



Resource suitability modulating spatial co-occurrence of soil-forager termites (Blattodea: Termitoidea)

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Abstract

Resource can regulate animal foraging range, which in turn determines the chances of species co-occurrence. Here, we addressed the question of whether resource determines the co-occurrence of soil-forager termite species (i.e. those foraging in subterranean tunnels). Eight quadrats (4 × 4 m) were marked in seven sites of Brazilian Atlantic rainforests, giving a total area sampled of 896 m². Inside each quadrat, we measured the co-occurrence of soil forager species and the resource suitability (N:C ratio of the soil and litter biomass). The number of records of more than one soil-forager termite species at a single foraging spot, relative to the total number of foraging spots detected in each forest, was taken as a surrogate for spatial co-occurrence. We tested whether termite co-occurrence was mediated by random or nonrandom processes. Data were subjected to linear regression to test how the termite species co-occurrence responds to resources. We compared this method with a null model analysis. Soil-forager termites comprised 885 records, 20 species and 14 genera. From those records, 29% indicated species co-occurrence. Co-occurrence was not random: occurred more frequently when resource suitability was very high or very low. This result suggests an optimised use of space by termite communities.

Key words

communities, foraging strategies, N/C ratio, soil insects, species co-occurrence.

INTRODUCTION

In natural environments, the relation between foraging range and resource suitability has a significant influence on the distribution of animals. Vertebrate and invertebrate species have been reported to regulate their foraging, which in turn leads to changes in their foraging range (i.e. in location, size, time and form of foraging) (Tremblay *et al.* 2005; Westphal *et al.* 2006; Lanan & Bronstein 2013; Grangier & Lester 2014). Shifts in the foraging range can modulate the occurrence of animals in the environment and, consequently, determine species co-occurrence on both local and global scales. Thus, understanding these factors could help to understand general patterns in community ecology, particularly for species reported as ‘ecosystem engineers’ (e.g. termites), which promote the maintenance of other species in their community (Jones *et al.* 1994).

A range of biotic and abiotic filters can regulate species distributions in natural environments and, thus, structure communities deterministically (i.e. nonrandom organisation). Factors such as resource suitability are known to influence the use of space (e.g. foraging distance) and, consequently, species co-occurrence, as already reported to different taxa (Tremblay *et al.* 2005; Lanan & Bronstein 2013; Zengeya *et al.* 2014). Among invertebrates, the co-occurrence of insects that share the same resource is related to differences in their foraging efficiency (Bennett *et al.* 2009). The spatial co-occurrence of

earthworm species was demonstrated to be mediated by the spatial aggregation of competitors based on habitat selection and resource exploitation (Jiménez *et al.* 2012).

However, the mechanisms that regulate the co-occurrence of termite species are poorly understood. The search for resources is a costly process for those termite species that need to invest in digging tunnels to explore the environment. Subterranean termites discover food in the soil by constructing a network of underground tunnels, which extend from the central nest to a food source. Therefore, it is reasonable to hypothesise that colonies of soil-foraging termites (i.e. all termites with a similar behaviour of foraging underground) adjust their foraging area as a compromise between their resources demand and the cost of digging a tunnel to get access to such resources. These insects are known to exhibit selective behaviour in the use of their resources in the field (Evans *et al.* 2005; DeSouza *et al.* 2009) and to adjust their tunnelling according to resources offered under laboratory conditions (Araújo *et al.* 2011). At a population level, several intrinsic factors have been reported to affect termite foraging and distribution, such as interspecific termite interactions (Adams & Levings 1987), predation risk (Korb & Linsenmair 2002) and soil texture (Pequeno *et al.* 2015). However, at a community level, it is unknown whether termite species co-occurrence could be regulated according to resources availability in the environment.

The current study addressed the question of whether resource suitability modulates the likelihood of termite species co-occurrence in a natural environment. To do so, we tested whether

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the distribution of termite species was regulated by random ('null model') or nonrandom processes. We then analysed whether the spatial co-occurrence of soil-foraging termite species responded to variation in resource availability.

MATERIAL AND METHODS

Study site and data collection

Fieldwork was carried out in seven sites of secondary forest fragments of Brazilian Atlantic rainforest in Viçosa town (29°45'S, 42°50'W), Minas Gerais, southeastern Brazil (Fig. 1). Selected sites represented distinct succession stages (recovery time ranging from 30 to 120 years) to detect variation in resource quantity and quality. The size of sites sampled ranged from 9.30 to 194 ha, and the minimal and maximal distance between sites were 500 m and 5 km, respectively. The altitude of the sites ranged from 694 to 758 m above sea level. Previous tests showed that site sizes did not affect the number of termite records ($F_{1,5}=3.92$, $P=0.10$) or species richness ($F_{1,5}=3.55$, $P=0.11$).

The original forest in the region is classified as Submontane Semideciduous Forest (Oliveira-Filho & Fontes 2000; Silva *et al.* 2003) but has been dramatically altered since the 1930s because of the expansion of agricultural and urban development. In the study sites, the terrain was rough with predominance of oxisol at the top of mountains, cambic oxisol on the slopes and fluvisol in the valleys (Resende 1985).

Sampling was performed during two consecutive autumn seasons in April 2006 and April–May, 2007. The average temperature and the accumulated precipitation during the period of study were 20.7 °C and 56 mm in 2006 and 19.3 °C and 58 mm in 2007, respectively.

Fieldwork procedure

To check whether resource suitability modulated the co-occurrence of soil-feeding termite species, eight quadrats (4 × 4 m) were marked at least 15 m apart (Fig. 2a) in each one of the seven sites selected. A total of 56 quadrats were sampled totalling 896 m². Inside each quadrat, the resource suitability and co-occurrence of soil-feeding species were measured as described below and in Figure 2b.

Estimating resource suitability

A quadrat with large amounts of high-quality resources was hypothesised to be of high suitability and, therefore, more rewarding than quadrats holding any other combination of resource quantity and quality. In other words, 'resource suitability' increased with simultaneous increments of resource quantity and quality. The amount of litter on the soil surface was considered as a measure of resource quantity. Plant litter acts as a primary resource for decomposer organisms and its quality regulates key processes, such as decomposition and nutrient flow. High-quality litter is also more readily mineralised (Aerts 1997). As litter decomposes, the nitrogen (N) content of the soil is enriched, adding quality to the N-poor cellulose-based termite diet. Accordingly, we chose the amount of N relative to carbon (C) in the soil as a surrogate for resource quality. Even so-called 'soil-feeding' termites depend on litter, because they feed on the organic layer of the soil (Brauman *et al.* 2000), which is largely formed of decomposing litter. Additionally, the litter sampled comprised roots, leaves, bark, seeds, fruits and wood debris (branches up to 20 cm in circumference) and fine debris (<3.35 mm). Therefore, the litter biomass sampled is likely to represent food to soil-foraging termites regardless of whether they feed in soil, litter or wood.

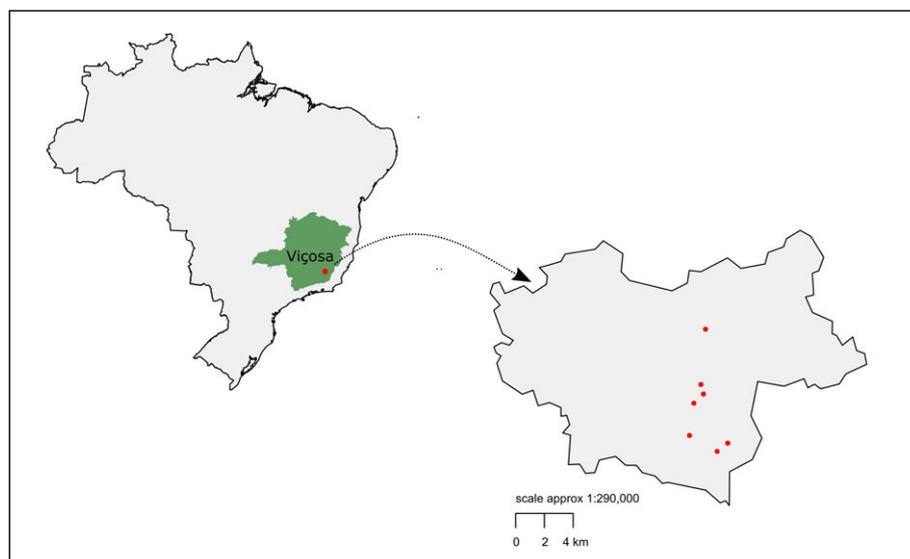


Fig. 1. Map showing the sampled sites (red points) in Viçosa, Minas Gerais, Brazil where fieldwork was conducted. Selected sites represented distinct succession stages (recovery time ranging from 30 to 120 years) to detect variation in resource quantity and quality. The size of sites sampled ranged from 9.30 to 194 ha, and the minimal and maximal distance between sites were 500 m and 5 km, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

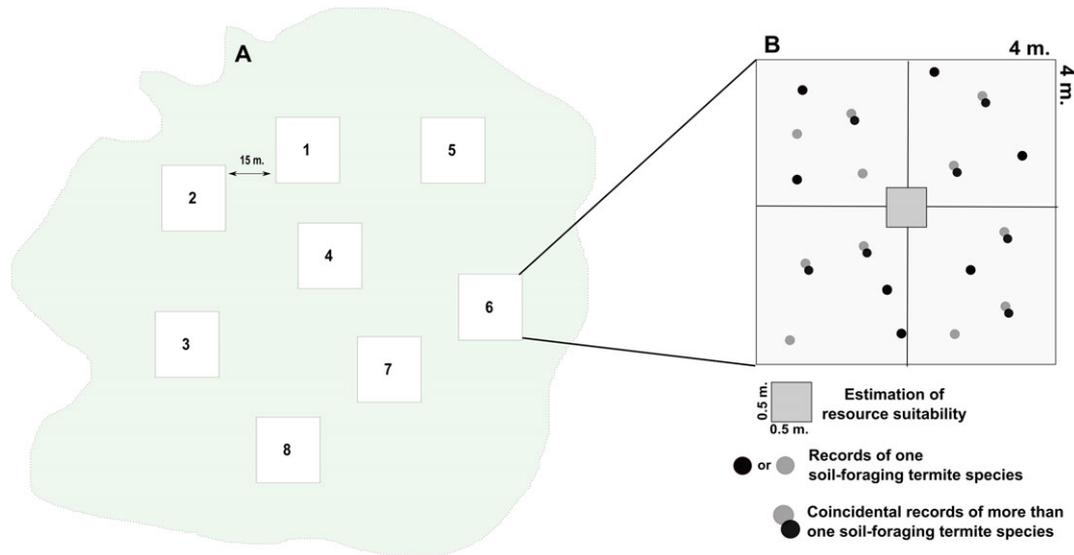


Fig. 2. Schematic design of the fieldwork procedure to test whether resource suitability modulated the co-occurrence of soil-feeding termite species. (a) In each one of the seven sites selected, eight quadrats (4×4 m) were marked at least 15 m apart. (b) Inside each quadrat, the resource suitability and co-occurrence of soil-feeding species were measured as described below. Resource suitability was measured in the centre of each quadrat by two variables that denote resource quantity and quality, respectively: (1) the amount of litter on the quadrat surface (g/m^2); and (2) the N/C ratio of soil samples collected inside the quadrat (dag/kg). To access the spatial co-occurrence of soil-foraging species, we probed the entire experimental quadrat surfaces by inspecting for the presence of termites. We only considered as records of overlap foraging those samples with different termite species that are known to display the same underground foraging behaviour independently of their feeding groups. Thus, the occasional co-occurrence of more than one soil-foraging species, i.e. the encounter of more than one species of soil-foraging termites in the sample, was considered an indicator of the spatial overlap of foraging areas (interspecific overlap). The search for termites occurred on mounds and potential resources, such as soil, litter, dead wood, trunks and the bases of trees occurring within the quadrat. See Material and Methods section for more details. [Color figure can be viewed at wileyonlinelibrary.com]

In summary, resource suitability was measured by two variables that denote resource quantity and quality, respectively: (1) the amount of litter on the quadrat surface (g/m^2); and (2) the N/C ratio of soil samples collected inside the quadrat (dag/kg), given in proportional values from zero to one. We used N/C rather than the traditional C/N ratio, because the numerical values of this former increase as the N content increases, and so does resource quality. This would make data analysis simpler compared with the latter, when numerical values decrease as quality increases.

All surface litter (amount of debris excluding fallen logs) from a 0.5×0.5 m area at the centre of each quadrat was collected (Fig. 2b), taken to the laboratory and processed according to Mendonça and Matos (2005). This included sieving litter through mesh 6 (mesh width = 3.35 mm), extracting coarse soil particles manually and removing remaining fine soil particles by soaking litter in a 2.5% NaOH aqueous solution. Resulting samples were then oven dried (70°C) until they achieved a constant weight, as measured by a two-digit precision scale. One soil sample ($10 \times 10 \times 10$ cm) was collected from beneath the litter layer in the centre of each quadrat. These soil samples were taken to the Laboratory of Soil Analysis at the Federal University of Viçosa (UFV), where total N and C contents were quantified, following standard procedures (Mendonça & Matos 2005). The determination of total organic C was done by wet oxidation with potassium dichromate in a strong acid with an external heat source (Yeomans & Bremner 1988). Total N content was

determined by sulfuric digestion and N-chlorination by Kjeldahl distillation (Bremner & Mulvaney 1982).

Estimating co-occurrence of soil-foraging termite species

Estimation of the foraging range of termite species is inherently difficult, because of their cryptic habits. Techniques proposed to determine termite home range include aggression tests (Nel 1968), individual marking with fat-soluble histological dye (Thorne *et al.* 1996; Evans 2006; Nobre *et al.* 2007) or fluorescent spray dye (Forschler 1994), DNA fingerprinting (Husseneder & Grace 2001), or analysis of cuticular hydrocarbons (Haverty *et al.* 1999). Less intrusive or expensive alternatives have also been used; e.g. Jones and Trosset (1991) succeeded in mapping territorial interference between two termite species by probing an arbitrarily defined area with baits laid on the soil surface. Here, we derived from Jones and Trosset (1991) a method that detected foraging locations occupied by two or more termite species. To do so, we probed the entire experimental quadrat surfaces, by inspecting for the presence of termites (Fig. 2b). We only considered as records of overlap foraging those samples with different termite species that are known to display the same underground foraging behaviour independently of their feeding groups. Thus, the occasional co-occurrence of more than one soil-foraging species, i.e. the encounter of more than one species of soil-foraging termites in the sample, was considered an indicator of the spatial overlap of

foraging areas (interspecific overlap). Thus, our emphasis was on the division of the same space by different species simultaneously, which does not necessarily equate to competition. However, this overlap might interfere with the chance of finding termites and so could help understand the soil-foraging termite distribution pattern in habitats with different resource availability.

Coincidental records of more than one soil-foraging termite species at a single foraging point indicated that these species were using (1) the same resource or (2) neighbouring foraging tunnels. These observations fulfilled our aims, given that our hypothesis was mainly concerned with the effects of resource suitability on spatial overlap (or co-occurrence) of termite species. This approach is suitable only for hypotheses aimed at the community level (such as the one tested here), because it measures only interspecific, rather than intraspecific, overlap.

Termites found in each inspection point inside the quadrats were manually collected with entomological forceps during daylight (between 10:00 and 15:00 h). Each quadrat (4 × 4 m) was subdivided into four subquadrats (2 × 2 m) (Fig. 2b) to ease standardisation and to homogenise sampling at more regular intervals across the quadrat. Two collectors inspected the quadrat simultaneously for 48 min. Collectors started working from opposite ends of the quadrat; each collector being assigned to a different set of two subquadrats and never inspecting the other collector's assigned area. Therefore, each subquadrat took 24 min to be inspected by a single collector, averaging 0.17 m² per min per collector, i.e. approximately 1 h of human effort per 10 m², as in Jones and Eggleton (2000). The search for termites occurred on mounds and potential resources, such as soil, litter, dead wood, trunks and the bases of trees occurring within the quadrat. Thus, a foraging spot was considered to be any one of the above items or places inside the quadrats in which termites were found.

Specimens collected were preserved in 80% ethanol, labelled and later identified to species (or morphospecies). Identifications followed specific literature (Mathews 1977; Constantino 2002), along with comparison with samples from the termite section of the Entomological Museum at the Federal University of Viçosa, Brazil, where voucher specimens from this study were deposited. Collected termites were classified into guilds according to Donovan *et al.* (2001) and Davies (2002) (Table 1).

Statistical analysis

Null model analysis was carried out using the EcoSim software, version 7.1 (Gotelli & Entsminger 2006). Data of termite registers in each quadrat were converted in a presence-absence matrix, in which rows represented different termite species and each column represented a different quadrat. We used the checkerboard score (*C-score*), a fixed-fixed model, as described by Gotelli (2006).

When quadrats inside each site presented with similar characteristics (e.g. succession stage) and were less than 15 m apart, we considered all quadrats inside a site to be from the same termite community. Therefore, the sites were considered to be an independent point in the analysis and represented the respective mean values of co-occurrence inside the quadrats. Thus, each

Table 1 Termite (morpho)species and the respective subfamily and abundance of soil-feeding termites, Viçosa, Minas Gerais, in Southeastern Brazil (2006/2007)

Taxon	Records	Donovan <i>et al.</i> (2001)	Davies (2002)	This work
Apicotermittinae	485			
<i>Anoplotermes</i> sp. 1	61	—	S	S
<i>Anoplotermes</i> sp. 2	265	—	S	S
<i>Anoplotermes</i> sp. 4	4	—	S	S
<i>Anoplotermes</i> sp. 5	23	—	S	S
<i>Anoplotermes</i> sp. 6	81	—	S	S
<i>Anoplotermes</i> sp. 7	35	—	S	S
<i>Anoplotermes</i> sp. 8	1	—	S	S
<i>Aparatermes abbreviatus</i> (Silvestri)	3	—	S	S
<i>Griegotermes</i> sp.	3	S	S	S
<i>Ruptitermes silvestrii</i> (Emerson)	9	—	S	S
Nasutitermittinae	22			
<i>Atlantitermes osborni</i> (Emerson)	14	—	S	S
<i>Subulitermes</i> sp.	8	—	S	S
Syntermittinae	135			
<i>Silvestritermes</i> sp.	5	S/W	S	S
<i>Cyrrillitermes cupim</i> Fontes	13	—	S	S
<i>Ibitermes curupira</i> Fontes	9	—	—	S
<i>Labiatermes</i> sp.	6	S	—	S
<i>Procornitermes lespesii</i> (Mueller)	102	S/W	—	S
Termitinae	232			
<i>Dentispicotermes cupiporanga</i> Bandeira & Canello	73	—	S	S
<i>Dihoplotermes inusitatus</i> Araújo	11	—	S	S
<i>Neocapritermes opacus</i> (Hagen)	148	—	S	S
Unidentified	11			
TOTAL	885			

Guilds definition according to Donovan *et al.* (2001) and Davies (2002). In the absence of definition at species level (e.g. for morphospecies), guilds definition follows the most referred guild for the respective genus. The column headed as 'this work' presents the guild identity assumed here, whose criterion was the coincident opinion between at least two of the authorities presented in previous columns. Termites from groups III and IV of Donovan *et al.* (2001) were considered as potential *soil-feeders*. Species stated here, consisted in the registers that comprised the co-occurrence analysis in this work.

S, soil; W, wood.

forest fragment had a single value for termite co-occurrence, as well as for resource quality and quantity. In all cases, only the records of potential soil-foraging species were analysed, i.e. only those species that were foraging in subterranean tunnels. To test how the proportion of termite species co-occurrence varied with resource quantity and quality, data were subjected to linear regression with binomial errors and corrected for overdispersion. The number of records of more than one soil-feeding termite species at a single foraging spot, relative to the total number of foraging spots detected in a given site, was taken as the response variable (*y-var*) and as a surrogate for spatial co-occurrence. Foraging spots were considered in the analysis only if at least one soil-feeding termite was found in it. Therefore, completely unoccupied areas did not enter the calculation, avoiding eventual bias from 'no-termite lands', known to occur between termite territories (Levings & Adams 1984). Explanatory variables included the N/C ratio of the soil (dag/kg; x_1) as a surrogate for resource quality and litter biomass (g/m²; x_2) as a surrogate for resource

quantity. Both x variables were averaged across the eight quadrats from each forest fragment.

Analyses were carried out in R (R Development Core Team 2011) using a generalised linear model (GLM), followed by residual analyses to verify error distribution and the suitability of the models used, including checks for overdispersion. Model simplification was achieved by eliminating nonsignificant terms ($P > 0.05$) from the model according to their respective complexity, starting from the most complex. When two nonsignificant terms presented the same complexity, the one explaining less deviance was extracted first. Each term deletion was followed by an analysis of deviance to recalculate the deviance explained by the remaining terms (Crawley 2007).

RESULTS

Termites were recorded in 708 of the spots inspected, of which 667 included at least one soil-foraging species. A total of 952 termite records were registered, comprising 27 species and 18 genera, all from the family Termitidae (Tables 1,2). The Apicotermittinae was the most abundant subfamily (52%), followed by Termitinae (25%), Syntermitinae (15%) and Nasutitermitinae (8%).

Among all foraging points, including both single and co-occurrence records, soil-foraging termites comprised 885 records (93%), 20 species and 14 genera (Table 1). Soil-foraging records were used in the co-occurrence analysis, and all of the represented termites belong to the soil-feeding guild (Table 1). Of the total number of foraging points containing soil-feeding termites, 29% contained more than one soil-foraging species, indicating a co-occurrence of termite species. The number of species involved in each co-occurrence record varied from two to four. Other registers (67) comprised a total of seven species, including wood and/or litter feeding (Table 2), which were not used in the soil-foraging co-occurrence analysis.

The null model analysis indicated that the observed C -score index was statistically greater than that expected by chance ($P = 0.03$, Table 3), indicating that termite species co-occurrence

was deterministically structured. Our results also showed that resource suitability modulated the co-occurrence of soil-foraging termite species at local scale. The co-occurrence of soil-foraging termites depended on the interaction between resource quantity and quality, rather than on the independent action of these variables ($\chi^2 = 28.049$, d.f. = 7, $P = 0.023$, Table 4). At both extremes of resource suitability, the spatial co-occurrence of soil-foraging species was observed more often than in sites with intermediate values (Fig. 3).

DISCUSSION

The result from the null model analysis showed that the spatial distribution of soil-foraging termite species was not randomly structured (Table 3). Therefore, the distribution of soil-foraging termite species must be governed by biotic and/or abiotic factors. Among a range of possibilities, our study showed that resource suitability modulated the spatial co-occurrence of soil-foragers at a local scale (Fig. 3). This could result from an adjustment in the home range of a termite colony in response to changes in resource suitability. Foraging efforts by termites seem to represent a compromise between tunnel extension and energy demands that might be governed by resource suitability. This compromise seems particularly applicable to termites. First, unlike other animals that search for food by flying or walking on the surface, soil-feeding termites forage within tunnels. This imposes severe energetic constraints on termites because, in addition to the intrinsic cost of digging a tunnel, there is an additional cost of abandoning tunnels that lead to poor foraging sites (Campora & Grace 2001). Second, despite foraging on extremely abundant resources, termites need to adopt strategies to overcome the high C/N ratio of their diet (Higashi *et al.* 1992; Traniello & Leuthold 2000); i.e. they must exhibit selective behaviour (Shellman-Reeve 1994; Evans *et al.* 2005; Evans 2006; DeSouza *et al.* 2009). Hence, it is reasonable to suppose that termite colonies adjust their home range to balance resource demands and foraging costs. Specifically, termites might build longer tunnels in patches where resources do not provide a suitable combination

Table 2 Termite (morpho)species and respective subfamily, abundance and feeding guild of non-soil-feeders termites, Viçosa, Minas Gerais, in Southeastern Brazil (2006/2007)

Taxon	Records	Donovan <i>et al.</i> (2001)	Davies (2002)	This work
Nasutitermitinae	55			
<i>Diversitermes castaniceps</i> (Holmgren)	20	—	—	W/L
<i>Nasutitermes jaraguai</i> (Holmgren)	18	W	W	W
<i>Nasutitermes rotundatus</i> (Holmgren)	5	W	W	W
<i>Nasutitermes</i> sp. 1	2	W	W	W
<i>Nasutitermes</i> sp. 2	10	W	W	W
Syntermitinae	12			
<i>Cornitermes cumulans</i> (Kollar)	8	W/L	W/L	W/L
<i>Syntermes dirus</i> Burmeister	4	—	W/L	W/L
Total	67			

Guilds definition according to Donovan *et al.* (2001) and Davies (2002). In the absence of definition at species level (e.g. for morphospecies), guilds definition follows the most referred guild for the respective genus. The column headed as 'this work' presents the guild identity assumed here, whose criterion was the coincident opinion between at least two of the authorities presented in previous columns. Species stated here was not considered on co-occurrence analysis.

L, litter; W, wood.

Table 3 Null model (fixed-fixed) analysis of soil-foragers termites using *C*-score

Null Model	Observed index	Mean of simulated indices	SES	P
Fixed-fixed				
<i>Quadrats</i>	39.41	38.49	1.94	0.03**

Further details in the Material and Methods section. SES, standardised effect size; P, probability that observed index was greater than the expected by chance. **, $P < 0.05$.

Table 4 Effects of resource suitability (resource quality = soil N/C ratio and resource quantity = litter biomass) on the proportion of co-occurrence in soil-feeding termites

Source	d.f.	Deviance	$P(>\chi^2)$	
N/C ratio (a)	1	1.524	0.3934	ns
Litter biomass (b)	1	0.046	0.8744	ns
a:b	1	28.049	0.0236	***
Error	4	29.620		
Total	7			

Generalised linear modelling with binomial errors, corrected for overdispersion. See further details in the Material and Methods section. df, degrees of freedom; ns, $P > 0.05$; ***, $P < 0.001$.

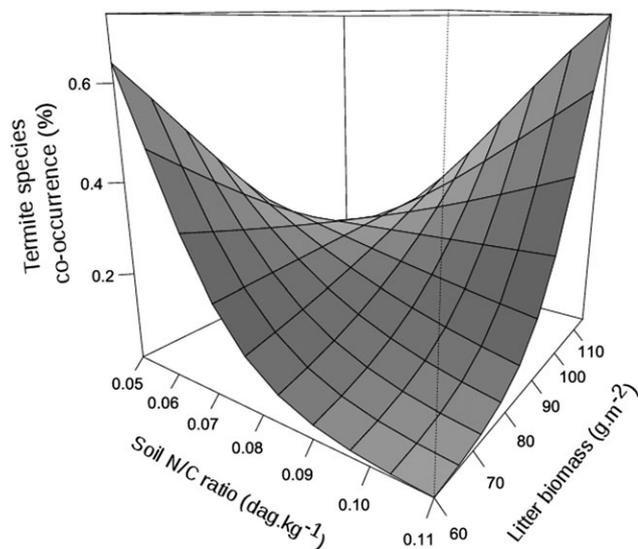


Fig. 3. Effect of resource suitability on the proportion of soil-forager termite co-occurrence. Suitability is taken as the combination of resource quality (soil N/C ratio in dag/kg) and resource quantity (litter biomass g/m^2), increasing with increments of both parameters. Co-occurrence of soil-feeder species is defined as a record of more than one species in a single point sample. The spatial co-occurrence of soil-foragers was observed more often at both extremes of resource suitability (low and high) than in sites with intermediate values.

of quality and quantity, than where both of these are optimal. The mechanism behind this behaviour might be that stimuli promoting excavation persist until a profitable patch is found. In fact, under laboratory conditions, termites tend to build more numerous and longer tunnels more quickly when they are subjected to a low supply of resources (Hedlund & Henderson 1999; Arab &

Costa-Leonardo 2005; Gallagher & Jones 2005; Araújo *et al.* 2011). The regulation of home ranges to balance the benefits and costs of foraging according to resource suitability might be an important determinant of community structure in termites and in other organisms.

Regardless of the mechanisms generating the U-shape pattern depicted in Figure 3, our results illustrate patterns in termite home range that are also observed in other animals. For example, *Bombus terrestris* (Hymenoptera: Apidae) modify their foraging behaviour when resources are abundant, spending less time travelling (Westphal *et al.* 2006). Similarly, ants prefer to use food sources close to their nest when resources are abundant (Brown & Gordon 2000), and the density of prey determines the choice of a feeding site for social wasps (Richter 2000). Even vertebrates have been reported using space in a similar manner to the termites studied here: e.g., brown bears exhibit the same U-shape pattern of home range overlap (McCloughlin *et al.* 2000).

Interestingly, the pattern found here can arise from both non-interactive and interactive processes (see Fig. 4). When food resources are so unsuitable that defence yields no net benefit to the home-range owner, we can expect abandonment of territorial behaviour (Carpenter & Macmillan 1976) and subsequent increases in home-range overlap (McCloughlin *et al.* 2000). To termites, as resource quality and quantity increase, overlap might be reduced to a minimum because of a reduced necessity for tunnel excavation and the contraction of home ranges generally. Further improvement in resource suitability could lead to colony growth and/or the settlement of new colonisers, with a consequent expansion of tunnel networks. However, a resource bonanza might undermine territorial behaviour if overlaps do not threaten energy acquisition. In termites, low levels of interaction seem likely given that subterranean species forage in the confines of their tunnels, and so neighbouring tunnels from another colony might frequently go unnoticed. Hence, termite tunnel networks are likely to coexist, overlapping or not, entirely as a result of colonies adjusting their foraging strategy in response to cost-benefit assessments of resources. Interactive processes could also cause overlap at intermediate levels of resource suitability. Contrary to high and low levels, where territorial defence is unnecessary or unattainable, respectively, at intermediate levels, defending a home range might convey a net benefit. Again, evidence from termite foraging behaviour adds support to this reasoning. For instance, in contrast to subterranean termites that excavate tunnels, arboreal-nesting mangrove termites expand their foraging ranges by building galleries on the surface. Territory invasion is then highly conspicuous, offering greater opportunity to defend territories and avoid overlap (Levings & Adams 1984; Adams & Levings 1987). Although all co-occurrences analysed comprised at least one soil-feeding species, we could not determine whether species were competing for resources. Recently, it has been shown that resource availability affect response to chemical cues and aggressiveness in *Nasutitermes* aff. *coxipoensis* (see Cristaldo *et al.* 2016), adding support that the mechanism proposed here can be responsible for the 'U-shape' pattern found in the present study.

In addition to the above explanations, other environmental factors can also act simultaneously with habitat quality and, thus,

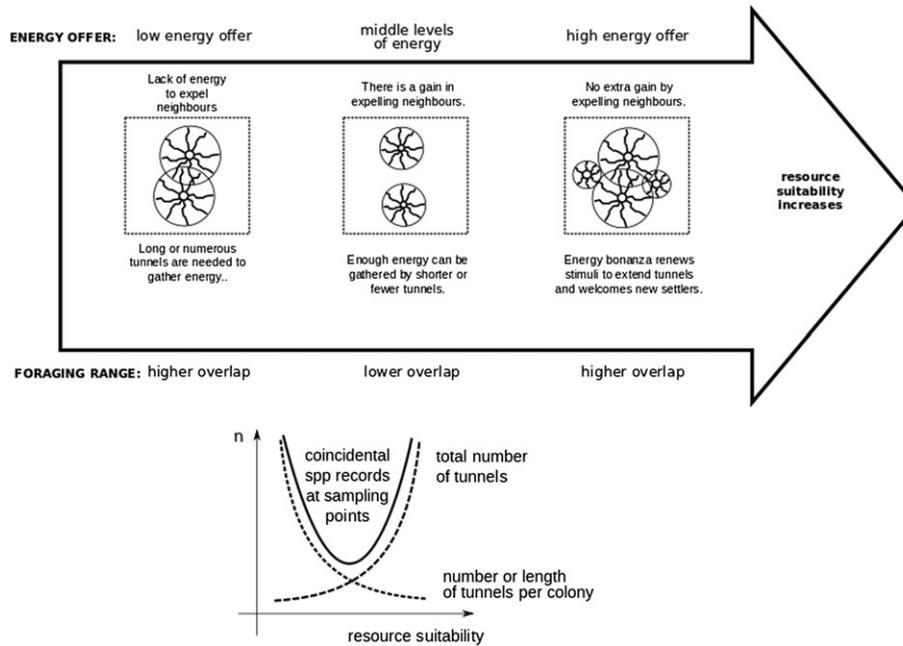


Fig. 4. Hypothetical mechanisms leading to U-shape correlation between termite co-occurrence and resource offer. Higher overlaps in home range of neighbouring colonies are bound to happen at low and high extremes of resource suitability, improving species detection by soil-probing sampling techniques. At intermediate resource levels, this overlap and hence sampling detection are lowest. This could happen by virtue of two opposing forces: decrements in tunnel length and numbers combined with renewed stimuli to extend tunnels as resources rise. See Discussion section for more details and also Cristaldo *et al.* (2016).

modulate the space use by termites. For example, microbial pathogens in soil and a low-quality diet can influence the reproduction and colony success of termites (Rosengaus *et al.* 2011), which could impact species co-occurrence. Other factors, such as predation risk and soil texture, can also influence termite foraging, as recently demonstrated in other studies at population level (Korb & Linsenmair 2002; Pequeno *et al.* 2015). However, most of soil-foraging termite species were not affected neither by soil structure nor chemical composition at community level (Bourguignon *et al.* 2015).

On other scales, e.g. at a regional scale, we suggest that the results of the present study could help to understand some common conflicting patterns of termite diversity: Eggleton *et al.* (1994) found a negative trend between termite generic diversity and net primary productivity (NPP) in tropical regions. However, in Brazilian biomes, termite diversity has been reported to be positively related to plant productivity in the semiarid 'Caatinga' (scrub forest; Melo & Bandeira 2004), negatively with increment of resource availability in Atlantic rainforest (Araújo *et al.* 2007), and no pattern was observed in the 'cerrado' (Brazilian savanna; Oliveira *et al.* 2013). The possible mechanism behind these conflicting results in termite diversity could be the regulation of foraging distance as a response of resource availability.

In the current study, soil-foraging termite colonies appeared to modulate their foraging range in accordance with resource suitability, instead of being randomly distributed. Overlap with neighbouring colonies of different species occurred more frequently when resource suitability measures were very high or very low. Our results could explain the absence (Oliveira *et al.* 2013) and also 'aberrant' inverse (Araújo *et al.* 2007) relations

between termite abundance and resource availability. The inverse relations could occur when colonies retract their foraging range in higher quality habitats, potentially impairing sampling detection and producing false low abundance records (e.g. Araújo *et al.* 2007). This study is, to the best of our knowledge, the first step to understanding the use of space by termite communities according to both resource quantity and quality variations under natural conditions.

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REFERENCES

Adams ES & Levings SC. 1987. Territory size and population limits in mangrove termites. *Journal of Animal Ecology* **56**, 1069–1081.

- Aerts R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* **79**, 439–449.
- Arab A & Costa-Leonardo AM. 2005. Effect of biotic and abiotic factors on the tunneling behavior of *Coptotermes gestroi* and *Heterotermes tenuis* (Isoptera: Rhinotermitidae). *Behavioral Processes* **70**, 32–40.
- Araújo APA, Araújo FS & Desouza O. 2011. Resource suitability affecting foraging area extension in termites (Insecta, Isoptera). *Sociobiology* **57**, 1–14.
- Araújo APA, Galbiati C & DeSouza O. 2007. Neotropical termite species (Isoptera) richness declining as resource amount rises, food or enemy-free space constraints? *Sociobiology* **49**, 93–106.
- Bennett J, Gillespie D, Shipp J & Vanlaerhoven S. 2009. Foraging strategies and patch distributions: intraguild interactions between *Dicyphus hesperus* and *Encarsia formosa*. *Ecological Entomology* **34**, 58–65.
- Bourguignon T, Drouet T, Šobotnik J et al. 2015. Influence of soil properties on soldierless termite distribution. *PLoS One* **10**, e0135341.
- Brauman A, Bignell DE & Tayasu I. 2000. Soil-feeding termites, biology, microbial associations and digestive mechanisms. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (eds T Abe, DE Bignell & M Higashi), pp. 233–259. Kluwer Academic Publishers, Netherlands.
- Bremner JM & Mulvaney CS. 1982. Nitrogen total. In: *Methods of Soil Analysis: Chemical and Microbiological Properties* (ed AL Page), pp. 595–624. ASA, Madison.
- Brown FMJ & Gordon MD. 2000. How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. *Behavioral Ecology and Sociobiology* **47**, 195–203.
- Campora CE & Grace JK. 2001. Tunnel orientation and search pattern sequence of the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology* **94**, 1193–1199.
- Carpenter F & Macmillan R. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science* **194**, 639–642.
- Constantino R. 2002. An illustrated key to Neotropical termite genera (Insecta: Isoptera) based primarily on soldiers. *Zootaxa* **40**, 1–40.
- Crawley MJ. 2007. *The R Book*, 942 pp. John Wiley and Sons, Chichester.
- Cristaldo PF, Araújo APA, Almeida CS et al. 2016. Resource availability influences aggression and response to chemical cues in the Neotropical termite *Nasutitermes* aff. *coxipoensis* (Termitidae: Nasutitermitinae). *Behavioral Ecology and Sociobiology* Online First. DOI: 10.1007/s00265-016-2134-y.
- Davies R. 2002. Feeding group responses of a Neotropical termite assemblage to rain forest fragmentation. *Oecologia* **133**, 233–242.
- DeSouza O, Araújo APA & Reis-Jr R. 2009. Trophic controls delaying foraging by termites: reasons for the ground being brown? *Bulletin of Entomology Research* **99**, 603–609.
- Donovan SE, Eggleton P & Bignell DE. 2001. Gut content analysis and a new feeding group classification of termites. *Ecological Entomology* **26**, 356–366.
- Eggleton P, Williams PH & Gaston KJ. 1994. Explaining global termite diversity: productivity or history. *Biodiversity and Conservation* **3**, 318,330.
- Evans TA. 2006. Foraging and building in subterranean termites: task switchers or reserve labourers? *Insectes Sociaux* **53**, 56–64.
- Evans TA, Lai JCS, Toledano E et al. 2005. Termites assess wood size by using vibration signals. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 3732–3737.
- Forschler BT. 1994. Fluorescent spray paint as a topical marker on subterranean termites (Isoptera, Rhinotermitidae). *Sociobiology* **24**, 27–38.
- Gallagher NT & Jones SC. 2005. Effects of resource availability on search tunnel construction by the eastern subterranean termites, *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). *Sociobiology* **45**, 1–12.
- Gotelli NJ. 2006. Null-model analysis of species co-occurrence patterns. *Ecology* **81**, 2606–2621.
- Gotelli NJ & Entsminger GL. 2006. EcoSim: Null model software for Ecology. Version 7.1, Acquired Intelligence Inc. & Kelsey-Bear.
- Grangier J & Lester P. 2014. Carbohydrate scarcity increases foraging activities and aggressiveness in the ant *Prolasius adenus* (Hymenoptera: Formicidae). *Ecological Entomology* **39**, 684–692.
- Haverty MI, Copren KA, Getty GM & Lewis VR. 1999. Agonistic behavior and cuticular hydrocarbon phenotypes of colonies of *Reticulitermes* (Isoptera: Rhinotermitidae) from northern California. *Annals of the Entomological Society of America* **92**, 269–277.
- Hedlund JC & Henderson G. 1999. Effect of available food size on search tunnel formation by the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Economic Entomology* **92**, 610–616.
- Higashi M, Abe T & Burns TP. 1992. Carbon–nitrogen balance and termite ecology. *Proceedings of the Royal Society of London B Biological Science* **249**, 303–308.
- Husseneder C & Grace JK. 2001. Evaluation of DNA fingerprinting, aggression tests, and morphometry as tools for colony delineation of the Formosan subterranean termite. *Journal of Insect Behavior* **14**, 173–186.
- Jiménez JJ, Decaëns T & Rossi JP. 2012. Soil environmental heterogeneity allows spatial co-occurrence of competitor earthworm species in a gallery forest of the Colombian ‘Llanos’. *Oikos* **121**, 915–926.
- Jones CG, Lawton JHH & Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**, 373–386.
- Jones DT & Eggleton P. 2000. Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *Journal of Applied Ecology* **37**, 191–203.
- Jones SC & Trosset MW. 1991. Interference competition in desert subterranean termites. *Entomologia Experimentalis et Applicata* **61**, 83–90.
- Korb J & Linsenmair EK. 2002. Evaluation of predation risk in the collectively foraging termite *Macrotermes bellicosus*. *Insectes Sociaux* **49**, 264–269.
- Lanan MC & Bronstein JL. 2013. An ant’s-eye view of an ant–plant protection mutualism. *Oecologia* **172**, 779–790.
- Levings SC & Adams ES. 1984. Intra- and interspecific territoriality in *Nasutitermes* (Isoptera: Termitidae) in a Panamanian mangrove forest. *Journal of Animal Ecology* **53**, 705–714.
- Mathews A. 1977. *Studies on Termites from the Mato Grosso State, Brazil*, 267 pp. Academia Brasileira de Ciências, Rio de Janeiro.
- McLoughlin PD, Ferguson SH & Messier F. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology* **14**, 39–60.
- Melo ACS & Bandeira AG. 2004. A qualitative and quantitative survival of termites (Isoptera) in an open shrubby Caatinga in northeast Brazil. *Sociobiology* **44**, 707–716.
- Mendonça ES & Matos ES. 2005. In: *Matéria orgânica do solo: métodos de análises* (eds ES Mendonça & ES Matos). D&M Gráfica e Editora Ltda, Viçosa.
- Nel JJC. 1968. Aggressive behaviour of the harvester termites *Hodotermes mossambicus* (Hagen) and *Trinervitermes trinervoides* (Sjöstedt). *Insectes Sociaux* **15**, 145–156.
- Nobre T, Nunes L & Bignell DE. 2007. Estimation of foraging territories of *Reticulitermes grassei* through mark release recapture. *Entomologia Experimentalis et Applicata* **123**, 119–128.
- Oliveira DE, Carrijo TF & Brandão D. 2013. Species composition of termites (Isoptera) in different Cerrado vegetation physiognomies. *Sociobiology* **60**, 190–197.
- Oliveira-Filho AT & Fontes MAL. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *Biotropica* **32**, 793–810.
- Pequeno PACL, Franklin E, Venticinque EM & Acioli ANS. 2015. Linking functional trade-offs, population limitation and size structure: termites under soil heterogeneity. *Basic and Applied Ecology* **16**, 365–374.
- R Development Core Team. 2011. R: A Language and Environment for Statistical Computing.
- Resende M. 1985. Clima e solo: suas relações com o ambiente agrícola. *Informe Agrapocuario* **12**, 43–49.
- Richter MR. 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annual Review of Entomology* **45**, 121–150.
- Rosengaus RB, Traniello JFA & Bulmer MS. 2011. Ecology, behavior and evolution of disease resistance in termites. In: *Biology of Termites: A Modern Synthesis* (eds DE Bignell, Y Roisin & N Lo), pp. 165–191. Springer, New York.
- Shellman-Reeve JS. 1994. Limited nutrients in a dampwood termite: nest preference. *Competition and Cooperative Nest Defence. Journal of Animal Ecology* **63**, 921–932.
- Silva AF, Oliveira RV, Santos NRL & dePaula A. 2003. Composição florística e grupos ecológicos das espécies de um trecho de floresta semidecídua submontana da Fazenda São Geraldo, Viçosa-MG. *Revista Árvore* **27**, 311–319.

- Thorne BL, Russek-Cohen E, Forschler BT *et al.* 1996. Evaluation of mark–release–recapture methods for estimating forager population size of subterranean termite (Isoptera: Rhinotermitidae) colonies. *Environmental Entomology* **25**, 938–951.
- Traniello JFA & Leuthold RH. 2000. Behavior and ecology of foraging in termites. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (eds T Abe, D Bignell & M Higashi), pp. 141–168. Kluwer Academic Publishers, Netherlands.
- Tremblay I, Thomas D, Blondel J, Perret P & Lambrechts M. 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits. *Parus caeruleus*. *Ibis (Lond. 1859)* **147**, 17–24.
- Westphal C, Stefan-Dewenter I & Tschamtko T. 2006. Foraging trip duration of bumblebees in relation to landscape-wide resource availability. *Ecological Entomology* **31**, 389–394.
- Yeomans JC & Bremner JM. 1988. A rapid and precise method for routine determination of organic carbon in soil. *Communications in Soil Science and Plant Analysis* **19**, 1467–1476.
- Zengeya FM, Murwira A & De Garine-Wichatitsky M. 2014. Seasonal habitat selection and space use by a semi-free range herbivore in a heterogeneous savanna landscape. *Austral Ecology* **39**, 722–731.

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