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Graveyards on the Move: The Spatio-Temporal Distribution of Dead Ophiocordyceps-Infected Ants

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Abstract

Parasites are likely to play an important role in structuring host populations. Many adaptively manipulate host behaviour, so that the extended phenotypes of these parasites and their distributions in space and time are potentially important ecological variables. The fungus *Ophiocordyceps unilateralis*, which is pan-tropical in distribution, causes infected worker ants to leave their nest and die under leaves in the understory of tropical rainforests. Working in a forest dynamic plot in Southern Thailand we mapped the occurrence of these dead ants by examining every leaf in 1,360 m^2 of primary rainforest. We established that high density aggregations exist (up to 26 dead ants/m^2), which we coined graveyards. We further established that graveyards are patchily distributed in a landscape with no or very few *O. unilateralis*-killed ants. At some, but not all, spatial scales of analysis the density of dead ants correlated with temperature, humidity and vegetation cover. Remarkably, having found 2243 dead ants inside graveyards we only found 2 live ants of the principal host, ant *Camponotus leonardi*, suggesting that foraging host ants actively avoid graveyards. We discovered that the principal host ant builds nests in high canopy and its trails only occasionally descend to the forest floor where infection occurs. We advance the hypothesis that rare descents may be a function of limited canopy access to tree crowns and that resource profitability of such trees is potentially traded off against the risk of losing workers due to infection when forest floor trails are the only access routes. Our work underscores the need for an integrative approach that recognises multiple facets of parasitism, such as their extended phenotypes.

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Introduction

Parasites negatively affect their hosts in multiple ways. Because disease prevention and containment is crucial in many arenas such as city living, agriculture and the conservation of endangered species, we know a great deal about parasite spatio-temporal dynamics [1]. In such an epidemiological approach, where the goal is to understand transmission dynamics the key information that is recorded is the location of the infected hosts in a population of healthy individuals and the history of transmission prior to the current sampling date [2]. This is a host centred approach to understanding parasite spatio-temporal dynamics. However, in certain host-parasite systems uninfected individuals may be completely absent in some populations because the parasites have manipulated the behaviour of the infected hosts so that they aggregate [3]. Often this is a parasite adaptation to increase fitness and so is viewed as an extended phenotype of the parasite [4]. This is an explicitly parasite centred approach and it has not been generally considered when examining parasite spatio-temporal dynamics.

Many examples of parasites altering host behaviour exist [3] and a few choice ones illustrate the often dramatic effects observed: nematodes and nematomorphs cause various insect hosts (e.g. crickets, ants) to drown themselves so the adult parasite can reproduce in water [5,6]; parasitoids cause bees to bury themselves alive [7] or spiders to build aerial cocoons so as protect the developing parasitoid pupa [8] and many arthropods, fish and mammals have altered behaviour that makes it much easier for predators to catch them which enables the parasite to be passed on trophically [3,9]. The field of parasite manipulation is currently going through interesting and significant changes as researchers move beyond merely cataloguing abnormal behaviour in infected individuals [10]. For example, determining the proximate mechanisms by which such changes are induced [11]; the effects of aggregated hosts on biodiversity [12] or intraspecific competition [13]. Here we want to add the spatio-temporal distribution of behaviourally manipulated hosts as an additional direction. We will use Carpenter ants (genus *Camponotus*) infected by the behaviourally manipulating fungal parasite, *Ophiocordyceps unilateralis* as a model.