinzeiros, estruturas naturais abundantes no Cerrado, desempenham papel vital como refúgios microclimáticos durante e após os incêndios, oferecendo abrigo e estabilidade térmica para diversos organismos. Este estudo investiga como cupinzeiros contribuem para a resiliência da herpetofauna do Cerrado durante e após incêndios, bem como que características estruturais desses abrigos afetam a abundância e a riqueza de espécies que buscam refúgio nesses locais. Testamos se a temperatura e a umidade interna dos cupinzeiros permanece mais estável que a temperatura e a umidade da superfície e do solo adjacente. Também avaliamos como diferenças de temperatura são influenciadas pelas características estruturais dos cupinzeiros. Buscamos testar a hipótese de que a temperatura e a umidade dentro dos cupinzeiros não foram afetadas pelos eventos de fogo estudados, onde esses parâmetros seriam mais estáveis dentro dos cupinzeiros em comparação com o ambiente ao redor. Para realizar nosso experimento, aproveitamos queimadas prescritas para simular incêndios naturais, registrando a temperatura e a umidade (com dataloggers) do interior de cupinzeiros em áreas sob efeito do fogo (UFE), em áreas um dia após o fogo (DAF) e em áreas sem fogo (AWF). Medimos o diâmetro, a altura, as temperaturas interna e externa, a umidade e características do habitat. Os cupinzeiros foram abertos para capturar e identificar a herpetofauna. Modelos Lineares Generalizados foram usados para relacionar a temperatura interna dos cupinzeiros às suas características estruturais. Analisamos 179 cupinzeiros, sendo 69 no tratamento AWF, 66 no tratamento UFE e 44 no tratamento DAF. Registramos 124 indivíduos de 15 espécies de répteis e 10 indivíduos de seis espécies de anfíbios utilizando os cupinzeiros como abrigo. O tratamento UFE apresentou a maior abundância (71 indivíduos) e riqueza de espécies (14 espécies), seguido pelo DAF com 37 indivíduos e 14 espécies e AWF, com 26 indivíduos e 10 espécies. A temperatura interna dos cupinzeiros variou entre 12,1ºC e 31,4ºC, enquanto umidade interna nunca esteve abaixo de 86.9%. Encontramos diferenças significativas nas temperaturas internas e externas dos cupinzeiros, com variações notáveis entre os tratamentos. Modelos GLM mostraram que a temperatura interna dos cupinzeiros no tratamento AWF não foi significativamente explicada pelas variáveis estudadas, enquanto no tratamento UFE, a temperatura interna não teve variáveis significativas associadas. No tratamento DAF, o volume dos cupinzeiros e o número de árvores explicaram a temperatura interna, com o volume tendo efeito positivo e o número de árvores com efeito negativo. A abundância e riqueza de espécies foram mais associadas ao volume dos cupinzeiros. O volume dos cupinzeiros teve efeito positivo significativo na abundância, enquanto o número de buracos e a temperatura interna variaram em seus efeitos, dependendo do tratamento. Nosso estudo reforça que cupinzeiros são amplamente utilizados pela herpetofauna do Cerrado, oferecendo abrigo essencial para várias espécies de répteis e anfíbios. A abundância de répteis dentro dos cupinzeiros sugere que esses animais buscam rotineiramente refúgio nessas estruturas, especialmente durante e após incêndios. Muitas espécies encontradas em áreas afetadas pelo fogo usam os cupinzeiros como abrigo temporário, embora não sejam residentes permanentes. Reptéis, particularmente lagartos, são mais representados, possivelmente devido à sua maior mobilidade, enquanto os anfíbios são menos abundantes nos cupinzeiros, refletindo sua preferência por ambientes úmidos e, teoricamente, menos propensos a incêndios. Além de proporcionar refúgio contra o fogo, os cupinzeiros servem como locais de alimentação e nidificação. As características estruturais dos cupinzeiros, como volume e número de buracos, influenciaram sua temperatura interna e, consequentemente, a disponibilidade de abrigo. A estabilidade térmica proporcionada pelos cupinzeiros durante e após os incêndios destaca sua importância como refúgios para a fauna do Cerrado e destaca o papel dessa estrutura não apenas na sobrevivência dos organismos mas também na gestão do fogo em áreas naturais.

Palavras-chave: Ecologia do fogo, Microclima, Queima prescrita, Incêndios florestais, Resiliência, Biodiversidade.

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ABSTRACT

Run to the Hills: Termite mounds as fire shelter for the Cerrado herpetofauna

Luis Felipe Carvalho de Lima

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Abstract da Dissertação de Mestrado apresentada ao Programa de Pós-graduação em Zoologia, Instituto de Ciências Biológicas, da Universidade de Brasília, como parte dos requisitos necessários à obtenção do título de Mestre em Zoologia.

In the Cerrado, wildfires are natural and seasonal phenomena that shape the biome's biodiversity, with a history of occurrences that has driven local fauna adaptation. While natural fires are crucial for maintaining certain species, the intensification of fire events due to human activities can destabilize the ecological balance, negatively impacting population survival and regeneration. Termite mounds, abundant natural structures in the Cerrado, play a vital role as microclimatic refuges during and after fires, providing shelter and thermal stability for various organisms. This study investigates how termite mounds contribute to the resilience of the Cerrado's herpetofauna during and after fires, as well as which structural features of these shelters affect the abundance and richness of species seeking refuge there. We tested whether the internal temperature and humidity of the termite mounds remain more stable than those of the surface and adjacent soil. We also assessed how temperature differences are influenced by the structural characteristics of the termite mounds. We hypothesized that the temperature and humidity inside the termite mounds were not affected by the fire events studied, with these parameters being more stable inside the mounds compared to the surrounding environment. To conduct our experiment, we took advantage of prescribed burns to simulate natural fires, recording the temperature and humidity (using dataloggers) inside termite mounds in areas affected by fire (UFE), in areas one day after the fire (DAF), and in areas without fire (AWF). We measured diameter, height, internal and external temperatures, humidity, and habitat characteristics. The termite mounds were opened to capture and identify the herpetofauna. Generalized Linear Models were used to relate the internal temperature of the termite mounds to their structural characteristics. We analyzed 179 termite mounds, with 69 in the AWF treatment, 66 in the UFE treatment, and 44 in the DAF treatment. We recorded 124 individuals from 15 reptile species and 10 individuals from six amphibian species using the termite mounds as shelters. The UFE treatment showed the highest abundance (71 individuals) and species richness (14 species), followed by DAF with 37 individuals and 14 species, and AWF with 26 individuals and 10 species. The internal temperature of the termite mounds ranged from 12.1ºC to 31.4ºC, while internal humidity never dropped below 86.9%. Significant differences were found between the internal and external temperatures of the termite mounds, with notable variations among treatments. GLM models showed that the internal temperature of the termite mounds in the AWF treatment was not significantly explained by the studied variables, while in the UFE treatment, no significant variables were associated with internal temperature. In the DAF treatment, mound volume and the number of trees explained internal temperature, with volume having a positive effect and the number of trees a negative effect. Species abundance and richness were more associated with mound volume. Mound volume had a significant positive effect on abundance, while the number of holes and internal temperature varied in their effects depending on the treatment. Our study reinforces that termite mounds are widely used by the Cerrado's herpetofauna, providing essential shelter for various reptile and amphibian species. The abundance of reptiles within the mounds suggests that these animals routinely seek refuge in these structures, especially during and after fires. Many species found in fire-affected areas use the termite mounds as temporary shelters, though they are not permanent residents. Reptiles, particularly lizards, are more represented, possibly due to their greater mobility, while amphibians are less abundant in the mounds, reflecting their preference for moist environments, theoretically less prone to fires. In addition to providing refuge from fire, termite mounds serve as feeding and nesting sites. The structural characteristics of the termite mounds, such as volume and the number of holes, influenced their internal temperature and, consequently, the availability of shelter. The thermal stability provided by termite mounds during and after fires highlights their importance as refuges for the Cerrado fauna and underscores the role of these structures not only in the survival of organisms but also in fire management in natural areas.

Key-words: Fire Ecology, Microclimate, Prescribed Burns, Wildfires, Resilience, Biodiversity.

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Introduction

As for other savannas around the world, wildfires are common phenomena in the Cerrado ecological history (Cole, 1960; Ferraz-Vicentini & Salgado-Labouriau, 1996), shaping the biome biodiversity (Simon et al., 2009; Simon & Pennington, 2012; Fidelis & Zirondi, 2021). The Brazilian Cerrado is the hotter and wetter of all savannas (Lehmann et al., 2014; Nascimento & Novais, 2020). The ecological history of fire in Cerrado involves the occurrence of natural fires, often caused by natural phenomena, such as ignitions caused by lighting during the transition between the dry and the rainy seasons (Ramos-Neto & Pivello, 2000; Klink et al., 2020). These natural fires typically consume mainly the biomass of the grassy layer present in the open fields and savanna phytophysiognomies (Schmidt et al., 2016, Pilon et al., 2021; Rodrigues et al., 2021). However, most fire events in the biome currently occur during the dry season, being caused by human activities (Berlinck & Batista, 2020; Klink et al., 2020), often intentionally, disrupting the natural fire regime (Bowman et al., 2011; Pivello, 2011; Schmidt & Eloy, 2020; Pivello et al., 2021).

Natural fire is an important driver of biodiversity in the Cerrado (Simon et al., 2009; Simon & Pennington, 2012; Fidelis & Zirondi, 2021). Many Cerrado animals seem to get some benefit from the occurrence of fires (Drummond, 2009; Costa et al., 2020), such as the endemic lizard *Micrablepharus atticolus*, which shows short-term demographic increases after fire (Sousa et al., 2015). However, in the long term, its demographic is negatively affected by extreme fire regimes and the complete absence of fires (Sousa et al., 2015). This illustrates the complex relationship between Cerrado fauna and wildfire events, highlighting the eventual sensitivity of some taxa to disturbances in their natural fire regime, i.e. intermediary fire patterns.

Changes in the frequency and intensity of fires lead to increased severity of these events (Trollope et al., 2002; Gorgone-Barbosa et al., 2016; Gomes et al., 2020; Schmidt & Eloy, 2020). Although fire is a natural component of the open physiognomies of the Cerrado, changes in the fire regime cause pervasive disturbances in the structure and composition of ecosystems (Medeiros & Miranda, 2008; Vieira & Mendonça, 2019; Berlinck & Batista, 2020; Klink et al., 2020; Cazetta & Vieira, 2021). High-intensity fires affect survival rates and the regeneration processes of populations, impairing the resilience capacity of some species (Sousa et al., 2015; Vieira & Mendonça, 2019; Cazetta & Vieira, 2021; Batista et al., 2023;

Bergstrom et al., 2023; Sousa et al., 2023; Lourenço et al., 2024).

Considering millennia of evolution and adaptation (Simon et al., 2009), the fauna of the Cerrado's open phytophysiognomies have developed several mechanisms, strategies, and behaviors to enable coexistence with fire (Pivello, 2011; Bond, 2015, Batista et al., 2023; Miranda et al., 2023; Souza et al., 2023). Thus, the herpetofauna inhabiting these phytophysiognomies are usually resilient against some fire regimes (Costa et al., 2013; Durigan et al., 2020; Ribeiro et al., 2020; Anjos et al., 2024), especially when wildfires are less widespread in the landscape, a common characteristic of natural wildfires (Russell et al., 1999; Certini et al., 2021; Santos et al., 2021). Ideally, the Cerrado fauna can also be resilient to prescribed fires, but very little data is available.

A common strategy adopted by the Cerrado herpetofauna during fires is the use of shelters available in the environment, such as burrows, logs, and termitaria (Costa et al., 2013). Termite mounds play a significant role in this context, providing thermal shelter for a large number of species (Fleming & Loveridge, 2003; Costa, 2005; Colli et al., 2006; Costa et al., 2009; Moreira et al., 2009; Rodrigues et al., 2009; Moro et al., 2014; de-Carvalho & Citeli, 2022). The refractory capacity of termite mounds may allow the maintenance of stable temperature and humidity in its internal layers, preventing abrupt variations even during dry seasons or wildfire events (Konaté et al., 1999; Jouquet et al., 2004; Vitt et al., 2007; Turner & Soar, 2008; Eggleton, 2011).

Termite mounds are widespread features in the Cerrado landscape, and termites themselves constitute the largest animal biomass in the biome (Redford, 1984). These insects play a crucial role in soil formation, moving large quantities of soil each year, contributing biomass, and significantly impacting nutrient cycling (Salick et al., 1983; Crowther et al., 2019; D'Angioli et al., 2024). The different construction strategies adopted by several termite taxa provide a range of microhabitats potentially used as shelter for different forms of life (Korb, 2010). In addition to mound-building termites, other invertebrates such as arachnids, centipedes, millipedes, and insects, as well as some vertebrates including reptiles, amphibians, small mammals, and birds, use these structures for numerous ecological interactions (Costa et al., 2009; Dias, 2011; Duleba & Ferreira, 2014; Lima & Brandão, 2024; present study).

Some species prefer specific kind of microhabitats for thermoregulation, based on environmental characteristics and their physiological needs (Adolph, 1990). In this context, the exterior layer of termite mounds is an important site for thermoregulation to lizards, providing a surface exposed to the sun and allowing them to control the solar incidence (and its internal temperature) due to the termitaria semi-elliptical shape (Rocha & Bergallo, 1990; Gandolfi & Rocha, 1998). In contrast, the microclimatic stability found in the termitaria inner layers provides favorable conditions for the survival of ectothermic and moisture-dependent vertebrates, such as most amphibians and reptiles (Closel & Kohlsdorf, 2012). In this context, termitaria display a relevant role within the open cerrado habitats, creating sites for thermoregulation, but also as a microclimatic refuge against environmental hashes, including fire (Costa et al., 2013; Costa et al., 2020).

Therefore, termite mounds are commonly used by the herpetofauna for various purposes, such as reproduction, feeding, refuge against predators, and thermal shelter (Brandão & Vanzolini, 1985; Riley et al., 1985; Colli et al., 2003; Pramuk & Alamillo, 2003; Vitt et al., 2007; Knapp & Owens, 2008; Lima & Eterovick, 2013; Duleba & Ferreira, 2014; Amorim et al., 2017; Brandão et al., 2020). Termites, in turn, serve as a nutritious, abundant, and easily accessible primary food source for numerous predators in the Cerrado (Redford & Dorea, 1984; Juarez & Marinho-Filho, 2002; Marques-Pinto et al., 2019). Thus, the richness of termites can impact the richness of insectivorous animals, especially influencing the presence of *taxa* highly dependent on these organisms and by the availability of the structures they provide (Costa, 2005; Colli et al., 2006; Moreira et al., 2009; Moro et al., 2014).

The fauna of open vegetation formations in the Cerrado is resilient to fire (Costa et al., 2013; Durigan et al., 2020; Ribeiro et al., 2020; Anjos et al., 2024), and we believe that the presence of termite mounds, which represent significant biomass (Redford, 1984, Redford & Dorea, 1984) and volume, may influence this resilience, allowing the survival during the passage of fire line (Costa et al., 2013), and by providing resources and shelter in the recently burned Cerrado (de-Carvalho & Citeli, 2022; Batista et al., 2023).

Although most of the studies on the using of termite mounds by animals Cerrado merely focused on describing the associated fauna (Costa et al., 2009; Moreira et al., 2009; Duleba & Ferreira, 2014). However, some few studies aimed to describe some ecological aspects that influence these interactions (Gandolfi &

Rocha, 1998; Vitt et al., 2007; Choosai et al., 2009; Costa and Vanin, 2010; Leitner et al., 2020), highlighting the need to investigate how termite mounds can be key drivers of biodiversity in open areas.

Given the importance of termite mounds for the Cerrado biome and the limited research on their ecological interactions with herpetofauna, our study aims to evaluate the role of these termitaria as microclimatic refuges during and after fires, and their contribution to the short-term resilience of these organisms. We investigated differences in species richness and abundance of herpetofauna using termite mounds as shelters in areas without fire, areas under fire effect, and areas one day after fire, and examined how these patterns were influenced by the characteristics of the termite mounds. We also tested the hypothesis that the internal temperature of termite mounds remained lower than the surface and adjacent soil temperatures across all treatments, and we assessed how this temperature differential was driven by the termitaria structural features. Additionally, we tested the hypotheses that the temperature and humidity inside the termite mounds were unaffected by the passage of the fire line, being more stable inside the mounds compared to the surrounding environment.

Material and Methods

Study area

The study was conducted in the Serra do Tombador Natural Reserve (STNR) (Fig. 1), a Private Natural Heritage Reserve maintained by the Boticario Foundation for Nature Protection (FBPN), located in the municipality of Cavalcante, state of Goiás, near the border with the state of Tocantins (13°39'08.2"S, 47°49'44.2"W; 779m above sea level). The STNR is a large private protected area, with 8,730.45 hectares, and harbors one of the most relevant herpetofauna taxocenoses in the Cerrado, with 40 species of reptiles and 34 species of amphibians, including species with restricted distribution, such as *Allobates goianus*, *Bokermannohyla pseudopseudis*, *Scinax rupestris*, and *Leptodactylus tapiti* (Guerra et al., 2022).

The local vegetation is mainly composed by natural grasslands, savannas, and forest formations, with the prevalence of open formations, corresponding to more than 77% of the landscape (RNST, 2011). The climate is tropical savanna with a dry winter season (Aw according to the Köppen-Geiger classification, Alvares et al., 2013), and markedly seasonal. The rainy season corresponds to November to March, with annual precipitation reaching up to 1,600 mm (Alvares et al., 2013), while the dry season corresponds to April to October.

As large wildfires threaten the local biodiversity, since 2018 the STNR staff has employed prescribed burns (*sensu* Bosnich et al., 2000; Medeiros et al., 2001) aiming to reduce part of inflammable biomass and to create firebreaks for wildfire management. This technique involves controlled burning of predetermined target areas eventually burned at different times in short time episodes. Prescribed burns are usually applied at the beginning of the dry season when the vegetation is dry enough to allow ignition but still moist enough to prevent the fire from spreading uncontrollably (Ray et al., 2005; Santos et al., 2021). In this way, prescribed burns have intensity and severity characteristics similar to natural fires (Durigan & Ratter, 2015; Schmidt et al., 2016; Gomes et al., 2020; Santos et al., 2021). As a result, incidental fires throughout the dry season are halted due to the lack of fuel (Schmidt et al., 2018) and by avoiding the costs of traditional fire combat.

Since the occurrence of natural wildfires would be unpredictable in time and space, we used these prescribed burns as a surrogate for natural wildfires (Fig. 2A). We sampled seven areas where prescribed burns were applied and seven areas without fire (Fig. 1), including grassland, bush field, cerrado *stricto sensu*, and rocky cerrado.

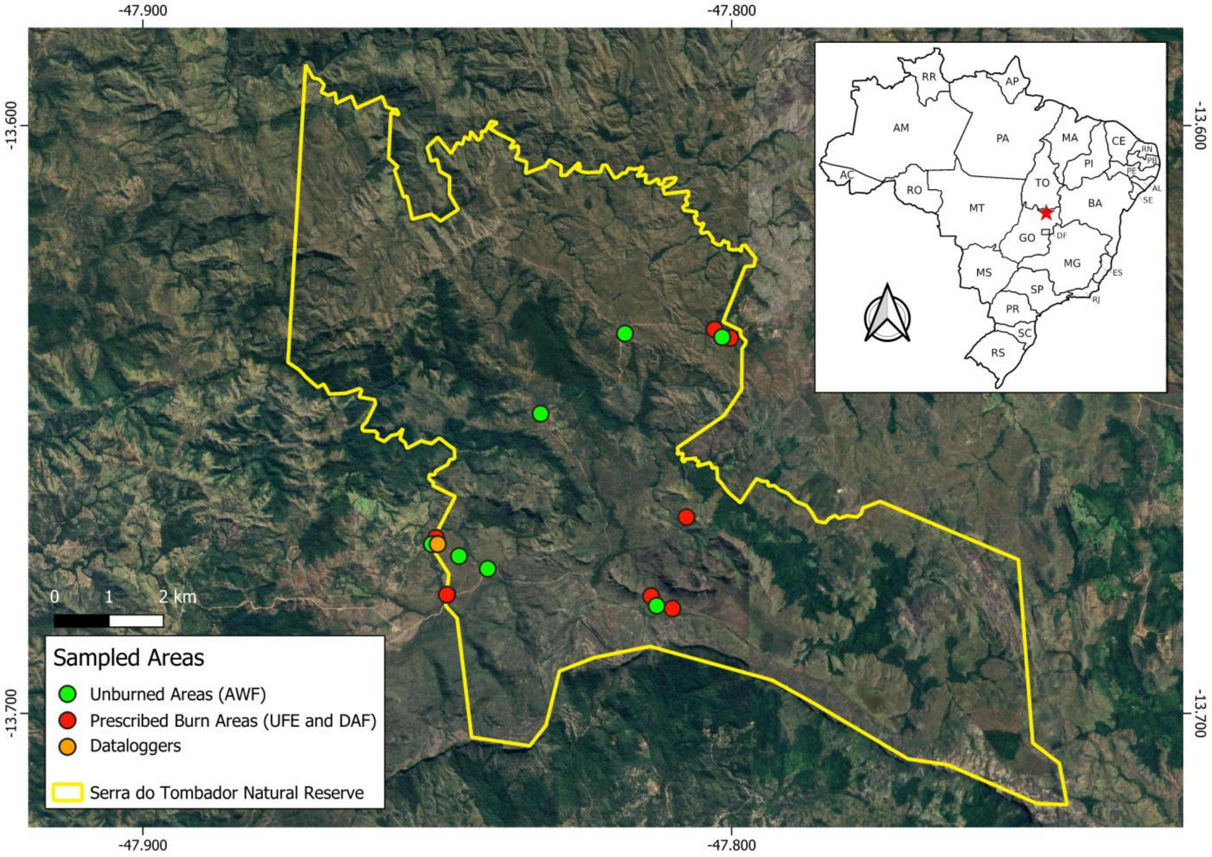

Figure 1 – Map of the Serra do Tombador Natural Reserve in Cavalcante, Brazil (inset map), showing the sampled areas. Green circles: locations where we sampled termite mounds in areas without fire (AWF); Red circles: locations where prescribed burns were conducted, and we sampled termite mounds affected by fire (UFE) and one day after the fire (DAF); Orange circle: area where we installed dataloggers inside termite mounds subjected to a prescribed burn, termite mounds in normal conditions, and in the external environment.

Sampling methods

Data sampling in the field was conducted during two expeditions to the STNR between April 21st and May 4th, and June 4th to June 15th, 2023. To evaluate the effect of the fire on the usage of termite mounds by the Cerrado herpetofauna, we accessed the herpetofauna richness (RI) and abundance (AB) in termite mounds (Fig. 2B) under three situations: under fire line effect (UFE; Fig. 2C), one day after the fire line passage (DAF; Fig. 2D), and areas without fire (AWF). As a way to simulate a scenario closer to natural fire, we used prescribed burns and firebreak burns used in the integrated fire management of the reserve (Fig. 2A). We selected termite mounds within the burned areas in UFE and DAF and randomly searched for termite mounds in open cerrado areas in AWF.

For each selected termite mound, we gathered the following data: major and minor diameters, maximum termitaria height, surface temperature (ST) and internal temperature (IT) of the mound, temperature of the soil one meter away from the mound (SOT), number of holes (NH), presence of associated trees (NT) and bushes (NB), habitat, geographical coordinates, and the associated vertebrates. To measure temperatures, we used an infrared thermometer model Perceptec DT8750 (temperature range: -50ºC to +750ºC) (Fig. 2A). Termite measurements were accessed using a measuring tape. We used the hemiellipsoid volume equation to access the termite volume (VOL), following Domingos 1983, given by:

$$V = \left(\frac{\frac{4}{3}\pi(x * y * z)}{2}\right)$$

where "x" corresponds to the major diameter, "y" corresponds to the height, and "z" corresponds to the minor diameter.

To sample herpetofauna in termitaria, each termite mound was carefully opened using tools (pickaxe, hoe, lever) (Fig. 2A), and all animals were manually captured, identified, measured, weighted, and released at the same location. Animals eventually found dead were collected and deposited in Coleção Herpetológica da Universidade de Brasília (CHUnB). After sampling, all large fragments of the termite mounds were piled up at the original site to allow for the reconstruction of the termitaria structure. Data collection was authorized by SISBIO license (#88336-1).

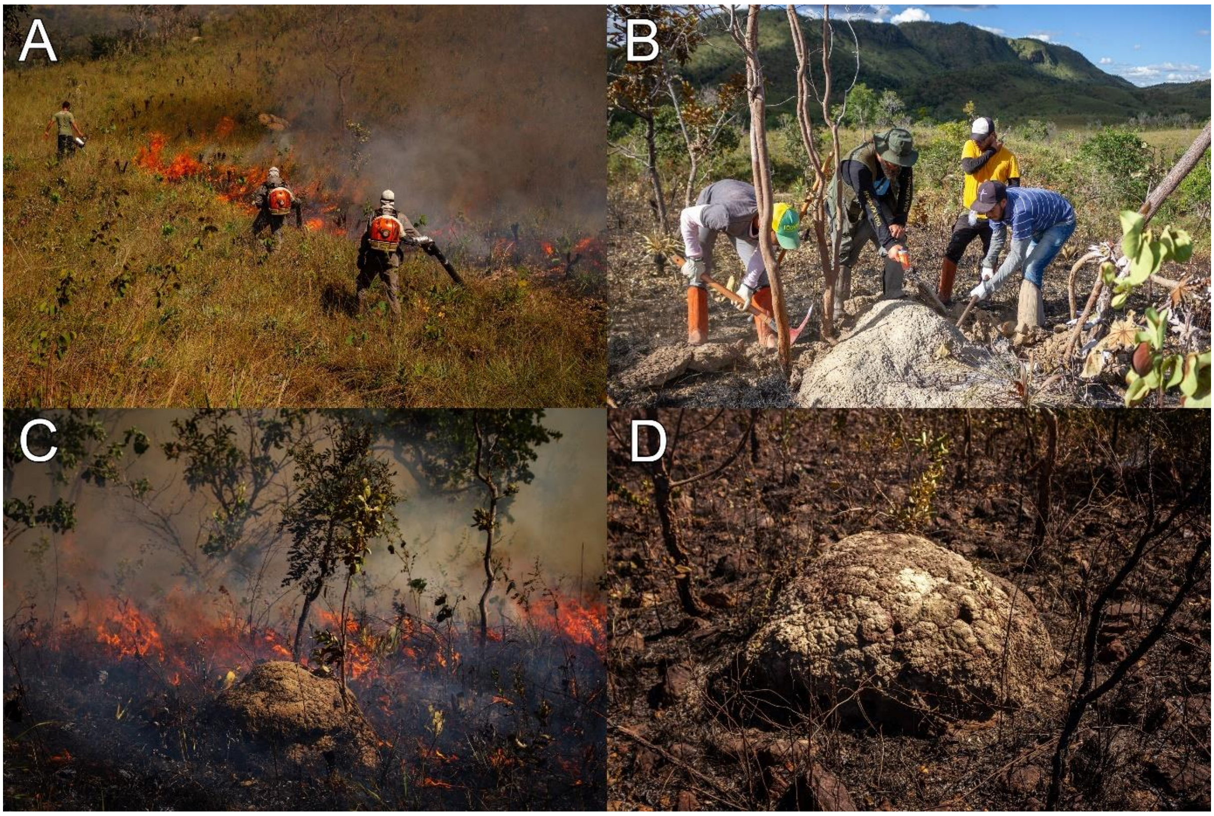

Figure 2 – Components of the methodology applied for data sampling. A) Reserve fire brigade conducting a prescribed burn in a bush field area. B) Research teamwork opening and collecting the surface temperature of a termite mound one day after the fire. C) Termite mound under fire line effect. D) Termite mound one day after the fire line passage.

We used portable dataloggers, model Perceptec DHT1432 (firmware V3.11, temperature range: -20ºC to +85ºC, humidity range: 0 to 100%RH), to obtain temperature (ºC) and humidity (%RH) data inside five termite mounds in the studied area (Fig. 1), being three under fire effect (UFE) and two under normal conditions (UNC). We made a hole large enough to insert the datalogger into the central part of the termite mound (Fig. 3A). The dataloggers were equipped with plastic mesh to prevent termites from accessing the circuit and were secured with wire for its retrieval (Fig. 3B). After installation (Fig. 3C), we sealed the termite mound using its clay material to isolate the dataloggers from external weather conditions (Fig. 3D). We also installed a sixth external datalogger fixed at a height of 1 meter to obtain environmental data under normal conditions (ENV). Each datalogger was programmed to capture data every 15 seconds for 24 hours, starting at 2:00 PM on June 9, 2023.

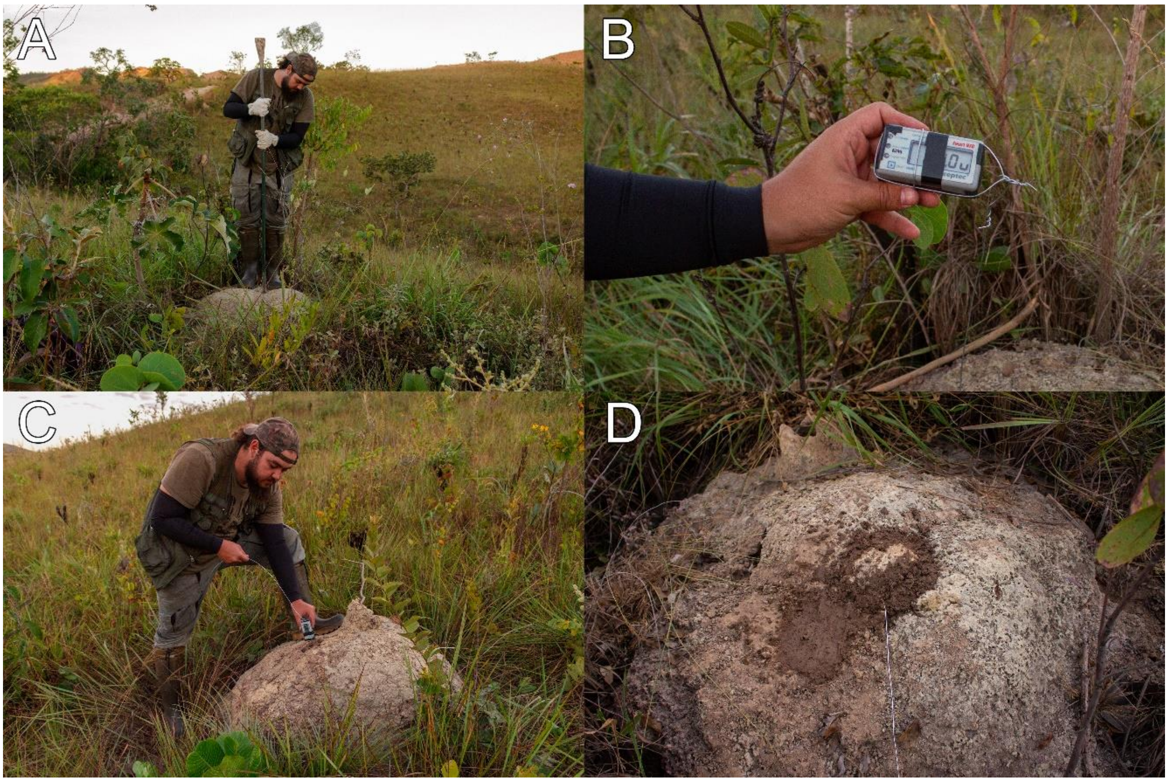

Figure 3 – Methodology for installing dataloggers inside termite mounds. A) LFCL opening a hole at the top of a termitaria with a crowbar for datalogger installation. B) Preparing the datalogger for installation inside the termite mound. C) LFCL installing the datalogger inside the mound. D) Termite mound sealed after datalogger installation. Photos: Emayre Campos.

Statistical Analyses

To compare the internal temperature of the termite mounds with the external temperature and assess how it responds to each treatment, we assessed statistical differences in internal temperature (IT), surface temperature (ST), and temperature of the soil around the mounds (SOT) measurements both within and between active sampling treatments (AWF, UFE and DAF). We used the Shapiro-Wilk W test to assess normality and the Levene's test to evaluate the homogeneity of the data. To test our first hypothesis, we applied the non-parametric Kruskal-Wallis test when the assumptions of normality and homogeneity of variances were violated. When the data were normally distributed but variances were not homogeneous, we used the Welch *F* test. Additionally, we used Dunn’s post hoc test to identify significant differences between specific data groups.

We used Zero-Inflated Poisson (ZIP) regression models to evaluate how the richness and abundance in each treatment could be explained by variables collected from the termite mounds. For this analysis, we excluded variables unrelated to the interior of the termite mounds. When two or more variables were highly related (e.g. measurements and volume of termitaria), we selected the most representative one. We generated 26 models for each response variable (RI and AB), incorporating all possible combinations of explanatory variables (VO, NH, NT, NB, IT), and compared them using the Akaike Information Criterion (AIC) to identify the best-fitting models (Bozdogan, 1987). We also created null models containing only the intercept (without explanatory variables) for each treatment. We considered models with ΔAIC ≤ 2 relative to the model with the lowest AIC as equally plausible models. We used the Log-Likelihood (Log-llh) to evaluate how well each model fit the observed data and McFadden's pseudo-R^2 (p-R^2) to assess each model's fit relative to the null model. We chose this type of modeling because our richness and abundance data are not linear and contain a large number of zeros, as most of the opened termite mounds did not contain reptiles or amphibians (Agarwal et al., 2002), although each unoccupied mound can be potentially used.

To evaluate how the internal temperature of the termite mounds in each treatment can be explained by their structural characteristics, we used Generalized Linear Models (GLMs) of the Gaussian family. We excluded all variables unrelated to the structural characteristics of the termite mounds, resulting in 11 models with all possible combinations of explanatory variables (VO, NH, NT, NB). To assess and compare the model fits, we used the same approach applied to the richness and abundance. All analyses were performed using R software (Version 4.4.1; R, 2024).

We excluded three termite mounds sampled in the AWF treatment from all analyses due to missing data (data analyzed: AWF n = 66; UFE n = 66; DAF n = 44).

Results

Abundance and species richness

We opened 179 termite mounds, comprising 69 for AWF treatment, 66 for UFE treatment, and 44 for DAF treatment. We found 124 individuals of 15 reptile species and 10 individuals of six amphibian species using the termitaria as shelter (Table 1). The most frequent species was the termitophilous phyllodactylid *Gymnodactylus amarali* (n = 33), *Norops meridionalis* (n = 23) and *Copeoglossum nigropunctatum* (n = 18), while 11 species were represented by only one individual each.

Figure 4 – Species found inside termite mounds with new records in the STNR and a documented reptile nest within a termite mound. A) *Adenomera juikitan* found in DAF. B) *Amphisbaena vermicularis* found in UFE. C) *Adelphostigma occipitalis* found in UFE. D) Unidentified reptile eggs found in UFE. Photos: A, C and D Luis Lima; B Afonso Meneses.

The UFE and DAF treatments had the highest richness, with 14 species each (Table 1). The highest abundance was found in UFE (n = 71), followed by DAF (n = 37), and AWF (n = 26). Three species were exclusively recorded in AWF, four only in UFE, and four only in DAF. Furthermore, three species (*Adenomera juikitan*, Fig. 4A; *Amphisbaena vermicularis*, Fig. 4B; *Adelphostigma occipitalis*, Fig. 4C) correspond to new records for the STNR herpetofauna checklist (Guerra et al., 2022). Additionally, we found seven unidentified reptile eggs (Fig. 4D) inside a termitaria in UFE. We also observed an unidentified rodent using one of the termitaria in AWF, that were not captured or photographed.

Table 1 - Species list and their abundance within termite mounds for each treatment.

TAXA	AWF	UFE	DAF	n
Amphibia				
Anura				
Dendrobatidae				
Ameerega flavopicta	1			1
Hylidae				
Boana albopunctata		1		1
Scinax similis	1			1
Leptodactylidae				
Adenomera juikitan			1	1
Leptodactylus syphax		1	1	2
Physalaemus cuvieri		2	2	4
Reptilia				
Squamata				
Amphisbaenidae				
Amphisbaena vermicularis		6	1	7
Dactyloidae				
Norops meridionalis	2	16	5	23
Gymnophtalmidae				
Cercosaura olivacea		6	1	7
Colobosaura modesta		1		1
Micrablepharus maximiliani	4	7	2	13
Mabuyidae				
Copeoglossum nigropunctatum		16	2	18
Phyllodactylidae				
Gymnodactylus amarali	12	7	14	33
Polychrotidae				
Polychrus acutirostris		1		1
Sphaerodactylidae				
Coleodactylus brachystoma			1	1
Tropiduridae				
Tropidurus oreadicus	4	5	4	13
Boidae				
Epicrates crassus			1	1
Colubridae				
Tantilla melanocephala			1	1
Dipsadidae				
Adelphostigma occipitalis		1		1
Philodryas nattereri	1	1	1	3
Viperidae				
Bothrops aff. *mattogrossensis*	1			1
Total	**26**	**71**	**37**	**134**

Structural characteristics and microclimate of termite mounds

The volume of the termite mounds (VOL) ranged from 0.1m³ to 18.3m³ (average: 1.8m³), with heights between 21cm and 124cm (average: 50cm), and diameters from 10cm to 321cm (average: 130cm for the larger diameter; 115cm for the smaller diameter). Only three termitaria in AWF, four in UFE, and three in DAF were inactive, with four of them infected by saproxylophagous beetles of the genus *Actinobolus* (Lima and Brandão, 2024). The termite mounds had between zero and 26 holes (NH), with an average and most frequent count of six holes. Up to 13 trees (NT) (average: 1; mode: 0) and seven bushes (NB) (average: 1; mode: 0) were found growing in association with an individual termite mound. The highest surface temperature (ST) recorded on a termite mound was 60.7ºC in UFE, while the lowest was 21ºC in DAF. The lowest temperature recorded in the soil close to the termite mound (SOT) was 12.2ºC in DAF and the highest was 58ºC in UFE. In contrast, the lowest internal temperature (IT) recorded inside a termite mound was 12.1ºC in UFE, while the highest was 31.4ºC also in UFE. However, the internal temperature exhibited less variation in AWF (Fig. 5A) compared to UFE (Fig. 5B) and DAF (Fig. 5C) (Appendix 1).

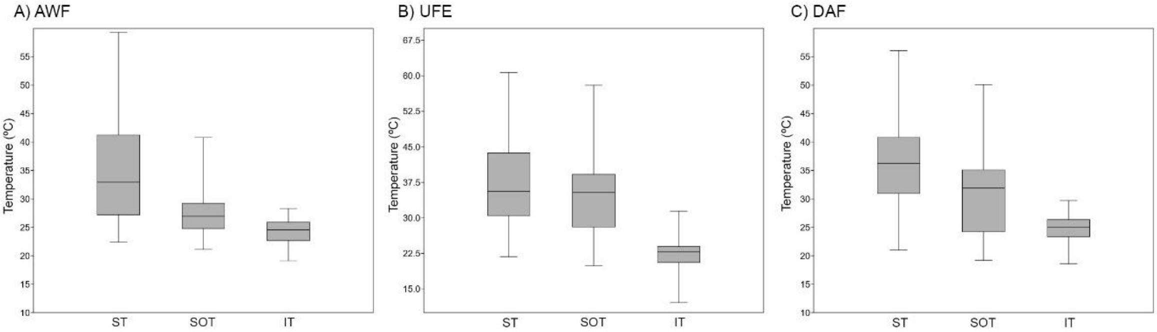

Figure 5 – Boxplots of temperature measurements in each treatment. Abbreviations: AWF = areas without fire, UFE = under fire line effect, DAF = one day after the fire line passage, ST = termitaria surface temperature, SOT = temperature of the soil around the mound, IT = termitaria internal temperature.

We found significant differences between IT, ST and SOT in AWF (Kruskal-Wallis: *H* = 73.48, *p* = 1.10E-16), UFE (Welch *F* test: *F* = 125.2, df = 104.2, *p* = 1.95E-28), and DAF (Welch *F* test: *F* = 57.92, df = 69.44, *p* = 1.59E-15).

We also found differences between all temperatures in AWF (Dunn's post hoc: SOT and ST *p* = 1.56E-05, ST and IT *p* = 1.01E-17, SOT and IT *p* = 2.11E-05) and

DAF (Dunn's post hoc: SOT and ST *p* = 2, ST and IT *p* = 2.60E-13, SOT and IT *p* = 1.84E-05). In UFE, there were significant differences between SOT and IT (Dunn's post hoc: *p* = 3.39E-19), and between ST and IT (Dunn's post hoc: *p* = 3.77E-20), but no significant difference between SOT and ST (Dunn's post hoc: *p* = 0.3). The internal temperature was significantly different between AWF and UFE (Welch *F* test: *F* = 10.67, df = 102, *p* = 6.20E-05; Dunn's post hoc: *p* = 7.24E-05), and between UFE and DAF (Dunn's post hoc: *p* = 3.49E-05), but not between DAF and AWF (Dunn's post hoc: *p* = 0.56). Soil temperature was significantly different (Kruskal-Wallis: *H* = 29.12, *p* = 4.74E-07) between all treatments (Dunn's post hoc: AWF and UFE *p* = 6.82E-08, UFE and DAF *p* = 0.02, AWF and DAF *p* = 0.01). Surface temperature, however, did not differ significantly between treatments (Kruskal-Wallis: *H* = 4.27, *p* > 0.12) although the maximum surface temperature was found in a termite after the fireline passage.

The temperatures recorded by our dataloggers inside the termite mounds showed similar coefficients of variation across both treatments and were significantly lower than the variation in ambient temperature (Table 2). The temperature inside the termite mounds is more stable and does not reach the extreme highs and lows of the external environment (Fig. 6A). When comparing the internal temperature curves, we observe similar patterns between treatments (Fig. 6B, 6C, 6D, 6E, 6F). The internal temperature appears to follow ambient temperature changes over 24 hours but does so gradually and steadily, without abrupt spikes. This pattern remained unchanged in the UFE mounds, with no temperature spikes recorded during the prescribed burn (Fig. 6D, 6E, 6F). Thus, termite mounds maintain milder microclimates compared to the external environment, with temperatures that are neither too hot nor too cold.

Similarly, ambient humidity varied considerably more than inside the termite mounds (Table 3). The lowest relative humidity recorded outdoors was 24.3% RH, while inside the termite mounds, it never dropped below 86.9% RH. As expected, there is an inverse relationship between temperature and humidity in the environment (Zebende et al., 2018), as temperature increases, humidity decreases. Humidity follows a similar pattern inside the termite mounds under normal conditions (Fig. 6B and 6C). Inside the termite mounds affected by fire, the humidity either stabilized (Fig. 5D) or followed temperature trends (Fig. 6E and 6F). However, in both treatments where dataloggers were installed inside termite mounds, humidity showed considerably lower coefficients of variation compared to environmental humidity

(Table 3). We also did not observe any spikes in humidity inside the termite mounds during the passage of the fire (Fig. 6D, 6E, 6F). Thus, termite mounds are able to maintain consistently high humidity levels.

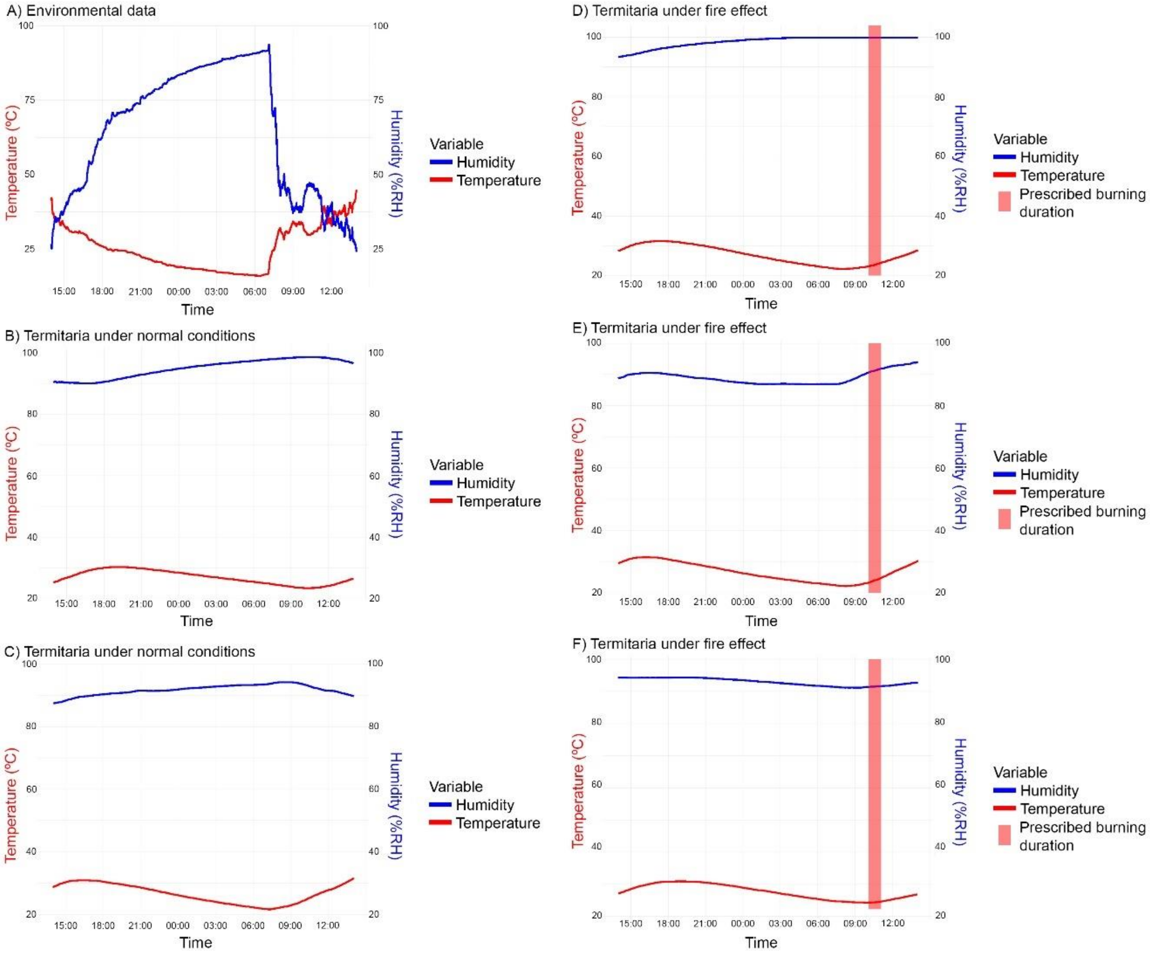

Figure 6 – Graphs of temperature and humidity recorded by dataloggers over 24 hours in three treatments.

Table 2 - Summary of descriptive statistics for temperature measurements from dataloggers in each treatment.

Treatment	Datalogger	Maximum (ºC)	Minimum (ºC)	Mean (ºC)	SD	CV (%)
ENV	A	44.6	16	25.47	7.28	28.6
UNC	B	30.3	22.3	26.99	2.23	8.3
	C	31.5	21.6	26.54	3.1	11.67
UFE	D	31.6	23.5	26.87	3.15	11.7
	E	31	24.3	27.62	2.32	8.39
	F	31.5	22.2	26.64	3.05	11.45

Table 3 - Summary of descriptive statistics for humidity measurements from dataloggers in each treatment.

Treatment	Datalogger	Maximum (%RH)	Minimum (%RH)	Mean (%RH)	SD	CV (%)
ENV	A	93.7	24.3	64.49	21.5	33.3
UNC	B	98.7	90.1	95.01	3.01	3.2
	C	94.3	87.5	91.8	1.62	1.76
UFE	D	99.9	93.4	98.49	1.86	1.9
	E	94	86.9	89	2.02	2.26
	F	94.4	91.1	92.92	1.15	1.23

The influence of structural characteristics and microclimate of termitaria on abundance and species richness

Of the 26 ZIP models generated to explain richness in each treatment (Table 4, Appendix 1), three AWF models, eight UFE models, and three DAF models had ΔAIC ≤2, indicating good fits. Internal temperature was included in two AWF models, in five UFE models, and in one DAF model. The number of bushes was included in one AWF model, five UFE models, and one DAF model. The number of holes was included in one AWF model, seven UFE models, and two DAF models. The number of trees was included in two AWF models, four UFE models, and one DAF model. The volume of the termite mounds was included in three AWF models, six UFE models, and two DAF models.

No variable from any well-fitted AWF model had significant effects on richness count ($p > 0.05$). In the well-fitted UFE models, the volume of the termite mounds was significant in all models ($p < 0.05$). The termite internal temperature, number of holes, and number of bushes were also significant ($p < 0.05$) in two models each, while the number of trees was significant ($p < 0.05$) in only one model. Most variables had a positive influence. However, an increase in the number of bushes negatively affected the richness within termite mounds under the fire effect. In the DAF models, internal temperature, number of bushes, and number of trees were significant ($p < 0.05$) in all the models they appeared in. An increase in the number of shrubs positively influenced richness, while increases in internal temperature and the number of associated trees had negative effects. The volume of the termite mounds was significant ($p < 0.05$) in only one of the models, positively influencing richness, while the number of holes had no significant effects on richness ($p > 0.05$) in the only model it appeared in. For detailed statistics see Appendix 2.

Of the 26 ZIP models generated to explain abundance in each treatment (Table 4, Appendix 2), one AWF model (N = 66), one UFE model (N = 66), and three DAF models (N = 44) had ∆AIC ≤2. The AWF model included the volume of the termite mounds and the number of holes. The UFE model included the volume of the termite mounds, the number of bushes, and internal temperature, whereas all variables were included in the DAF models. Two of these models featured the volume of the termite mounds and the number of trees, while the other variables appeared only once.

Only the volume of the termite mounds had a significant positive effect on total herpetofauna abundance ($p < 0.05$) in the well-fitted AWF model. In the well-fitted UFE model, internal temperature had significant positive effect, while and the number of bushes had a significant negative effect on abundance ($p < 0.05$). In the well-fitted DAF models, internal temperature, the number of bushes, and the number of trees were significant ($p < 0.05$) in all the models where they were included. The volume of the termite mounds was significant ($p < 0.05$) in only one model, while the number of holes was not significant ($p > 0.05$) in the sole model in which it appeared. The number of bushes and the volume had a positive influence, while increases in internal temperature and the number of associated trees had negative effects on abundance in DAF. For detailed statistics see Appendix 3.

Table 4 - Three best ZIP models to explain richness (RI) and abundance (AB) within termite mounds for each treatment. Abbreviations: RV) Response Variable; EV) Explanatory Variables.

Treatment	RV	EV	AIC	∆AIC	Log-llh	p-R²
AWF	RI	Null	96.34	2.42	-46.17	
		VOL+NT+IT	93.92	0	-38.96	0.16
		VOL+NH	94.35	0.42	-41.17	0.11
		VOL+NT+NB+IT	95.17	1.24	-37.58	0.19
	AB	Null	96.34	0.23	-46.17	
		VOL+NH	96.11	0	-42.05	0.16
		VOL+NH+NT	98.41	2.3	-41.21	0.18
		VOL+NH+NT	98.64	2.53	-41.32	0.17
UFE	RI	Null	171.63	16.83	-83.81	
		VOL+NH+NT+IT	154.8	0	-39.11	0.15
		NH+NB+IT	155.28	0.48	-43.49	0.06
		VOL+NH+NB	155.5	0.7	-41.09	0.11
	AB	Null	171.63	-3.37	-83.81	
		VOL+NB+IT	175	0	-79.5	0.17
		VOL+NH+NT+NB+IT	178.69	3.69	-77.35	0.19
		VOL+NT+NB+IT	179.6	4.6	-79.8	0.16
DAF	RI	Null	103.09	8.9	-49.54	
		VOL+NT+IT	94.19	0	-39.1	0.21
		NH+NB	95.09	0.9	-41.54	0.16
		VOL+NT	96.02	1.83	-42.01	0.15
	AB	Null	103.09	2.4	-49.54	
		VOL+NT+IT	100.69	0	-42.35	0.22
		VOL+NT	102.2	1.51	-45.1	0.17
		NH+NB	102.31	1.62	-45.15	0.17

The influence of the structural characteristics of termite mounds on the microclimate

Of the 11 GLMs generated to explain the internal temperature of the termite mounds in each treatment (Table 5, Appendix 3), six AWF models (N = 66), six UFE models (N = 66), and three DAF models (N = 44) had ∆AIC ≤2. The volume of the termite mounds was included in four AWF models, two UFE models, and all three DAF models. The number of holes was included in five AWF models, four UFE models, and one DAF model. The number of trees was included in two AWF models, three UFE models, and all three DAF models. The number of shrubs was included in three AWF models, five UFE models, and two DAF models.

Only the number of holes was significant ($p < 0.05$) in explaining internal temperature in the second-best AWF model. An increase in the number of holes had a negative effect on internal temperature. The best AWF model comprised the number of holes and the volume of the termite mounds, but these variables did not have significant effects on IT in this model. The best UFE model comprised the number of holes and the number of bushes, however, none of the variables had significant effects on IT in any model for this treatment. In the DAF treatment, the volume of the termite mounds and the number of trees were significant ($p < 0.05$) in explaining IT in all well-fitted models. The number of associated trees had a negative effect on internal temperature, while the volume of the termite mounds had a positive effect. The best DAF model comprised the number of bushes, the number of trees, and the volume of the termite mounds, although the number of bushes did not have significant effects ($p > 0.05$). For detailed statistics see Appendix 4.

Table 5 - Three best GLMs to explain the internal temperature (IT) of termite mounds for each treatment.

Treatment	Model	AIC	∆AIC	Log-llh	p-R²
AWF	Null	289.28	3.04	-142.64	
	RI~NH+VOL	286.24	0	-139.12	0.02
	RI~NH+NT	287.16	0.92	-139.58	0.02
	RI~NH+NB+VOL	287.89	1.65	-138.94	0.03
UFE	Null	338.06	1.24	-167.03	
	RI~NH+NB	336.82	0	-164.41	0.02
	RI~NH+NT+NB	337.7	0.87	-163.85	0.02
	RI~NH+NT	338	1.17	-165	0.01
DAF	Null	214.08	7.48	-105.04	
	RI~NT+NB+VOL	206.6	0	-98.3	0.06
	RI~NT+VOL	206.98	0.38	-99.49	0.05
	RI~NH+NT+NB+VOL	208.51	1.9	-98.25	0.06

Discussion

The use of termite mounds by herpetofauna

In this study, we reinforce that termite mounds are widely used by the Cerrado herpetofauna (Vitt et al., 2007; Moreira et al., 2009; Duleba & Ferreira, 2014). The high abundance of reptiles inside the termite mounds indicates that these animals routinely seek shelter in these structures (Table 1 and Fig. 4). Whereas some Cerrado lizards, such as *Gymnodactylus amarali*, are typically found in termitaria (Vitt et al., 2007), other species were found exclusively or more often in areas under fire effect, suggesting that these species seek termite mounds as a temporary refuge from wildfires, but may not necessarily be residents or frequent visitors. For instance, *Norops meridionalis*, which typically inhabits the ground or perches on low vegetation in the savanna environments of the Cerrado (Vitt, 1991), usually seeks shelter to protect itself from fire (Miranda et al., 2023). Other species, such as *Copeoglossum nigropunctatum* and *Cercosaura olivacea*, appear to use termite mounds similarly.

Reptiles, mainly lizards, were the most representative vertebrates in our sampling (Table 1). This is possibly linked to their greater mobility (Hertz et al., 1988) and diversity in the Cerrado (Nogueira et al., 2011; Alexandre et al., 2023), enabling them to escape and find shelter more easily than other animals (Batista et al., 2023). This may explain why they are relatively resilient to wildfires (Russell et al., 1999; Sousa et al., 2015; Costa et al., 2020; Certini et al., 2021; Santos et al., 2021; Sousa et al., 2023). In this context, the abundance and density of termite mounds are likely important drivers of resilience, influencing lizard diversity in the open areas of the Cerrado (Costa et al., 2008).

On the other hand, amphibians were less represented in termitaria, despite its high local diversity (Guerra et al., 2022). Anurans are more related to humid Cerrado environments (Santoro & Brandão, 2014), being naturally less abundant in fire-prone Cerrado habitats. Furthermore, during dry season, most anurans concentrate in areas close to water, not burned in our experiment. Considering that prescribed burns and firebreaks are applied in areas with dry soil and vegetation to facilitate burning, these environments are naturally less suitable for amphibians (Brasileiro et al., 2005; Prado et al., 2005; Maffei et al., 2011). Therefore, the lower richness and abundance of frogs inside termitaria is not an unexpectable result.

In addition to providing refuge from fire, termite mounds can serve various purposes for herpetofauna. The termite specialist *Gymnodactylus amarali* relies on these structures for feeding and to avoid the daily fluctuations in temperature and humidity typical of the Cerrado (Colli et al., 2003; Vitt et al., 2007; Amorim et al., 2017). *Ameerega flavopicta* feeds on termites and often uses termite mounds as calling sites (Lima & Eterovick, 2013; Brandão et al., 2020), as well as shelters for predator protection (LFCL pers. obs.). The use of termite mounds as nesting sites for reptiles (Fig. 4C) is also well documented (Brandão & Vanzolini, 1985; Riley et al., 1985; Knapp & Owens, 2008).

The fact that *Amphisbaena vermicularis* was found only in burned areas was probably incidental, considering that it is a naturally elusive species. The use of termite mounds by this species is possibly related to its feeding habits (Pramuk & Alamillo, 2003, Amorim et al., 2024), as it has fossorial habits, being less sensitive to fire (Batista et al., 2023). This is an inherent bias in rare or hard-to-sample species, resulting in an inaccurate description of how some species utilize termite mounds. The observed species turnover between treatments indicates that different species use termite mounds in different contexts, suggesting that some species only use termitaria as shelter during or after the passage of fire.

None of the variables were significant in explaining the richness of species in termite mounds in areas without fire. This suggests that other ecological factors not considered in our models may be more relevant in explaining species richness within termite mounds under normal conditions. It is also possible that in environments with homogeneous vegetation and higher availability of resources and shelters, the use of termitaria may be limited to termitophilous species and occasional tenants (Moro et al., 2014).

Flammable biomass is consumed by fire, causing temporary changes in habitat structure by primarily removing the low vegetation layers (Pilon et al., 2021; Rodrigues et al., 2021). However, herpetofauna seems to be minimally affected directly by the fire line passage. The main impacts on this group are due to exposure to opportunistic predators and the reduced availability of resources, thermoregulatory balance, and shelter after the fire (Esque et al., 2003; Attum e Eason, 2006; Wilgers e Horne, 2007; Webb e Shine, 2008; Costa et al., 2013; Costa et al., 2020; Santos et al., 2021).

Competition for shelters increases during and after a wildfire event due to fire effects on its availability (Banks et al., 2012; Batista et al., 2023). The volume of termite mounds proved to be a strong determinant of richness under fire effect and had a significant impact on both richness and abundance one day after the fire. This suggests that larger mounds provide a more suitable refuge habitat and support a greater species richness and animal abundance. This explains why volume was also significant in determining abundance in our studied areas without fire. The number of holes plays a similar role by facilitating access to the interior of the mounds during fires. Mounds with more holes can dilute competition for access and allow different species to use various spaces.

Some species with higher mobility and low territorial fidelity abandon burned areas in search of safer locations with more abundant resources (Steenvoorden et al., 2019; Batista et al., 2023). Other species with reduced mobility or territorial behavior that probably used termitaria as shelter likely continued to use termite mounds after the fire. This likely happens due to the limited availability of shelters in the environment, especially by vegetation cover loss. Additionally, the increment in solar radiation incidence due to the consumption of plant cover by fire may drive the choice of termite mounds as shelter, as they offer more stable and milder conditions inside (Costa et al., 2020). Moreover, since many invertebrates and other vertebrates also seek shelter in termite mounds, they become important feeding centers in an environment with low resource availability after the fire (Vitt et al., 2007; Costa et al., 2009).

Bushes were an important predictor of richness and abundance in termite mounds under fire effect and one day after fire. However, the increase in their number caused divergent effects in both treatments. They provide structural complexity around the termite mounds, which can benefit species that perch and increase their chances of survival against predators one day after the fire (Longland & Bateman, 2002; Steenvoorden et al., 2019; Batista et al., 2023). On the other hand, shrubs can affect the richness and abundance by hindering access to the mounds, acting as a barrier of flammable material during wildfires. Another possibility is the effect of bushes and small trees on smoke and coal in the termitaria area.

The internal temperature of the termite mounds also had a divergent effect on species richness and abundance in the same two treatments (UFE and DAF). During wildfires, the increase in internal temperature seems to favor the use of termite mounds by ectotherms, likely because higher temperatures enhance metabolic and sensory activity (Bennett & John-Alder, 1984; Glanville & Seebacher, 2006; Crawshaw, 2015), allowing for quicker motor responses in emergency situations and the need to escape (Batista et al., 2023). However, one day after the fire, these animals seem to prefer termite mounds with lower temperatures, likely to avoid external climate fluctuations (Colli et al., 2003; Vitt et al., 2007), as there is no immediate need to seek shelter from the fire.

Although adapted to the environmental harasses usually related to the Cerrado climatic characteristics, most reptiles and amphibians in the biome cannot withstand high temperatures for long periods (Diele-Viegas et al., 2018; Díaz-Ricaurte et al., 2020; Díaz-Ricaurte et al., 2021; de-Lima et al., 2022; Souza-Oliveira et al., 2024). Therefore, most species control their body temperatures actively, moving in the environment according to their thermal needs (Rocha & Bergallo, 1990; Glanville & Seebacher, 2006; Dubiner et al., 2024). By providing milder microclimates, termitaria are actively searched by Cerrado herpetofauna (Vitt et al., 2007; Moreira et al., 2009; Duleba & Ferreira, 2014). This role is even more relevant during the Cerrado wildfires.

Here, we assess the use of termite mounds by herpetofauna under normal conditions and how these structures may aid in the survival of these organisms during fires and shortly thereafter. However, further research is needed to evaluate the role of termite mounds in the resilience of reptile and amphibian populations throughout the regeneration process of their habitats (Meddens et al., 2018). Considering that some species may benefit from some fire frequencies in the biome (Costa et al., 2013; Sousa et al., 2015; Costa et al., 2020), we believe termite mounds are crucial for herpetofauna Cerrado resilience when faced with wildfires.

Termite mounds as a microclimate refuge

Corroborating our hypothesis, the internal temperature of termite mounds was significantly lower than both the surface temperature of the mounds and the soil near them across all treatments. This highlights the importance of termite mounds as microclimatic refuges for herpetofauna, as external temperatures can reach critical and potentially lethal levels for many organisms (Diele-Viegas et al., 2018; Herrando-Pérez et al., 2018; Pontes-da-Silva et al., 2018; Claunch et al., 2020; Borghetti et al., 2021; de-Lima et al., 2022; Souza-Oliveira et al., 2024).

The volume of the mounds, the number of holes, and the number of associated trees were the most important factors explaining this result. Larger mounds take a long time to develop (Domingos, 1983; Korb, 2010) and offer greater thermal insulation (Ndlovu & Pérez-Rodríguez, 2018), but they also have a larger surface exposed to solar radiation. This could explain the increase in temperature observed in larger termite mounds one day after the fire, coupled with the reduced shade provided by the vegetation depletion (Joseph et al., 2016; Ndlovu & Pérez-Rodríguez 2018; Wildermuth et al., 2021). However, while holes enhance animal access to the mound interiors, they also may reduce thermal insulation, allowing external temperatures to influence the internal environment of the mounds (Lima & Brandão, 2024). This factor was only significant in the AWF models, which explains the temperature differences observed in mounds in areas without fire compared to the other treatments. Nevertheless, this influence does not appear to impair habitability.

Associated trees provide shade, which facilitates the cooling of the termite mounds surface (Joseph et al., 2016; Ndlovu & Pérez-Rodríguez 2018; Wildermuth et al., 2021). Furthermore, tree roots associated with the mounds promote soil water infiltration (Liu et al., 2019) and help retain moisture (Leung et al., 2015). In contrast, bushes have shallower roots that do not reach the mound interiors and do not cast large shade over the termite mounds.

It is expected that the internal temperature of termite mounds would be influenced by trends in external environmental temperature (Joseph et al., 2016; Ndlovu & Pérez-Rodríguez, 2018). The temperature and humidity recorded by the datalogger outdoors exhibited much greater variability compared to the interior of the mounds, even in the presence of fire, corroborating our hypothesis. The absolute minimum and maximum temperatures outside the termite mounds exceeded the minimum and maximum limits recorded inside the mounds in both treatments (UNC and UFE) (Table 2, Fig. 6), and the humidity inside the mounds consistently remained at high levels (Fig. 6), showing that the internal environment of termite mounds is more stable and milder than external environments.

Despite our small number of dataloggers, the recovered patterns corroborate our active findings, highlighting the stability of internal temperatures and humidity conditions in the mounds, including under fire conditions (Table 3). Additionally, they underscore the extensive use of these structures as refuges for herpetofauna during fire events and their role as microclimatic refuges, mitigating environmental climate variations. Larger sample sizes in future experiments should enhance our understanding of termite mounds as fire refuges for fauna.

Corroborating our hypothesis, there was no significant difference between the internal temperature and humidity of termite mounds affected by fire and those in normal conditions. We also did not observe any drastic peaks or changes in temperature and humidity inside termite mounds affected by the recent passage of the fire line. Thus, we reinforce that termite mounds are effective shelters against fire, maintaining milder and more stable conditions compared to the surrounding environment.

Conclusion

Our study underscores the critical role of termite mounds as refuges for herpetofauna in the Cerrado in different contexts. The presence of fire and the temporary alterations it induces in the environment are significant drivers of how these microhabitats are utilized by these organisms. On the other hand, termitaria structural and microclimatic characteristics played a subtle role in their attractiveness to herpetofauna.

Future research should focus on understanding the long-term ecological impacts of fire on termite mound microhabitats and their associated faunal communities. Investigating how different species adapt to the changes in microclimate and how these adaptations influence their survival and reproduction could provide valuable insights into the resilience of Cerrado herpetofauna. Additionally, exploring the role of termite mounds in supporting species other than herpetofauna, such as insects and small mammals, could broaden our understanding of their ecological significance in fire-affected landscapes. We also highlight that fire management in the Cerrado landscape should account for the presence, volume and density of termitaria in the areas to be burned.

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Appendix 1 - Descriptive statistics summary of temperature measurements recorded during active sampling of termite mounds in each treatment.

	Treatment	**Surface**	**Soil**	**Internal**
Maximum (ºC)	**AWF**	59.3	40.8	28.3
	UFE	60.7	58	31.4
	DAF	56.1	50.1	29.7
Minimum (ºC)	**AWF**	22.4	21.1	19.1
	UFE	21.8	19.9	12.1
	DAF	21	19.2	18.6
Mean (ºC)	**AWF**	34.2	27.54	24.35
	UFE	37.02	34.78	22.44
	DAF	36.28	31.16	24.64
SD	**AWF**	8.29	4.14	2.12
	UFE	9.01	8.46	3.06
	DAF	7.33	7.45	2.66
CV (%)	**AWF**	24.2	15	8.7
	UFE	24.3	24.3	13.7
	DAF	20.2	23.9	10.8

Appendix 2 – ZIP models with ∆AIC ≤2 used to explain species richness inside termite mounds for each treatment.

Treatment	Model	AIC	∆AIC	Log-llh	p-R²	Variable	Estimate Coefficient	*p*-Value
AWF	RI~VOL+NT+IT	93.92	0	-38.96	0.16	VOL	0.03	0.73
						NT	0.12	0.53
						IT	0.14	0.25
	RI~VOL+NH	94.35	0.42	-41.17	0.11	VOL	0.04	0.5
						NH	-0.02	0.82
	RI~VOL+NT+NB+IT	95.17	1.24	-37.58	0.19	VOL	0.03	0.68
						NT	0.12	0.53
						NB	0.09	0.43
						IT	0.22	0.1
UFE	RI~VOL+NH+NT+IT	154.8	0	-67.4	0.2	VOL	0.28	0.01 *
						NH	0.02	0.59
						NT	0.06	0.2
						IT	0.11	0.05 *
	RI~NH+NB+IT	155.28	0.48	-69.64	0.17	NH	0.09	0.02 *
						NB	-0.05	0.63
						IT	0.03	0.51
	RI~VOL+NH+NB	155.5	0.7	-69.75	0.17	VOL	0.25	0.02 *
						NH	0.05	0.27
						NB	-0.21	0.04 *
	RI~VOL+NH+NT+NB+IT	155.54	0.74	-65.77	0.22	VOL	0.29	0.01 *
						NH	0.02	0.6
						NT	0.05	0.32
						NB	-0.12	0.23
						IT	0.1	0.08
	RI~VOL+NH+NT	155.74	0.94	-69.87	0.17	VOL	0.23	0.04 *
						NH	0.03	0.48
						NT	0.09	0.06
	RI~VOL+NH	156.42	1.62	-72.21	0.14	VOL	0.24	0.03 *
						NH	0.05	0.32
	RI~VOL+NB+IT	156.66	1.86	-70.33	0.16	VOL	0.24	0.02 *
						NB	-0.23	0.03 *
						IT	0.11	0.04 *
	RI~NH+NT+NB+IT	156.72	1.92	-68.36	0.18	NH	0.08	0.02 *
						NT	0.09	0.05 *
						NB	-0.03	0.81
						IT	0.02	0.76
DAF	RI~VOL+NT+IT	94.19	0	-39.1	0.21	VOL	0.5	0.02 *
						NT	-0.69	0.01 *
						IT	-0.18	0.01 *
	RI~NH+NB	95.09	0.9	-41.54	0.16	NH	-0.03	0.48
						NB	0.42	0.03 *
	RI~VOL+NT	96.02	1.83	-42.01	0.15	VOL	0.29	0.13
						NT	-0.45	0.04 *

Appendix 3 - ZIP models with ∆AIC ≤2 used to explain abundance inside termite mounds for each treatment.

Treatment	**Model**	**AIC**	**∆AIC**	**Log-llh**	**p-R²**	**Variable**	**Estimate Coefficient**	***p*-Value**
AWF	AB~VOL+NH	96.11	0	-42.05	0.16	VOL	0.11	0 *
						NH	-0.03	0.66
UFE	AB~VOL+NB+IT	175	0	-79.5	0.17	VOL	0.18	0.06
						NB	-0.24	0.02 *
						IT	0.15	0.01 *
DAF	AB~VOL+NT+IT	100.69	0	-42.35	0.22	VOL	0.52	0.01 *
						NT	-0.74	0 *
						IT	-0.16	0.01 *
	AB~VOL+NT	102.2	1.51	-45.1	0.17	VOL	0.33	0.08
						NT	-0.51	0.02 *
	AB~NH+NB	102.31	1.62	-45.15	0.17	NH	-0.02	0.56
						NB	0.4	0.03 *

Appendix 4 – GLMs with ∆AIC ≤2 used to explain species richness inside termite mounds for each treatment.

Treatment	**Model**	**AIC**	**∆AIC**	**Log-llh**	**p-R²**	**Variable**	**Estimate Coefficient**	***p*-Value**
AWF	IT~NH+VOL	286.24	0	-139.12	0.02	NH	-0.13	0.09
						VOL	-0.16	0.14
	IT~NH+NT	287.16	0.92	-139.58	0.02	NH	-0.16	0.04 *
						NT	-0.25	0.26
	IT~NH+NB+VOL	287.89	1.65	-138.94	0.03	NH	-0.12	0.15
						NB	-0.1	0.57
						VOL	-0.16	0.15
	IT~NH+NT+VOL	287.92	1.68	-138.96	0.03	NH	-0.14	0.08
						NT	-0.13	0.59
						VOL	-0.13	0.28
	IT~NB+VOL	288.07	1.84	-140.04	0.02	NB	-0.18	0.28
						VOL	-0.19	0.07
	IT~NH+NB	288.12	1.88	-140.06	0.02	NH	-0.15	0.07
						NB	-0.11	0.54
UFE	IT~NH+NB	336.82	0	-164.41	0.02	NH	-0.18	0.12
						NB	-0.38	0.12
	IT~NH+NT+NB	337.7	0.87	-163.85	0.02	NH	-0.19	0.09
						NT	0.19	0.31
						NB	-0.36	0.14
	IT~NH+NT	338	1.17	-165	0.01	NH	-0.2	0.08
						NT	0.22	0.25
	IT~NB+VOL	338.64	1.82	-165.32	0.01	NB	-0.36	0.16
						VOL	-0.28	0.39
	IT~NT+NB	338.74	1.91	-165.37	0.01	NT	0.15	0.42
						NB	-0.38	0.13
	IT~NH+NB+VOL	338.74	1.92	-164.37	0.02	NH	-0.17	0.18
						NB	-0.37	0.14
						VOL	-0.1	0.78
DAF	IT~NT+NB+VOL	206.6	0	-98.3	0.06	NT	-0.96	0.01 *
						NB	-0.55	0.14
						VOL	1.04	0.01 *
	IT~NT+VOL	206.98	0.38	-99.49	0.05	NT	-0.97	0.01 *
						VOL	1.08	0 *
	IT~NH+NT+NB+VOL	208.51	1.9	-98.25	0.06	NH	0.02	0.77
						NT	-0.94	0.01 *
						NB	-0.58	0.14
						VOL	1.03	0.01 *