

Elevational environmental stress modulating species cohabitation in nests of a social insect

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Abstract. 1. Termite nests may offer shelter to a number of species, alleviating the effects of environmental harshness. Certain elevational gradients provide variation on edaphoclimatic features, possibly generating harsh environmental conditions and boosting the number of immigrants seeking shelter within termitaria. Therefore, it is expected that metrics describing the community of termitaria cohabitants would correlate with elevation.

2. To test this hypothesis, we surveyed the termitophiles inhabiting 20 nests of *Nasutitermes coxipoensis* along an elevational gradient in a tropical mountain in Brazil. We assessed the richness, abundance, and composition (β -diversity) of termite nests' cohabitants, testing nest volume and elevational position as explanatory covariates.

3. We found a positive correlation between the elevation at which termitaria were located and the richness and abundance of cohabiting termitophiles. Additionally, no correlation was found between elevational distance and dissimilarity of cohabitant communities between termitaria. Hence, the understanding that termitaria work as an 'oasis' of favorable microclimate is reinforced by our findings that the composition changed but was not correlated to elevation.

4. In short, environmental harshness boosts the establishment of distinct species of termitophiles in termitaria and it does so regardless of the invading species identity.

Key words. *campo rupestre*, facilitation, inquilines, Isoptera, Serra do Cipó, stress-gradient hypothesis.

Introduction

By offering shelter to a variety of organisms, termitaria (da Cunha *et al.*, 2003; Costa *et al.*, 2009; Costa & Vanin, 2010), are key structures in the habitats where they are found (Redford, 1984; Leitner *et al.*, 2020). Despite not yet fully understood, the mechanisms that modulate such species cohabitation seem to include some of the cohabitants' behavioral traits (e.g., avoidance of encounters with termitarium builders; Cristaldo *et al.*, 2014), along with abiotic and biotic factors, such as termite

nest volume and the presence of the colony builder or of ants (Cristaldo *et al.*, 2012; Lisboa *et al.*, 2013; Marins *et al.*, 2016; Monteiro *et al.*, 2017).

Recently, Monteiro *et al.* (2017) showed that termite nests can provide ameliorated conditions to a considerable number of termitophile species in places under temporary environmental disturbance—fire, in their case. Such results, together with the fact that positive biotic interactions are favoured under harsh environments (Bertness & Callaway, 1994), render the idea that termitaria cohabitation may also be boosted by permanent harshness. After all, in addition to temporary abiotic factors (such as wildfire, storms, floods, earthquakes, tsunamis, volcanic eruptions), permanent abiotic factors like extremes of osmotic pressure, atmospheric pressure, and solar radiation can also

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modulate species interactions (Wingfield, 2013). This is in line with the Stress Gradient Hypothesis (SGH) which predicts that the frequency, intensity, and importance of certain species interactions are directly affected by abiotic stress levels (Brooker & Callaghan, 1998; Maestre *et al.*, 2009). Little is known, however, about the effects of these permanent abiotic factors on termitaria-cohabitants system.

High-montane systems provide a natural experiment for the effects of permanent harshness and SGH, because elevation increments show a strong correlation with environmental stress increments. Moreover, providing that such gradients are bound to determine species interactions (Callaway *et al.*, 2002; Henriques & Cornelissen, 2019) these gradients may ultimately drive termitaria cohabitation. The Espinhaço Mountain Range in Brazil seems particularly suitable to test such a hypothesis (Silveira *et al.*, 2019). On top of providing a harsh environment comprising of rocky outcrops along an elevational gradient extending *c.a.* 600 m, it is also home to *Nasutitermes coxipoensis* (Holmgren), a termite species that builds nests along this entire gradient (Nunes *et al.*, 2017).

Here we investigate how the elevational gradient in Serra do Cipó (in the Espinhaço Mountain Range) affects the richness, abundance, and composition (β -diversity) of cohabitants in *N. coxipoensis* termite nests. In this tropical montane system, a decrease in species richness is normally observed with increasing elevation (Fernandes *et al.*, 2016; Mota *et al.*, 2016; Nunes *et al.*, 2017; Perillo *et al.*, 2017). However, due to the already known habitat amelioration provided by termitaria (Monteiro *et al.*, 2017), we expect to find an inverse pattern, in which the richness and abundance of cohabiting termitophiles should increase with the elevational location of termitaria.

To obtain evidence of the process behind species assortment of such invasions, we will test whether the dissimilarity (β -diversity) of the cohabitant community in termite nests is positively affected by the elevational distance. Increments in β -diversity with increasing geographical distance is a very common pattern in ecological communities, commonly called distance-decay relationship (Fitzpatrick *et al.*, 2013; Perillo *et al.*, 2017; Antão *et al.*, 2019). Our results will be important for understanding the effects of prevalent environmental harshness (i.e. stress) upon termitophily, broadening the knowledge on abiotic determinants of this cohabitation. Ultimately, these will contribute to understanding the role of permanent environmental harshness upon nest sharing and positive species interactions.

Materials and methods

Study site

Termite nests were collected along an elevational gradient in Serra do Cipó, on the southeastern portion of the Espinhaço Mountain Range, Minas Gerais state, Brazil (19°100' S and 19°220' S, 43°290' O and 43°360' O; Fig. 1). The climate at Serra do Cipó is classified as dry-winter subtropical highland (CwbKöpper), with an annual average temperature and precipitation of 20 °C and 1500 mm, respectively (Madeira & Fernandes, 1999; Fernandes *et al.*, 2016). Soils are acidic, sandy,

shallow, and oligotrophic, mainly composed of quartzite and arenite, with little water retention capacity, and high aluminium concentration levels (Negreiros *et al.*, 2009, 2012). Vegetation is very heterogeneous and includes small and large patches of Atlantic Forest, shrub-savanna, seasonally dry forests, and riparian forest in drainages (Giulietti *et al.*, 1987; Fernandes *et al.*, 2016; Mota *et al.*, 2016). Along the elevational gradient, a change from *cerrado stricto sensu* to *campo rupestre* is observed, with a decrease in vegetation complexity, woody plant species richness (Mota *et al.*, 2018), and variation in climatic conditions (Fernandes *et al.*, 2016). From the 900 m elevation, the *campo rupestre*, a system with more than 65 million years of stability, stands out for its high faunal and floral diversity and a large number of endemic species (Silveira *et al.*, 2016, 2019).

Model organism

In this study, we used termite nests of *Nasutitermes coxipoensis* (Holmgren), a common species in tropical regions, often found in association with grass and sandy soils (Almeida *et al.*, 2016). However, in the *cerrado* and *restingas*, these termites are found on lateritic surfaces, such as the *campo rupestre* (Mathews, 1977; Buschini *et al.*, 2008), thus becoming one of the most abundant species in the study system (Nunes *et al.*, 2017). The outer nest surface is irregular, with granular protuberances suggesting a protrusion of the nest's inner cells (Fig. 2). This surface consists of a crumbly thin layer (3–4 mm thick). The aerial surface of the nest (i.e. its hypogeic portion) can be easily removed. Nest wall colors vary from light brown to reddish brown (Laffont *et al.*, 2012).

Data collection

We surveyed 20 termite nests between June 2015 and September 2016. All nests were located at a minimum distance of 130 meters from each other and a mean distance (\pm standard deviation) of 6.57 km (\pm 3.93 km). Nest geographic coordinates, elevation (m.a.s.l.), and volume (L) were recorded in the field. We arbitrarily chose nests with volumes above 20 L, since termitophiles are more likely to be found in such volumes (Cristaldo *et al.*, 2012). Sampled nests were distributed along an elevational gradient between 825 and 1411 m. We avoided nests in which ant colonies were present due to the evidence that ants can act as a protective mutualist, reducing the diversity of cohabitants in termitaria (Monteiro *et al.*, 2017). Nest volumes were calculated considering its shape to be an approximate spherical dome to apply the following equation: $V = \pi d^2 h / 6$, where d represents the basal diameter, and h the mound height (Tamura *et al.*, 1990).

In the laboratory, we divided the whole termite nest into small pieces passing the resulting material through two different sieves. After a visual inspection, we discarded the material retained in the thickest mesh (0.3 mm), the filtrate in the thinner mesh (500 nm), and stored the remainder in 80% alcohol. In a stereomicroscope, the material was carefully screened, and all cohabitants found therein were collected with entomological forceps, placed in 80% alcohol, labelled and identified to the lowest possible taxonomic level.

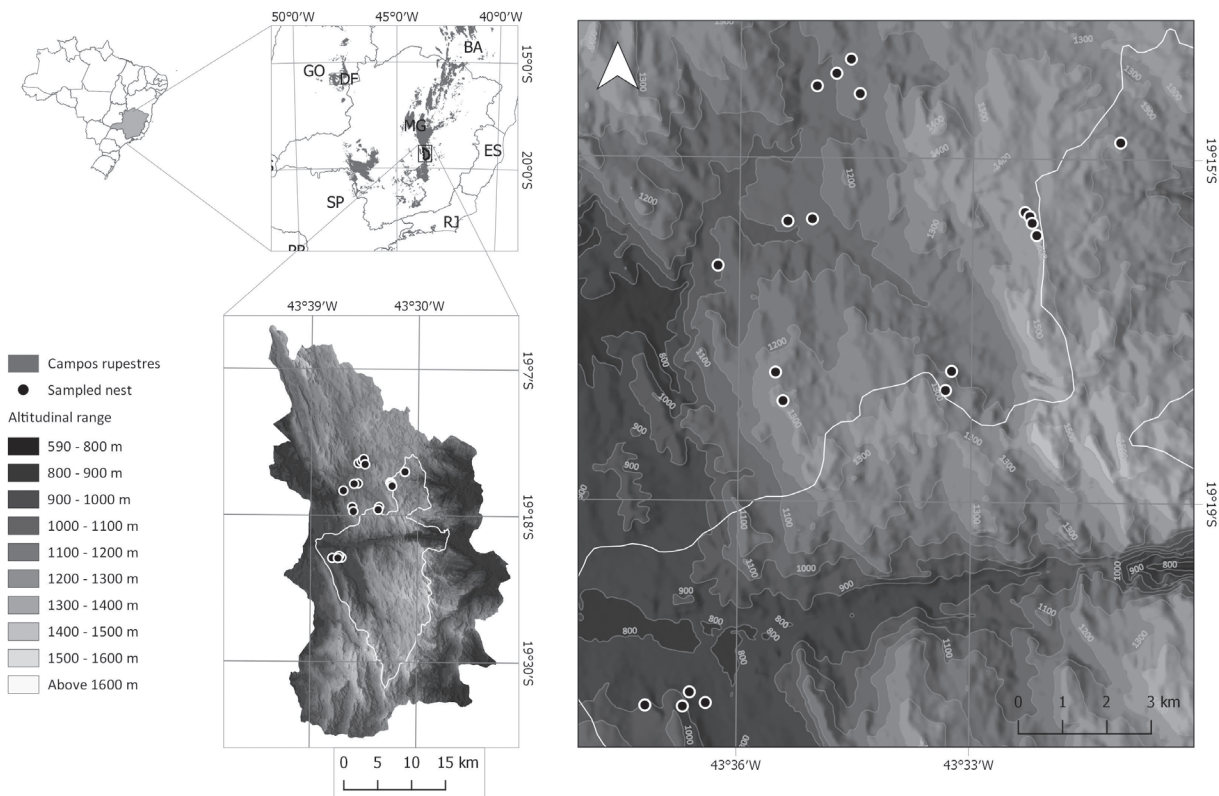


Fig. 1. Location of 20 termite nests *Nasutitermescoxiipoensis* (Holmgren) at Serra do Cipó, in the southeast portion of the Espinhaço Mountain Range, Minas Gerais state, Brazil.

Data analyses

Before generating the predictive models, we performed a generalised linear model (GLM) to assess the effect of seasonality on termitophiles diversity due to the temporal variation within the sampling period (22 months). As there was no significant difference in diversity between seasonal periods (Abundance: Negative binomial family; Deviance = 2.42; d.f. = 1, 18; $P = 0.11$; Richness: Negative binomial distribution; Deviance = 1.24; d.f. = 1, 18; $P = 0.26$), it seems safe to consider that sample seasonality did not play a confounding effect on the observed patterns (Supporting Information S1: Fig. S1).

Thus, to verify the effects of elevational stress on termitophilous nest occupation, we used a GLM with species richness or abundance of termitophiles as response variables (in independent analyses), and elevation and termitaria volume as explanatory variables. Volume was included in the models due to its importance as a predictor of cohabitant presence in termitaria (Cristaldo *et al.*, 2012; Marins *et al.*, 2016). For each response variable, a complete model was constructed and the minimal adequate model was created by removing non-significant explanatory variables ($P > 0.05$, Supporting Information S1: Tables S2 and S3; Figs. S2 and S3). All models were initially fitted under Poisson distribution errors, a choice later confirmed by residual analysis. When necessary, we corrected over-dispersed models using negative binomial errors (Lindén & Mäntyniemi, 2011; Crawley, 2013).

To evaluate elevational β -diversity patterns of termite-associated fauna, we performed Mantel tests with 10 000 permutations using pairwise matrices (Nekola & White, 1999). Prior to calculating the matrices of beta diversity metrics, we performed a Pearson correlation analysis by Mantel test between the elevational and geographical distance matrices (Euclidean distance) and observed that both variables are correlated ($r = 0.53$, $P < 0.001$), allowing us to keep only the elevational distance. We calculated three matrices with β -diversity metrics: (i) β_{sor} , which represents the total compositional variation between all nest pairs; (ii) β_{sim} , which represents the compositional change due to turnover; and (iii) β_{sne} , which is the dissimilarity resulting from nestedness calculated by the difference between β_{sor} and β_{sim} (Baselga, 2010). To quantify which processes contribute most to the cohabitant community along the elevation, we calculated the proportional turnover values (β_{sim}) and nestedness (β_{sne}) based on total dissimilarity (β_{sor}). For this, we computed three values of multiple-nest dissimilarities accounting for the spatial turnover and the nestedness components of beta diversity, and the sum of both values (Sorensen) (Baselga & Orme, 2012). Thus, the contribution of $\beta_{sim} = \beta_{sim}/\beta_{sor}$, while the contribution of $\beta_{sne} = \beta_{sne}/\beta_{sor}$. All analyses were performed in R (R Core Team, 2020) using the packages *vegan* (Oksanen *et al.*, 2019) for Mantel tests and *betapart* (Baselga & Orme, 2012) for β -diversity matrices.



Fig. 2. Pictures showing details of the *Nasutitermes coxipoensis* (Holmgren) nest, Serra do Cipó, Minas Gerais, Brazil. (a) Nest in a sandy soil environment. (b) Nest in a rocky outcrop environment. (c) Detail of the nest collection. (d) Detail of the soldier caste patrolled after a slight disturbance in the nest wall..[Colour figure can be viewed at wileyonlinelibrary.com].

Results

Richness and abundance of cohabitants

Out of the 20 termite nests of *Nasutitermes coxipoensis* surveyed, we recorded 483 cohabitant individuals belonging to 65 morphotypes of four invertebrate classes: Insecta (385 individuals; 79.71%); Arachnida (84; 17.39%); Diplopoda (9; 1.86%); Chilopoda (3; 0.62%), and Isopoda (1; 0.20%). Among insects, we found two social orders (Insecta: Blattodea: Isoptera and Hymenoptera: Formicidae), of which three morphotypes belong to Isoptera: Termitidae and 12 belong to Hymenoptera: Formicidae (Table S1). Cohabitant abundance and richness was positively correlated with elevation with no significant effect of volume nor any interaction between elevation and volume (Richness: *Deviance* = 4.63; d.f. = 1, 18; $P < 0.05$; Abundance: *Deviance* = 8.11; d.f. = 1, 18; $P < 0.01$; Fig. 3).

Composition of cohabitants

We verified that the cohabitant community dissimilarity (β -diversity) among nests was not related to elevational distance, either for turnover or nestedness components (Mantel- β sor: $r = 0.07$, $P = 0.23$; β sim: $r = 0.02$, $P = 0.41$; β sne: $r = 0.03$; $P = 0.35$; Fig. 4). In fact, the turnover component represented 94.09% of the β -diversity.

Discussion

Here we present evidence that the elevational gradient can positively affect macro-symbiosis in *Nasutitermes coxipoensis* nests: more individuals and more species of termitophiles were found in nests located at higher elevations compared to lower elevations. We also found that the elevational distance was not correlated to the β -diversity of cohabitants among termite nests, nor was it correlated to turnover and nestedness components of such β -diversity.

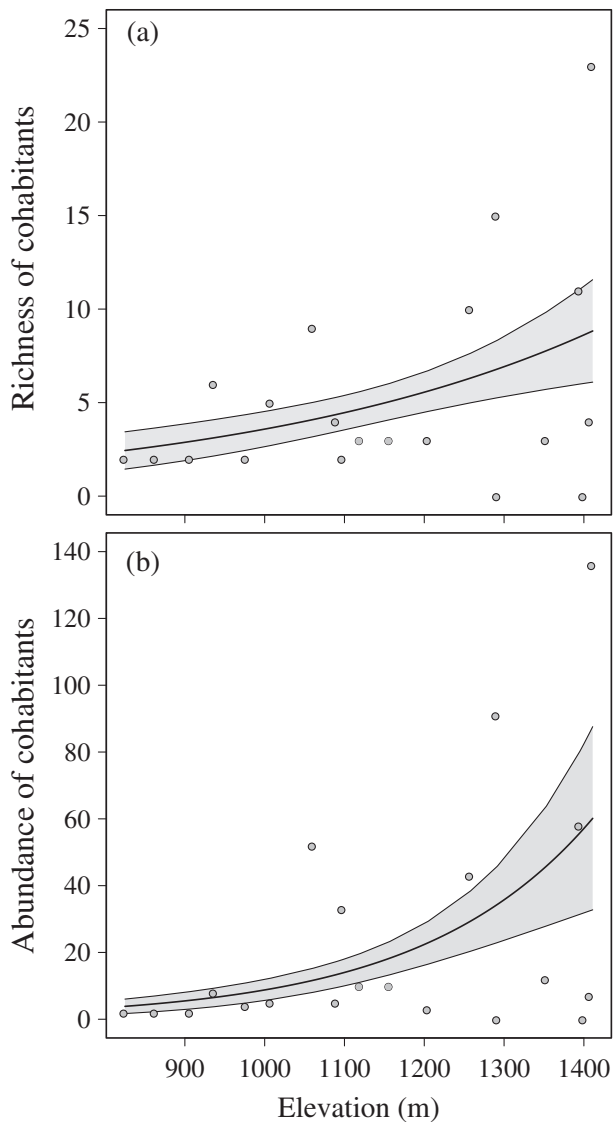


Fig. 3. Relationship between cohabitant species richness (a) and abundance (b) in function of the elevation in *Nasutitermescoxipoensis* (Holmgren) termitaria at Serra do Cipó, Southeastern Brazil.

It is tempting to attribute this positive correlation between elevation, abundance, and richness of termitophiles to environmental harshness. Indeed, this environment shows a greater climate instability in high altitude areas as opposed to lower places (Streher *et al.*, 2017; Silveira *et al.*, 2019). This positive effect of stressful conditions on symbiotic interactions is supported by previous records not only for termitophiles (Monteiro *et al.*, 2017), but also for other organisms (Bertness & Callaway, 1994; Callaway & Walker, 1997; Bertness *et al.*, 1999). Symbioses between fungi and plants, for instance, are more frequent in harsh ecosystems (Smith & Read, 2009). An example comes from the same environment studied here. Arbuscular mycorrhizal fungi (AMFs) on campo rupestre are more diverse in intermediate elevations, where their host plants grow on soils

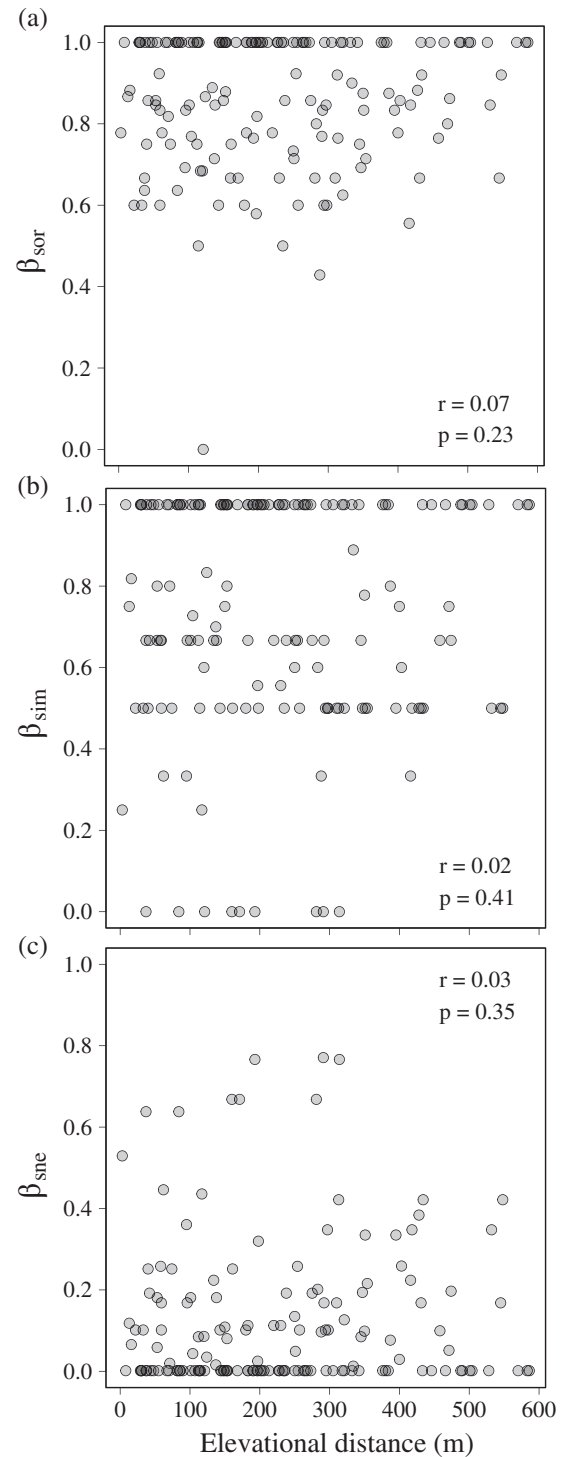


Fig. 4. Relationship between species pair-to-pair dissimilarity of cohabitants in *N. coxipoensis* nest and elevational distance at Serra do Cipó, Southeastern Brazil. (a) Represents total dissimilarity calculated by the Sorensen index. (b) Represents the dissimilarity by community compositional change (turnover) and (c) represents the dissimilarity by the nestedness component only. The coefficients of determination (r) and significance (P , computed using Mantel tests) of each relationship are shown.

promoting nutritional stress due to high aluminum concentration, high sand content, and low nutritional content in the soil (Coutinho *et al.*, 2015).

The novelty we bring here is that, for the specific case of termitophiles, permanent environmental harshness seems to affect termitophily in a manner similar to short-term stressful conditions such as the wildfires reported by Monteiro *et al.* (2017). This seems to indicate that one of the actual (and still unknown) drivers of termitaria cohabitation lies in the response of the associated species to harmful conditions. Hypothetical mechanisms could involve (i) lack of energy to remove invaders (see Araújo *et al.*, 2017), and (ii) higher eagerness of invaders to occupy termitaria when escaping stressful situations.

While such mechanisms remain to be thoroughly studied, our result corroborates the work of Monteiro *et al.* (2017), reinforcing the idea that termite nests favor the presence of cohabitants in stressful environments. This adds a new perspective to the importance of termitaria as diversity hotspots and termites as keystone species (Redford, 1984; Pringle *et al.*, 2010; Leitner *et al.*, 2020). Termites not only provide suitable habitat for other organisms in normal conditions, but they also reduce environmental harshness by providing shelter against stressful conditions. Moreover, they do so under permanent and temporary stress conditions.

Several studies have highlighted the temperature and humidity stability within termite nests as compared to external environmental conditions (Korb & Linsenmair, 1999, 2000; Korb, 2003). This seems to be particularly valid for *N. coxipoensis* nests, especially at the high elevations studied here. Being dome-shaped and possessing walls without large reentrances, such nests would be better prepared to conserve heat and preserve microclimatic stability than cathedral-shaped mounds (Korb, 2003). This should create a microclimatic amelioration in the windy and cold scenario of high elevations in Serra do Cipó, thus favouring termitophile survival. Our results indicate that there is no specificity of the termitarium fauna at any given elevation, suggesting the lack of environmental filters (Cottenie, 2005; Fitzpatrick *et al.*, 2013), dispersal idiosyncrasies (Astorga *et al.*, 2012; Wang *et al.*, 2012) among termitophile species and/or a marked action of stochastic factors (Hubbell, 2001). It seems that termitophiles seek warmer and more stable habitat, once they are living in a harsh environment, but which organism find and enter the nest is a random process. This apparently supports the idea that termites themselves are not acting as severe barriers to invasions in termitaria, much in line with what was found by Marins *et al.* (2016) and Monteiro *et al.* (2017). In other words, termitaria are a kind of open space providing shelter and suitable microclimates for a non-specialised variety of organisms in a harsh environment, working like an ‘oasis’ of favorable microclimate. This hypothesis is reinforced by our findings that the species composition changed regardless of elevation.

Our results revealed that species turnover was the main process structuring the differences in species composition between termite nests, with no detectable effects from an elevational distance. As a consequence, it is possible to describe these communities at a regional scale but one can not predict their structure. On the other hand, we observed that the higher the site where

the termitarium was located, the higher the number of species cohabiting therein. This suggests that the community of cohabitants of termitaria is affected by environmental filters at a local scale (Kraft *et al.*, 2015). Together, these results indicate that these communities would be structured (i) by stochastic processes at the regional scale and (ii) by niche processes at the local scale (Chase, 2005; Zhou & Zhang, 2008a,b; Thompson *et al.*, 2020). Therefore, it seems that we are facing an interesting combination of processes connected to stochastic (i.e. neutral theory, geographical barriers, and dispersal abilities) and deterministic (i.e. niche-based theory, response to environmental variations) processes. That is, a set of “nearly neutral” rules (Zhou & Zhang, 2008a) may structure these communities of termite cohabitants.

In conclusion, we showed that permanent harshness in the form of elevational-driven stress (Lobregat *et al.*, 2018; Henriques & Cornelissen, 2019), favours macro-symbioses within *N. coxipoensis* nests. Moreover, we provide strong evidence that, in addition to small-scale abiotic factors (see Cristaldo *et al.*, 2012), large-scale ones may also play a definitive role in termitaria invasion by termitophiles. Such factors may indeed be more relevant than a defensive action on the part of termites themselves, at least in stressful conditions. These results establish open avenues for further research on invasion processes governing termitophily. Issues asking for indepth analysis would include: “why is the species composition of cohabitants a random subset of an external pool of species?” or “what is the pattern of the termitophile diversity in temporarily stressful conditions”; and also “how do the key assumptions of the neutral and niche models modulate on termitophile community structure?” Regardless of the solution for the issues above our results achieved, summed with those from previous works, seem to point to the conclusion that termites may be perceived as ecosystem engineers *par excellence*. After all, more than merely providing shelter, they do so with markedly weak restrictions.

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Author contributions

Arleu B. Viana-Junior and Paola Mitraud conceived the study and termitarium field sampling; Arleu B. Viana-Junior, Wesley Dáttilo, and Frederico de s. Neves contributed to the data analysis; Arleu B. Viana-Junior, Og Desouza, and Frederico de s. Neves designed the study; and Arleu B. Viana-Junior, Wesley Dáttilo, Og Desouza and Frederico de s. Neves wrote the manuscript and reviewed the final version, contributed to results interpretation, and to the writing–review of the manuscript.

Data availability statement

Data available in article supplementary material.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1: List of cohabitant morph species and their distributions among inspected termitaria in Serra do Cipó, Minas Gerais, Brazil.

Supporting Information S1: Description of the statistical process showing the simplification tables and diagnostic plot of each models.

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