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Linking functional trade-offs, population limitation and size structure: Termites under soil heterogeneity

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Abstract

Organismal fitness is fuelled by resources. However, resource acquisition often involves conflicting functional demands that may ultimately shape broader ecological patterns. For instance, termites play major roles in ecosystem functioning through their foraging and building activities. Yet, while experiments suggest improved foraging in sand, nest construction depends on clay. Hence, these functions may trade off, with species optima reflecting interspecific variation in building requirements. We investigated whether a foraging–building trade-off could affect termite populations by using three species differing in building requirements, namely *Neocapritermes braziliensis*, *Anoplotermes banksi* and *Labiotermes labralis*. We characterized their populations in relation to soil texture and food amount across a tropical rain forest landscape, and then compared the observed patterns. Colony density was unrelated to food amount in the three species. However, *A. banksi* was denser at balanced mixtures of sand and clay, consistent with a compromise between foraging and building demands. Further, the species building more mineralized nests (*L. labralis*) was more abundant on clayish soils, whereas the species relying less on soil for nest construction (*N. braziliensis*) was more abundant on sandy soils. Changes in colony density correlated with changes in size structure: in *N. braziliensis* and *A. banksi*, colony mass variability increased with density due to a sharp decrease in minimum colony mass, consistent with higher productivity and/or size-asymmetric competition. This study suggests a novel functional trade-off that may help drive population density and size structure both within and across termite species.

Zusammenfassung

Die Fitness von Organismen wird von Ressourcen gespeist. Indessen stellt die Ressourcennutzung häufig widerstreitende funktionelle Anforderungen, die schließlich größere ökologische Muster formen können. Termiten spielen durch ihre Nahrungssuche und Bautätigkeit eine wichtige Rolle für die Ökosystemfunktion. Während Experimente nahelegen, dass die

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Nahrungssuche in Sand erleichtert ist, wird für den Nestbau Lehm benötigt. Damit ergeben diese Funktionen einen Zielkonflikt, wobei die Optima der Arten interspezifische Unterschiede bei den Bauansprüchen widerspiegeln. Wir untersuchten, ob ein Nahrungssuche-Nestbau-Zielkonflikt Termitenpopulationen beeinflussen könnte, am Beispiel von drei Arten mit unterschiedlichen Nestbauansprüchen: *Neocapritermes braziliensis*, *Anoplotermes banksi* und *Labiotermes labralis*. Wir beschrieben ihre Populationen in Hinblick auf Bodenstruktur und Nahrungsverfügbarkeit in einer tropischen Regenwaldlandschaft und verglichen dann die gefundenen Muster. Die Koloniendichte war bei keiner der Arten mit der Nahrungsverfügbarkeit verbunden. Aber *A. banksi* war häufiger bei einer ausgewogenen Mischung von Sand und Lehm, in Übereinstimmung mit einem Kompromiss zwischen Nahrungssuche- und Nestbauansprüchen. Die Art mit den am stärksten mineralisierten Nestern (*L. labralis*) war auf Lehmböden am häufigsten, während die Art, die weniger Erde beim Nestbau verwendet (*N. braziliensis*), auf sandigen Böden häufiger war. Änderungen der Koloniendichte korrelierten mit Änderungen der Größenstruktur: bei *N. braziliensis* und *A. banksi*, nahm die Variabilität des Koloniengewichts wegen eines deutlichen Rückgangs des minimalen Gewichts mit der Koloniendichte zu. Dies spricht für höhere Produktivität und/oder größenbedingte asymmetrische Konkurrenz. Diese Untersuchung legt einen neuen funktionalen Zielkonflikt nahe, der dazu beitragen könnte, die Populationsdichte und Größenstruktur innerhalb und zwischen Termitenarten zu steuern.

Keywords: Environmental filter; Granulometry; Size inequality; Social insect; Species distribution

Introduction

Resource availability is a major limiting factor of animal fitness (White, 2008). However, foraging is often subject to conflicting demands. For instance, conditions that favour resource abundance may simultaneously impose costs on its acquisition (e.g. lower foraging efficiency, higher risk of predation or parasitism), thus exposing animals to selection for a balance between parallel requirements (Hutchings, Judge, Gordon, Athanasiadou, & Kyriazakis, 2006; Verdolin, 2006). Such trade-offs can affect patterns of growth and habitat use (Roberts & Liebgold, 2008; Pomeroy, 2006; Lewis, 2001; McIvor & Odum, 1988; Crowder & Cooper, 1982), and may ultimately scale up to landscape patterns of abundance and diversity (Grol, Nagelkerken, Rypel, & Layman, 2011; Dussault et al., 2005; Grenouillet, Pont, & Seip, 2002; Hall, Stanford, & Hauer, 1992). Thus, functional trade-offs provide a framework for identifying mechanistic links between organismal performance and ecological patterns at broader scales.

Most resources provided by primary producers to animals are not consumed as living tissue, but rather enter food webs as organic detritus, thus supporting an abundant detritivore fauna (Hagen et al., 2012). Termites are dominant detritivores in many ecosystems (King, Warren, & Bradford, 2013). Being mainly soil-dwelling animals, termites commonly excavate underground tunnels to forage, and many species use soil to build nests that shelter their colonies from environmental hazards (Krishna, Grimaldi, Krishna, & Engel, 2013). However, as foraging and building activities can have different requirements, soil heterogeneity may have contrasting effects on these functions, which may scale up to population traits. Yet, while termite impacts on soils have been extensively documented, little is known about how soils affect termite populations (Jones, Rahman, Bignell, & Prasetyo, 2010).

Experiments indicate that termite tunnelling rate is higher, and energy expenditure lower, in coarser, sandier soils (Cornelius & Osbrink, 2010; Brown, Kard, Payton, & Kuehl, 2009; Houseman & Gold, 2003). This is because, for a given space, the number of soil particles decreases as particle size increases. Consequently, in sandier soils, fewer particles need to be removed while tunneling a given distance. This suggests that, for a given food level, foraging efficiency should be higher in such substrates. However, experiments and field data also indicate that termites favour finer, clayish particles during nest construction (Sarcinelli, Schaefer, Fernandes Filho, Mafia, & Neri, 2013; Jouquet, Lepage, & Velde, 2002; Lee & Wood 1971), which improves the structural stability of nests (Jouquet, Tessier, & Lepage, 2004). This suggests that sandy soils favour foraging while hampering nest construction, whereas clayish soils favour nest construction while hampering foraging.

Assuming both activities to be equally important, a compromise may be achieved under a balanced mixture of clay and sand, so that both requirements can be reasonably satisfied. However, termites evolved different degrees of dependence on soil as building material (Amelung, Martius, Bandeira, Garcia, & Zech, 2002; Lee & Wood 1971), so that the optimal clay-to-sand ratio may vary among species. If a species makes relatively little use of soil in nest construction, any compromise between foraging and nest-building may be displaced towards sandier soils, as these would favour foraging, thus being more energetically rewarding. In contrast, species that depend heavily on soil for building activities may have the balance shifted towards soils even richer in clay.

Assuming that local colony density mirrors local productivity (Korb & Linsenmair, 1999), optimal soil textures should support denser populations. Further, more productive populations may support larger colonies, thus experiencing a higher rate of recruitment relative to mortality. If so, such populations could be enriched with younger, smaller