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1 Bioturbation as a means to circumvent sodium limitation by termites? Suspected
2 processes and ecological consequences

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15

16 **Abstract**

17 Bioturbation by termites is considered a key process in the regulation of soil properties in
18 tropical soils. The concentration of clay and the presence of 2:1 clay minerals in termite-soil
19 are usually explained by the need of termites to build stable biogenic structures and/or to have
20 access to water only available in the lower soil layers. However, while these hypotheses are
21 attractive, they do not always offer a sufficient explanation for understanding termite
22 bioturbation behavior. Here, we used ecological stoichiometry theory to propose a third
23 hypothesis: that bioturbation can also be explained by the limitation of termites for Na⁺. This
24 chemical element is missing from the vegetation consumed by termites, while it plays an
25 important role in the regulation of termites' physiological processes. In old and highly
26 weathered soils, such as those found in the tropics, a significant source of Na⁺ for termites likely
27 comes from 2:1 minerals, which are only available in the deeper soil layers. Therefore, this
28 article aims to propose the hypothesis of the use of bioturbation by termites as a means to fulfil
29 their need for Na⁺. The impacts of this ecological process on ecosystem functioning and soil
30 fertility are discussed.

31

32 **Keywords:** Tropical soils, clay, 2:1 clay minerals, soil fertility

33 Bioturbation, i.e., the displacement of soil along the soil profile and the modification of its
34 properties, is mostly performed by termites in the tropics. In particular, the greater amount of
35 clay minerals in termite constructions, sometimes having specific soil physical, biological and
36 chemical properties from that observed in the surrounding environment, has been described in
37 numerous studies, due to its significant impact on soil dynamics and fertility. Three mechanisms
38 are commonly proposed to explain the impact of termites on clay dynamics in soil (Jouquet et
39 al. 2016):

40 (1) Termites enrich their soil-constructions (epigeous mounds and sheeting, and
41 belowground tunnel and chamber walls) in clay particles in order to make them stable and
42 resistant to environmental hazards (e.g., degradation by rain and predators, or changes in
43 temperature and humidity);

44 (2) Termites penetrate deep into the soil to collect the moisture associated with clay
45 particles that is needed to maintain their activity, and sometimes that of their symbiotic fungus
46 (in the case of fungus-growing termites). In doing so, they bring to the surface moist soil
47 enriched in clay particles;

48 (3) The chewing or consumption of soil by termites is associated with a modification of
49 clay mineralogical properties, most likely due to ionic exchanges between clays and saliva
50 and/or digestive fluids.

51 While these hypotheses are attractive, they do not always offer a sufficient explanation
52 for understanding termite bioturbation behavior. The search for clay in the deeper soil horizons,
53 sometimes at several meters depth, remains difficult to understand if clays are already available
54 on the soil surface (in the A and B horizons), and/or if nest-structures are built belowground,
55 where they are less subject to environmental hazards than those produced on the ground.
56 Moreover, experiments under controlled conditions provide evidence that water uptake by
57 termites is possible through the direct absorption of water, and perhaps the recycling of urine

58 and/or trophallactic exchanges (i.e., fluid-exchanges via mouth-to-mouth or anus-to-mouth
59 exchanges). Therefore, if access to the water available at several meters depth requires the
60 formation of deep galleries and the displacement of soil, why do termites need to spend energy
61 in bringing soil material and why do they accumulate on the ground or in the first soil layer
62 minerals that are only found in the deepest soil layers?

63 Here, we suggest that ecological stoichiometry theory offers an interesting but hitherto
64 unexplored insight for explaining the specific interactions between termites and clay minerals.
65 This theory states that animals tend to increase their foraging efforts searching for the rarest
66 nutrients, and not only C, N and P. While the importance of the C to N balance in termites has
67 been described (Higashi et al. 1992), there is a clear lack of information on how termites
68 regulate the other elements. The question is especially interesting when looking at the Na⁺
69 dynamics. This element is considered as the “seventh macronutrient” for many animals (*sensu*
70 Kaspari 2020). While plants usually contain low concentrations of Na⁺, this element plays an
71 important role in the regulation of several key physiological processes of animals, mostly
72 herbivores and decomposers (Kaspari 2020). Na⁺ can also contribute to the detoxification of
73 tannin-rich food and the enhancement of P recycling by the gut microbiome (Kaspari 2020).
74 However, while termites obtain C, N and P from plant materials, soil organic matter, and
75 interactions with microbes, such as N-fixing bacteria and fungi, the substrates they feed on are
76 comparatively impoverished in Na⁺. For instance, Yoshimura et al. (2002) evidenced a 90-fold
77 increase in the concentration of Na⁺ in termite bodies in comparison with the wood they feed
78 on. As a consequence, termite activity increases in response to an addition of Na (+ NaCl) to
79 the soil and litter, from a 7-fold increase in termite density in a Peruvian Amazon forest (Kaspari
80 et al. 2009) to 17-fold in Ecuador (Kaspari et al. 2014) and 20-fold in Panama rainforest (Clay
81 et al. 2014). From these examples, and given the fact that tropical soils and plant materials are

82 usually characterized by low availability in Na^+ (Sanchez 2019), one can question where the
83 Na^+ needed for termites comes from.

84 The answer to this question is perhaps hidden in two recent publications dealing with
85 termite bioturbation in a South-Indian forest (Jouquet et al. 2020) and in the Brazilian Cerrado
86 (Bruand et al. 2022). Both studies were carried out in Ferralsols, where clays are dominated
87 by kaolinite and where soils are depleted in basic cations, such as Na^+ , from the exchange sites
88 in clay and soil organic matter (SOM) surfaces. In these soils, Na^+ usually leaches out of the
89 soil surface because of the cumulative effect of the weathering processes of clay minerals, and
90 its concentration is usually very low in the first soil layers, while it is the highest close to the
91 saprolite. In both sites, the presence of 2:1 clay minerals in termite mound soil and in the first
92 soil layer is attributed to the rise of these minerals from the deeper soil layers to the surface. In
93 India, Jouquet et al. (2020) evidenced that the soil used by termites mostly came from a kandic
94 horizon situated at approximately 1 m depth and characterized by high Na^+ content in
95 comparison with the topsoil (0.11 vs. 0.02 $\text{cmol}^{(+)} \text{kg}^{-1}$). Similarly, Bruand et al. (2022) showed
96 that 2:1 clay minerals found in the soil surface, and that were likely to be brought by termites
97 from the deep soil layers, contained high levels of exchangeable Na^+ . Consequently, in line with
98 ecological stoichiometry theory these two examples show a potential congruence between the
99 selection of clay minerals enriched in Na^+ by termites and the ecological need of termites to
100 search for the Na^+ necessary for their activity. In other words, these examples offer a new
101 possible explanation for the bioturbation behaviour of termites, which could be seen as a means
102 for termites to achieve and maintain their Na^+ content (Kaspari 2020).

103 The consequences are important, not only in terms of soil fertility, but also at large scale
104 in providing Na^+ to the food web (Figure 1). Termites and the soil reworked by termites could
105 play a major role at the starting point of the food web in becoming sources of Na^+ for fungi and
106 animals. Termites are preyed upon by many animals, including ants and several mammals, and

107 the Na⁺ in termite biomass is likely to be a direct input in Na⁺ into the food web. Greater Na⁺
108 concentration in termite-soil also could explain why large herbivores, such as elephants, destroy
109 or simply lick or eat parts of termite mounds in search of salts (Jouquet et al. 2011). While Na⁺
110 can negatively impact soil structure because it disperses soil aggregates, fungi are considered
111 to be limited for Na⁺ (Scharnagl et al. 2017), and any increase in the availability of this element
112 is likely to stimulate the cohesion of soil and the decomposition of SOM, the dynamics of
113 nutrients (i.e., mineralization or immobilisation of nutrients within the microbial biomass), as
114 well as indirectly increase the availability of P to plants (Kaspari 2020). To conclude and to
115 paraphrase Sharnagl et al. (2017), termite bioturbation could be then seen as a “nature’s potato
116 chip maker” in providing important sources of Na⁺ to animals and fungi. This process and the
117 interaction between termite bioturbation, the presence, abundance, dynamics and abandonment
118 of mound nests, Na⁺ limitation, and soil fertility require further investigation. Such information
119 could have broad implications for the management of soil fertility and other key ecological
120 processes such as the regulation of biodiversity, the decomposition of litter and the
121 sequestration of C in soil, especially in Na⁺ limited environments.

122

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129

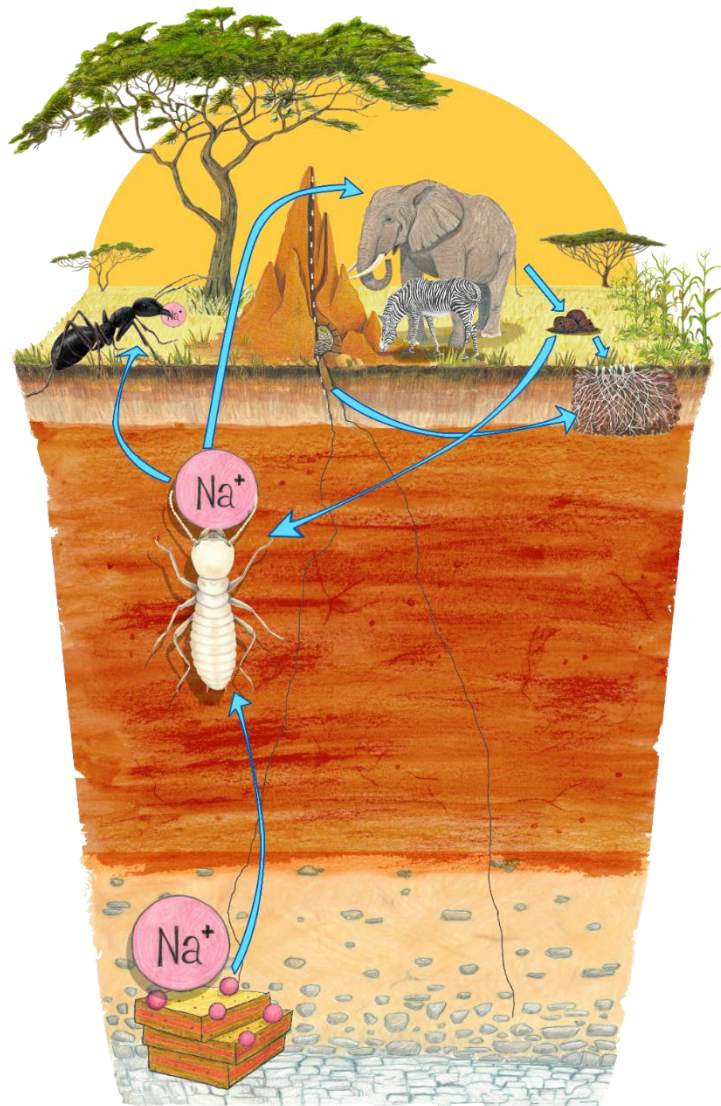
130 **Conflict of Interest:** The authors declare that they have no conflict of interest

131

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158

159 **Figure 1.** Schematic representation of the cascading effect of termite bioturbation. Na^+ is
160 brought to the surface from belowground minerals. Termite biomass and biostructures
161 constitute patches of Na^+ at the landscape scale. Redistribution of Na^+ by termites occurs
162 directly by predation (here by ants), and indirectly via the licking or consumption of termite-
163 soil by herbivores and the development of fungi with potential positive impacts on plants, and
164 as a feedback loop on herbivores. Recycling of Na^+ by termites mostly occurs via the
165 consumption of herbivores' dung. (© IRD – Cristal Ricoy Martinez).