

# Trophic controls delaying foraging by termites: reasons for the ground being brown?

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## Abstract

Why is the ground brown, when detritivores and decomposers have the numbers and ability to speed up the turnover of dark-coloured soil organic carbon? We consider this soil analogue to the ‘green world’ hypothesis measuring in the field how fast termites occupied cellulosic baits of varying quantity and quality and how predation risks by ants affect such encounters. Single baits with ants were occupied by termites later than triple baits without ants, implying that termites may spend longer searching for suitable food than feeding on it, thereby delaying decomposition rates of both chosen and neglected items. Because termites’ feeding speeds up dissimilation of polymers by decomposers, such results may imply that bottom-up and top-down forces, ultimately, impair carbon processing and release from soil. We argue that the ground is brown partly because of delays imposed upon termites’ use of resources by bottom-up and top-down forces.

**Keywords:** detritivory, carbon flux, decomposition, trophic controls, predation risks, Insecta: Isoptera

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## Introduction

The world is green, despite the astonishing abundance and diversity of herbivores with the capacity to consume all known plant tissues. Soon after Hairston *et al.* (1960) formally put forward hypotheses to explain why this is so, prolific debate populated ecological literature. Currently, ecologists tend to agree (Begon *et al.*, 2006) that the world is green not only because herbivores are limited by predators (‘top-down’ forces), but also because plants present effective chemical and physical defences that make them inedible by herbivores (‘bottom-up’ forces: Murdoch, 1966).

Expanding on Murdoch’s ideas, Abe & Higashi (1991) brought detritivores and decomposers to the scene, proposing that the world is green because consumers are either able to feed on cytoplasm (most herbivores) or on cell wall (detritivores and decomposers), with a marked scarcity of destructive consumers, i.e. generalists feeding on both cell components. According to Abe & Higashi (1991), this scarcity of generalists, together with the abundance of cell-wall specialists, could be ‘[...]viewed as one cause preserving the green earth by reducing the consumption of the living part of plants while enhancing the decomposition of the dead part[...], thereby speeding up the return of nutrients to the living part.

Detritivores and decomposers, in fact, shift the ‘green world’ puzzle one step down, to encompass the soil food web and a further enigma – the ground is brown. Why is it so, given the existence of detritivores and decomposers with

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the numbers and ability speed up the turnover of dark-coloured soil organic carbon? Allison (2006) convincingly hypothesizes that the ground is brown because both bottom-up and top-down forces operate on detritivores and decomposers, impairing their effective processing of soil organic carbon (SOC) into carbon dioxide, hence keeping the ground brown because carbon is kept locked into soil.

Here, we explore such an idea using termites (Insecta: Isoptera) in a field experiment, investigating whether bottom-up and/or top-down forces can delay resource encounter (and hence, usage) by these insects. Our rationale is that such delays would prevent prompt release of CO<sub>2</sub> from organic matter to the atmosphere, thereby contributing to enhanced amounts of humic complexes which confer the dark appearance of the ground. We base our reasoning on the fact that termites play a key role in release from dead organic matter in tropical soils. By feeding on the wide decomposing continuum from fresh litter to humus, termites can affect the entire dynamics of soil carbon, both directly, by digesting cellulose (Slaytor, 2000), and indirectly, by breaking litter down, thereby easing microbes' action on otherwise unexposed surfaces of litter items. Wood-feeding termites and their microbiota, for instance, can oxidise  $\approx 99\%$  of the carbon they intake, releasing it mainly as CO<sub>2</sub> (Slaytor, 2000). Soil-feeding termites, meanwhile, are well known to feed on highly humified material and are even suspected to process complex polyaromatic components of soil organic matter (SOM) which have been previously modified by microorganisms (Brauman *et al.*, 2000). In short, we argue here that one of the reasons for the ground being brown (in the tropics) is that trophic controls prevent termites from processing all available litter and humus, the remaining material being left to form impervious dark-coloured humic complexes in the soil.

### Hypotheses

Being one of the few groups of animals whose main diet consists of cellulose, termites could be thought to experience no shortage of food. In addition, as they forage within tunnels, most termite foragers could be considered to be released from strong predation risks. The corollary of these hypotheses is that termites would not be constrained by food types and status, readily occupying the first item they find in the field. Unoccupied resources would exist simply because termite foragers have not found them yet. If this is so, food processing by termites is not constrained by either bottom-up or top-down forces, which stands as our null hypothesis. An alternative idea is that termite foraging, albeit time-dependent due to the need to build tunnels/galleries, is also affected by any trait that would make a resource more worthwhile to explore than a competing one. According to this view, resources in larger amounts, presenting more nutrients and free from predation risks, would be the first to be occupied, providing evidence that trophic controls may contribute to delays in termite foraging and hence to the ground being brown.

### Materials and methods

#### *Study site*

The experiment was carried out in the municipality of Coimbra (S20–50.049' × W42–47.452'; altitude 650 m above

sea level), Minas Gerais State, Southeastern Brazil. The climate is wet subtropical, with a dry season between May and September, annual mean precipitation of 1400 mm and annual mean temperature of 19°C (Valverde, 1958). The study area is a grassland neighboring a small fragment (7 ha) of Brazilian coastal rainforest ('Atlantic rainforest') naturally separated from it by a 3-m-wide stream at the bottom of a valley. The experimental site presents a flat topography and is visually homogeneous regarding vegetation and soil. Both grassland and forest are immersed in a matrix composed of a mosaic of implanted pastures and small-scale agricultural fields.

#### *Experimental procedure*

The experiment aimed to check how fast termites are found on feeding (cellulosic) resources of varying quantity and nutrient content (i.e. bottom-up effects), and how predation risks (top-down) affect such an encounter rate. Cellulosic baits (unbleached, unscented, uncolored, single ply toilet paper rolls 12-cm tall × 10-cm Ø weighing 100 g) were used to mimic feeding resources. Such baits are well known to be promptly accepted and consumed by termites from all guilds in the field (Dawes-Gromadzki, 2003). Two 12 × 12 grids were set up. Baiting points within grids were placed 1 m apart, each point holding one of the four instances of a factorial combination of high or low resource quantity × high or low resource quality. These four treatments were placed systematically through the grid such that every treatment neighbored all the others from all possible locations, thereby assuring that each bait type had equal chances of being chosen by termites. Although such a grid design does not favour independence between bait locations, this interdependence was intentional as it allows equal chances of termite 'choice' (if it exists) for any bait type, as explained above. Baits on grid edges were not inspected; rather, they were installed to ensure that every baiting point was affected by the same number of neighboring baits (eight). Thus, the sampling area in each grid corresponded to 10 × 10 baits = 100 baiting points.

Variation in resource quantity was simulated by supplying a baiting point with a single bait or three side-by-side triangularly disposed baits. Two pieces of expanded polystyrene with the same size and weight as the paper roll were allocated beside single baits (mimicking a 3-bait station) to ensure that shading and pressure on the soil surface were the same at all points. This was intended to limit differences in 'thermal shade', which are known to affect food location by termites (Ettershank *et al.*, 1980). Variation in resource quality was simulated by adding nitrogen to the baits, which was based on the fact that termites are known to seek nitrogen-rich resources in the field (Shellman-Reeve, 1994). This was achieved by 'enriching' baits with 100 ml of a 3% w/v water solution of NH<sub>4</sub>NO<sub>3</sub>, as used by Curtis & Waller (1997) as the nitrogen source for termites in artificial diets. Baits, which were not nitrogen-enriched, received 100 ml of water.

Every week, termites and ants were collected under baits with the aid of entomological forceps. Baits were returned to their original location immediately after inspection/collection. Predation risks were estimated by recording the presence/absence of ants on the baits, since ants are known to be major predators of termites (e.g. Sheppe, 1970; Leal & Oliveira, 1995). A bait was classified as occupied only when

it contained galleries and termites were actually found feeding on it. A bait was recorded as free from predation risk only if ants were never spotted on it throughout the whole experiment. Sampling took place in the warm-wet period of January to March 2004, from 8:00 to 12:00 h. The experiment was repeated, with a new set of baits, in the cool-dry period of April to June 2004, to allow for differences in seasonal patterns of foraging (Moura *et al.*, 2006).

#### Statistical analyses

Data were taken as the number of days it took for termites to occupy baits, whether or not they were subsequently abandoned. For this, data were subjected to censored survival analysis with a Weibull distribution (Crawley, 2007), performed with survival package in R (R Development Core Team, 2006). Survival analysis, or failure time data analysis, means the statistical analysis of data where the response of interest is the time,  $t$ , from a well-defined time origin to the occurrence of some given event (end-point) (Martinussen & Scheike, 2006). In our specific case, the time origin is the moment of bait installation in the field, and the end-point is the first day termites were spotted on such bait. The analysis aimed to inspect whether resource traits would affect the time elapsed until a bait was first spotted with termites. Here, we are inspecting, therefore, the 'survival' of a bait in the field; its 'death' being considered to happen at the moment it was first found with termites. Similar uses of such an analysis for termites (but not for baits) can be found in DeSouza *et al.* (2001) and Miramontes & DeSouza (1996).

The general model for this analysis followed the equation:

$$\log_e S(t) = -\mu^{-\alpha} t^\alpha \quad (1)$$

where  $S(t)$  is the accumulated proportion of baits occupied until time,  $t$ ; the mean time,  $\mu$ , is the time elapsed until 50% of the baits of a given resource type are found with termites; and  $\alpha$  is the shape parameter for the survival curve. When  $\alpha = 1$ , the probability of finding a bait does not change as time elapses. If  $\alpha < 1$  this probability reduces as time elapses, the converse happening when  $\alpha > 1$ .

Statistical analysis was used to check whether the resource traits, bait quantity (single or triple baits), bait quality (nitrogen added/not-added), and predation risk (absence/presence of ants), would affect the mean time,  $\mu$ , spent until termites are found on the bait. The analysis began by estimating  $\alpha$  for the whole dataset and proceeded with hypotheses testing. Under the null hypothesis for a given  $\alpha$ , the mean time,  $\mu$ , to find a bait does not differ between resource traits and, hence, time,  $t$ , alone explains  $S(t)$ . Alternatively, if resource traits affect bait encounter by termites, a typical  $\mu$  can be calculated for each resource trait, and histograms can be plotted to ease visualisation of the differences between bait types. This would be taken as evidence that its corresponding regulatory force (bottom-up or top-down) was in effect speeding up the decomposition process of some items at the expense of others, which would point to a contribution of this regulatory force to delay SOC processing and, ultimately, to the brown ground.

Modelling proceeded by building a full model, including all of the above parameters and their second and third order interactions, plus a blocking term ('season') to distinguish between the two runs of the experiment. To inspect redundancy of effects, various full models were

Table 1. Termites (Insecta: Isoptera: Termitidae) recorded in cellulosic baits disposed in a grassland bordering an 'Atlantic forest' relict in southeastern Brazil. Diet types are based on the genus and are in accordance with Araújo *et al.* (2007). Soil feeders may sometimes be reported as 'humivorous'.

| Subfamily & species                                   | Diet        | Records    |
|---|-------------|------------|
| <b>Apicotermitinae</b>                                |             |            |
| <i>Anoplotermes</i> sp. 1                             | soil        | 52         |
| <i>Anoplotermes</i> sp. 2                             | soil        | 10         |
| <i>Anoplotermes</i> sp. 3                             | soil        | 5          |
| <i>Grigotermes bequaerti</i> (Snyder & Emerson, 1949) | soil        | 15         |
| <i>Ruptitermes xanthochiton</i> (Mathews, 1977)       | soil        | 7          |
| <i>Ruptitermes silvestrii</i> (Emerson, 1925)         | soil        | 49         |
| <b>Nasutitermitinae</b>                               |             |            |
| <i>Cornitermes cumulans</i> (Kollar, 1832)            | litter/wood | 35         |
| <i>Embratermes heterotypus</i> (Silvestri, 1901)      | soil/wood   | 3          |
| <i>Nasutitermes jaraguae</i> (Homlgren, 1910)         | wood        | 13         |
| <b>Termitinae</b>                                     |             |            |
| <i>Neocapritermes opacus</i> (Hagen, 1858)            | soil/wood   | 1          |
| <b>Total</b>  |             | <b>190</b> |

created, composed of the same terms entered in a different order. Model simplification, was performed by backward term extraction, removing one term at a time. Terms returned to the model if their removal provoked a change of deviance with  $P < 0.05$ .

#### Voucher specimens

Specimens of ants and termites were preserved in 80% alcohol, labelled and subsequently identified to species or morphospecies as appropriated. Termite identifications followed the literature (Constantino, 1999, and papers therein), being subsequently confirmed by comparison with the collection of the Termite Section of the Entomological Museum (UFVB) of the Federal University of Viçosa (UFV) (<http://www.insecta.ufv.br/museu>) where voucher specimens were deposited. Further confirmation of termite identities was kindly provided by R. Constantino from the University of Brasilia and A. Acioli from the Federal University of Amazonas. Ants were identified by comparison with the collection of the Community Ecology Laboratory of UFV.

#### Results

In the first half of the study period (January to March 2004, end of wet-warm season), rainfall attained a daily average of 10.2 mm, dropping to 1.9 mm in the second half (April to June 2004, beginning of the cool-dry season). Daily mean temperatures were 22.0 and 18.7°C, respectively.

Termites collected comprised ten species from seven genera and three subfamilies, all belonging to a single family (Termitidae) (table 1). Among those, at least seven species feed on soil and on highly humified wood (Apicotermitinae and Termitinae) and three (Nasutitermitinae) feed on litter and wood at initial stages of decomposition. Termites were easily spotted extracting fragments of the bait. Apicotermitinae termites frequently dug galleries on the lower end of the bait, whereas *Nasutitermes jaraguae* (Nasutitermitinae)

Table 2. Ant species (Hymenoptera: Formicidae) collected in cellulosic baits disposed to collect termites in a grassland bordering an 'Atlantic forest' relict in southeastern Brazil. Trophic groups are based on Brown Jr. (2000).

| Subfamily & species                         | Trophic group |
|---|---------------|
| Ecitoninae                                  |               |
| <i>Labidus coecus</i>                       | predator*     |
| Dolichoderinae                              |               |
| <i>Linepithema</i> sp. 1                    | generalist    |
| Myrmicinae                                  |               |
| <i>Cyphomyrmex</i> prox. <i>transversus</i> | fungus grower |
| <i>Mycocepurus goeldii</i>                  | fungus grower |
| <i>Pheidole</i> sp. 1                       | omnivore*     |
| <i>Pheidole</i> sp. 2                       | omnivore*     |
| <i>Solenopsis</i> sp. 1                     | omnivore*     |
| Ponerinae                                   |               |
| <i>Hypoponera</i> sp. 1                     | generalist    |
| <i>Odontomachus haematodus</i>              | predator*     |
| <i>Pachycondyla obscuricornis</i>           | predator*     |

\* denotes ants known to prey upon termites.

conspicuously bore many galleries through the bait. Ants (Hymenoptera: Formicidae) comprised ten species from nine genera and four subfamilies, among which eight species are predators, generalists or omnivores and two species are fungus cultivators (table 2). On several occasions, ants were spotted preying on termites in the baits.

The minimal statistical model achieved (equation 2) presented  $\alpha = 1.26$ , indicating that the probability of finding termites on a bait increased as time elapsed. That is, termites were not promptly spotted on the bait; they started to be found only after some initial time lag. This model also shows that some resource traits (but not their interactions) did modify the time needed until the bait was first spotted with termites. That is, all baits took some initial time lag to be occupied by termites, but for some bait types such a time lag was shorter than for others. Therefore, we have evidence disproving our null hypothesis in favour of the alternative one, namely, that food types and status would constrain termite use of resources.

The time,  $\mu$ , that baits of a given resource trait took to be occupied in the field by termites can be estimated by

$$\log_e \mu = 5.394 - 0.448q + 0.470r - 1.191s \quad (2)$$

where  $s$  refers to the season when the data was collected,  $q$  is bait quantity and  $r$  is predation risk (the resource traits referred to in the 'Material and methods' section). This  $\mu$  value, when replaced in equation 1 above, gives the accumulated proportion  $S(t)$  of baits found with termites after a given time,  $t$ , has elapsed. To calculate  $\log_e \mu$  (and hence  $\mu$  for each resource trait), it is sufficient to replace the value 0 or 1 in equation 2, respectively, for  $q =$  single or triple baits;  $r =$  ants absent or present;  $s =$  warm-wet or cool-dry.

As a general pattern (fig. 1), resource use by termites was severely delayed during the warm-wet period by low bait quantity and by the presence of ants. Bait quality showed no significant effect, indicating that in the present case, nitrogen additions did not pose strong constraints on termite foraging. Baits took longer to be occupied in the first run of the experiment (warm-wet season) than in the subsequent period (cool-dry season). In both periods, single baits took longer to be occupied than triple baits. Accordingly, regardless of season and bait quantity, baits with ants took longer to be occupied by termites than baits without ants.

## Discussion

Trophic control in soil food webs is receiving increased attention in recent years, because it is becoming evident that top-down and bottom-up forces belowground may severely impact aboveground dynamics (Moore *et al.*, 2003). In fact, in temperate soils, whether carbon is kept in the soil or released as  $\text{CO}_2$  to the atmosphere will depend in large part on the interruption and/or delay of decomposer activity (Ekschmitt *et al.*, 2008). Such activity depends on (i) bottom-up forces, represented by the quality of the substrate and the rate of its encounter by decomposers (Ekschmitt *et al.* 2005) and (ii) top-down controls upon microbes (Moore *et al.*, 2003). Detritivores, in turn, may also impact carbon flux since their action accelerates the decomposition of soil carbon (Fox *et al.*, 2006). It follows that the concurrent action of bottom-up and top-down controls upon detritivores and decomposers may

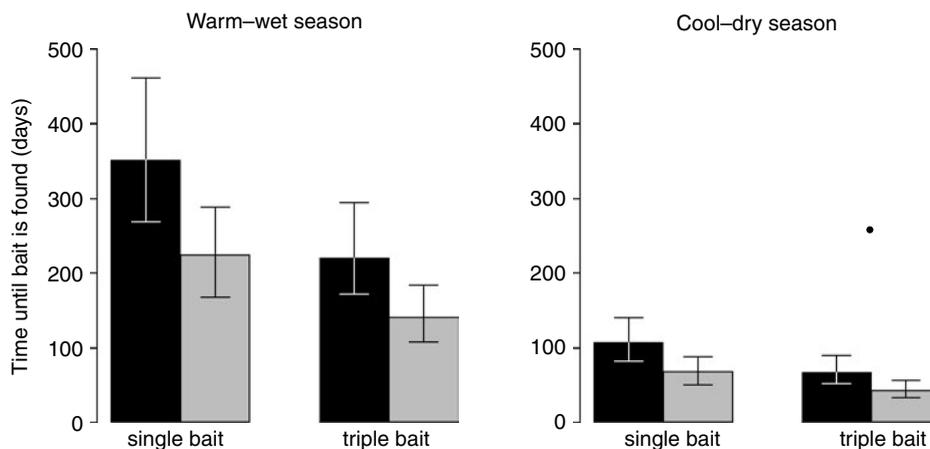


Fig. 1. Number of days (mean  $\pm$  SE), as a function of bait quantity (single or triple bait) and status (with or without ants), spent in the field until cellulosic baits are found to have termites for two consecutive seasons in the same year in a grassland bordering an 'Atlantic forest' relict in southeastern Brazil. Differences between treatments are significant, see table 3 (■, with ants; □, without ants).

Table 3. Analysis of deviance table for the survival model used to check whether resource traits would affect the promptness in which a bait is found having termites, more than time alone would do. Modelling proceeded under Weibull distribution; full details are given in the 'Material and methods' section.

| Source               | Df  | Deviance | ( $P > \chi^2$ ) |     |
|----------------------|-----|----------|------------------|-----|
| Model                | 8   | 46.02945 | 2.34e-07         | *** |
| presence of ants (a) | 1   | 1.02043  | 0.03829          | *   |
| bait quantity (b)    | 1   | 4.39519  | 0.02209          | *   |
| bait quality (c)     | 1   | 2.21461  | 0.06190          | ns  |
| season               | 1   | 35.65276 | 4.53e-09         | *** |
| a:b                  | 1   | 1.87014  | 0.17146          | ns  |
| a:c                  | 1   | 0.76917  | 0.38047          | ns  |
| b:c                  | 1   | 0.00038  | 0.98443          | ns  |
| a:b:c                | 1   | 0.10677  | 0.74385          | ns  |
| Residual             | 190 |          |                  |     |

ns  $P > 0.05$ ; \*  $P < 0.05$ ; \*\*\*  $P < 0.01$ .

delay litter and SOC processing, thereby contributing to the ground being brown (Allison, 2006).

While stressing the notion of detritivores and decomposers as crucial for the fate of carbon in tropical terrestrial ecosystems, our results seem to conform closely to the hypothesis above. Termites in the field were found occupying certain food types much earlier than others. More specifically, predation risks severely delayed bait occupation by termites; and, under the same predation risk, the smaller the bait, the longer it took to be occupied (table 3, fig. 1). This could be driven by previous evaluation by termites of the value of exploring a given resource and/or by predation upon and removal of termites in ant-occupied baits. No matter the mechanism, a combination of top-down and bottom-up forces seems to be playing a key role in this process.

We argue that such results would pose trophic controls upon termites as an important bottleneck for the carbon cycle. After all, apart from releasing carbon directly as CO<sub>2</sub> (Slaytor, 2000) and exposing carbon to microbes by disassembling plant debris, termites also unlock carbon directly to the atmosphere as CO<sub>2</sub> (Martius *et al.*, 1996), which emphasises their role as carbon processors in ecosystems. Besides being effective wood and litter processors, termites are also able to ingest mineral-containing soil horizons, as well as highly humified organic litter material (Brauman *et al.*, 2000), thus promoting further processing of SOC. Therefore, by impairing the effective use of resources by termites, top-down and bottom-up forces would limit prompt transformation in CO<sub>2</sub> of all carbon that is available as dead organic matter, thereby enhancing the pools of humic complexes in the soil. That is, rather than readily exploring the first item they found in the field, termites would favour items that are larger and risk-free. As a consequence, carbon present in smaller or risky items remains locked in organic form in the soil, enhancing the pools of humic complexes rather than being released to the atmosphere. Such a reasoning is supported by the findings by Hedlund & Henderson (1999) that termites (in the laboratory) will vary their rate of consumption with the size of their food, i.e. they eat small food more slowly.

*The relative strength of trophic controls*

A closer look into the final statistical model (equation 2) reveals some interesting patterns, if we compare the impact of its numerical estimates on the mean time ( $\mu$ ) taken to find termites on a bait. To ease comprehension, we invite the reader to check the reasoning below against fig. 1 along with equation 2. Firstly, the effects of season were much more

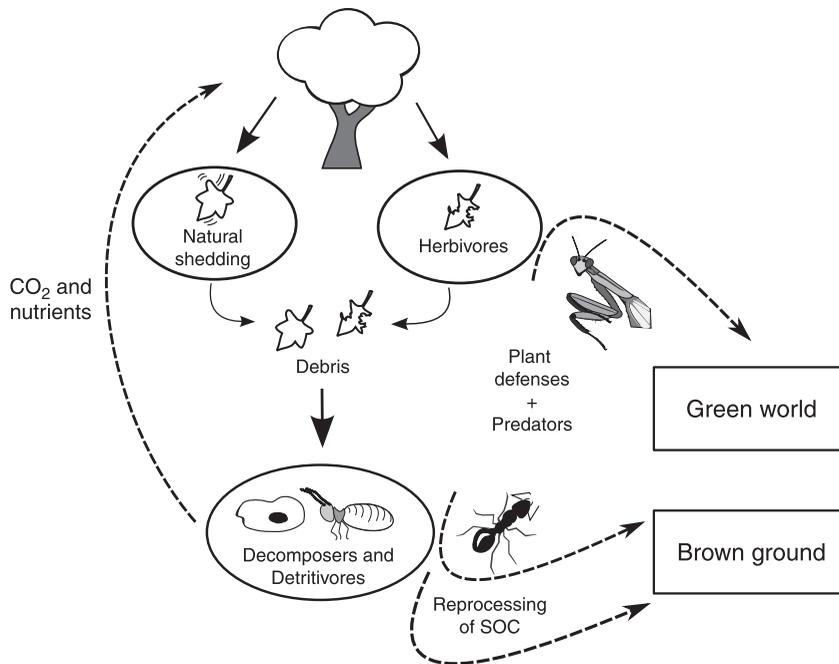


Fig. 2. Pathways connecting the green world to the brown ground and back, combining reasonings of Hairston *et al.* (1960) and Murdoch (1966) for the green world, with hypotheses of Allison (2006) for the brown ground. See text for details.

marked than the effects of bait quantity and predation risk, as season (*s*) contributed to 1.191 units to  $\log_{e}\mu$ , a value that is more than twice as big as the values for bait quantity, *q*, and predation risk, *r*. It is worth noting that the seasons reported here differed a lot in terms of rainfall (daily averages: 10.2 mm in warm-wet season and 1.9 mm in cool-dry season) but seemed similar in terms of temperature (daily mean temperatures: 22.0 and 18.7°C, respectively). In addition, we could not detect any visual differences in litter accumulation (hence, resource offer) between seasons. All this might indicate that what we saw as seasonal effects could be mostly attributable to rainfall, which is in line with previous findings by Jones & Gathrone-Hardy (1995) and Cabrera & Rust (1996), who reported that rainfall impairs termite activity. We warn, however, that this is mostly speculative, since the experiment was not aimed to inspect seasonal effects; and, hence, no proper replication was set up for seasons.

The estimates for bait quantity and for predation risk (respectively, *q* and *r* in equation 2) present very similar values (0.448 and 0.470), denoting that their impact on the mean time to find a bait is of comparable magnitude, with predation risk being slightly more important than bait quantity. In other words, bottom-up and top-down effects seem to have operated with similar strengths. This is easily spotted in fig. 1, where single-baits-without-ants and triple-baits-with-ants take about the same time to be found with termites, in both seasons. Such results are supported by previous reports, which have shown (i) that termite foraging can be severely limited by predation risk from ants (Gonçalves *et al.*, 2005), (ii) that termites abandon less and consume more larger baits as opposed to smaller ones (Evans & Gleeson, 2006), or even (iii) that termites tend to explore longer food items which are not under predation risk (Korb & Linsenmair, 2002).

Surprisingly enough, bait quality (= nitrogen additions to the bait) did not affect the mean time until bait occupancy ( $P=0.0619$ ; table 3) which could be related to the ability of termites to fix nitrogen (Yamada *et al.*, 2006).

Perhaps, more interestingly, the final statistical model did not include any interaction term, which would imply the independence of all factors studied. That is, despite differences between seasons, the general pattern does not change, termites seem to avoid smaller items that are under predation risk no matter the season (fig. 1). This seems to reinforce the idea that while climate determines the intensity of foraging activity of termites, trophic controls are responsible for 'fine tuning' such activities, determining where and how foraging would proceed.

### Conclusion

The evidence gathered here for tropical soil food webs seems to support the idea that decomposers and detritivores, in general, and termites, in particular, may connect the green world to the brown ground, as depicted in fig. 2. As plants shed their dead parts naturally, decomposers act upon them, unlocking SOC and minerals. These would be ultimately reused by plants, thereby closing the cycle. Herbivores speed up the process, producing additional plant debris out of living plant tissue far quicker than natural shedding would. However, delays are imposed in this process by predators (Hairston *et al.*, 1960) and plant defences (Murdoch, 1966), which secure the failure of herbivores in destroying plants

and lead to the green world. Detritivores act upon such debris and speed up decomposition processes by breaking litter into smaller portions and exposing surfaces which, otherwise, would stay for much longer out of the reach of decomposers. Termites take an important role in this process, due to their ability to process plant matter directly into CO<sub>2</sub> (as a decomposer would do), coupled with their well-known action as detritivores. Again, as evidenced by our results, predators and food unsuitability delay the action of termites, thereby establishing an important bottleneck to the system. Such delays increase residence times of carbon in soil, hence contributing to the increment of pools of humic complexes, hence making the ground brown. Additionally, reprocessing of SOC into compounds impervious to enzymatic action of decomposers (including perhaps termites, especially soil-feeding ones), prevents SOC from re-entering soil food web, "making the ground more brown than the world is green" (Allison, 2006).

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