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► **To cite this version:**

Pascal Jouquet, Ary Bruand. Bioturbation as a means to circumvent sodium limitation by termites? Suspected processes and ecological consequences. *Biology and Fertility of Soils*, 2023, 59 (6), pp.567 - 570. 10.1007/s00374-023-01752-2 . insu-04145733

**HAL Id: insu-04145733**

**<https://insu.hal.science/insu-04145733v1>**

Submitted on 29 Jun 2023

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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<sup>+</sup>. 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<sup>+</sup> 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<sup>+</sup>. 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<sup>+</sup>  
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<sup>+</sup>, 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<sup>+</sup> 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<sup>+</sup>. For instance, Yoshimura et al. (2002) evidenced a 90-fold  
77 increase in the concentration of Na<sup>+</sup> 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  $\text{Na}^+$  (Sanchez 2019), one can question where the  
83  $\text{Na}^+$  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  $\text{Na}^+$ , from the exchange sites  
88 in clay and soil organic matter (SOM) surfaces. In these soils,  $\text{Na}^+$  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  $\text{Na}^+$  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  $\text{Na}^+$ . Consequently, in line with  
98 ecological stoichiometry theory these two examples show a potential congruence between the  
99 selection of clay minerals enriched in  $\text{Na}^+$  by termites and the ecological need of termites to  
100 search for the  $\text{Na}^+$  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  $\text{Na}^+$  content (Kaspari 2020).

103 The consequences are important, not only in terms of soil fertility, but also at large scale  
104 in providing  $\text{Na}^+$  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  $\text{Na}^+$  for fungi and  
106 animals. Termites are preyed upon by many animals, including ants and several mammals, and

107 the Na<sup>+</sup> in termite biomass is likely to be a direct input in Na<sup>+</sup> into the food web. Greater Na<sup>+</sup>  
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<sup>+</sup>  
110 can negatively impact soil structure because it disperses soil aggregates, fungi are considered  
111 to be limited for Na<sup>+</sup> (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<sup>+</sup> to animals and fungi. This process and the  
117 interaction between termite bioturbation, the presence, abundance, dynamics and abandonment  
118 of mound nests, Na<sup>+</sup> 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<sup>+</sup> limited environments.

122

123 **Acknowledgments:**

124 As in any opinion paper, the concepts and ideas formulated in this article result from dialogs  
125 with many colleagues and peers, who are all acknowledged. We also thank the reviewers and  
126 the editor for their constructive remarks and significant help in improving the manuscript.  
127 Finally, we are grateful to Cristal Ricoy Martinez for the illustration, and L. Ganesha for his  
128 unconditional support.

129

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

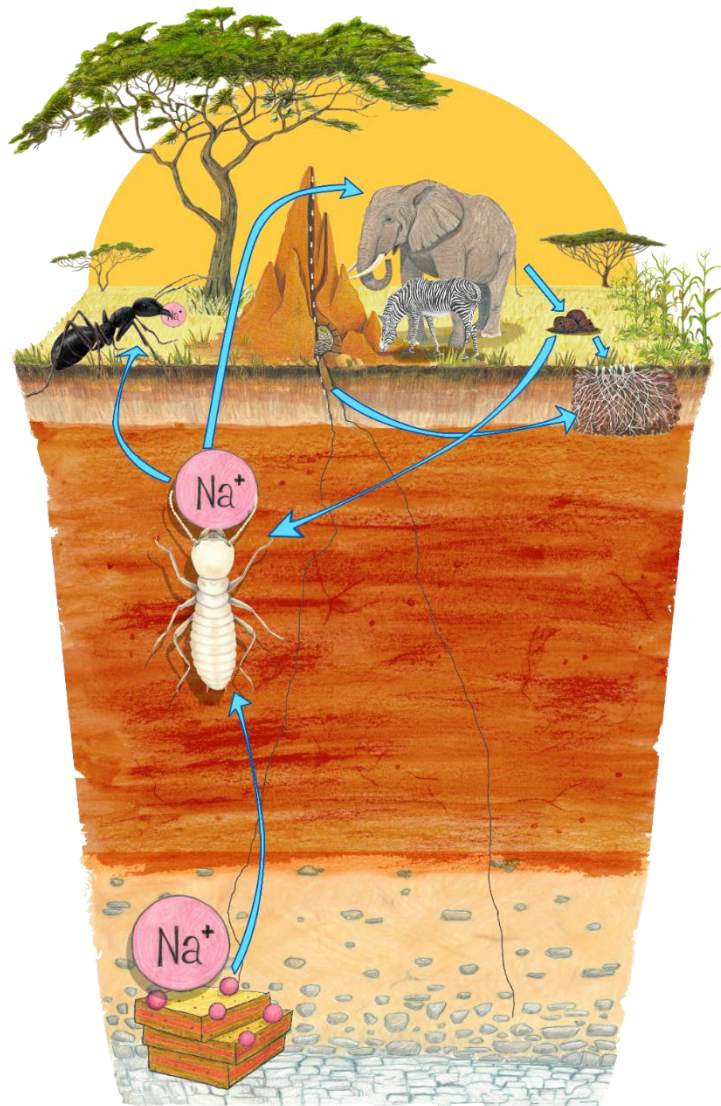
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158

159 **Figure 1.** Schematic representation of the cascading effect of termite bioturbation.  $\text{Na}^+$  is  
160 brought to the surface from belowground minerals. Termite biomass and biostructures  
161 constitute patches of  $\text{Na}^+$  at the landscape scale. Redistribution of  $\text{Na}^+$  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  $\text{Na}^+$  by termites mostly occurs via the  
165 consumption of herbivores' dung. (© IRD – Cristal Ricoy Martinez).