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Metapopulation processes affecting diversity and distribution of myrmecophiles associated with red wood ants

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Abstract

Red wood ants support a diverse community of myrmecophiles in their nest mounds. Given that nest mounds provide fairly constant and distinct habitat patches for myrmecophiles, metapopulation and metacommunity dynamics can be expected to play an important role in structuring myrmecophile communities. Here, we investigate how site, site size (i.e. number of mounds per site), mound isolation, mound size, moisture, pH and red wood ant host (*Formica rufa* and *Formica polyctena*) affect the (meta)community composition and species richness. We demonstrate that community composition is structured by site and within-site isolation. In addition, species richness per unit volume is negatively correlated with increasing nest mound isolation. Mound size and site size at a higher spatial scale had no effect on community composition or diversity. The latter suggests that few mounds are required to support the minimum viable metapopulation size. We did not find support that the environmental variables mound moisture and pH affect the myrmecophile community or its species richness. Finally, the communities of the two closely related wood ant species *F. rufa* and *F. polyctena* were very similar. Overall, our results demonstrate, in accordance with metapopulation theory, that isolated mounds support fewer myrmecophile species. Diverse myrmecophile metacommunities also occur in small red wood ant sites, with well connected nest mounds. We discuss the powerful potential of ant nests, and particularly red wood ant mounds, for metapopulation and metacommunity research.

Zusammenfassung

Rote Waldameisen beherbergen eine diverse Gemeinschaft von Ameisengästen in ihren Nesthaufen. Da die Nesthaufen recht konstante und eigenständige Habitate bilden, kann erwartet werden, dass Metapopulations- und Metagemeinschaftsdynamik eine wichtige Rolle bei der Bildung von Myrmekophilengemeinschaften spielen. Wir untersuchten wie der Standort, die Anzahl der Nester je Standort, die Isolation der Nester, die Nestgröße, Feuchtigkeit, pH und die Art der Wirtsameise (*Formica rufa* oder *Formica polytena*) Zusammensetzung und Artenreichtum der (Meta-)Gemeinschaft beeinflussen. Wir zeigen, dass die Zusammensetzung der Gemeinschaft durch den Standort und die Isolation der Nester innerhalb des Standortes strukturiert wird. Der Artenreichtum pro Volumeneinheit ist negativ mit zunehmender Isolation der Nesthaufen korreliert. Die Größe der Nesthaufen und die Zahl der Nester pro Standort hatten keinen Effekt auf Zusammensetzung und Diversität der Gemeinschaft. Letzteres legt nahe, dass wenige Nester benötigt werden, um eine minimale überlebensfähige Größe der Metapopulation aufrechtzuerhalten. Wir fanden keinen Anhaltspunkt dafür, dass Feuchtigkeit im Nest und der pH-Wert Zusammensetzung oder

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Diversität der Gemeinschaft beeinflussten. Schließlich waren die Myrmekophilengemeinschaften der beiden nah verwandten Waldameisenarten *F. rufa* und *F. polyctena* sehr ähnlich. Insgesamt zeigen unsere Ergebnisse in Übereinstimmung mit der Metapopulationstheorie, dass isolierte Nesthaufen weniger Myrmekophilenarten beherbergen. Diverse Metagemeinschaften von Ameisengästen treten auch in kleinen Waldameisenpopulationen mit gut vernetzten Nesthaufen auf. Wir diskutieren das große Potential von Ameisennestern und insbesondere der Nesthaufen von Roten Waldameisen für Forschungen zu Metapopulationen und Metagemeinschaften.

Keywords: *F. rufa* group; Myrmecophiles; Symbionts; Isolation; Metacommunity; Metapopulation; Ant guests

Introduction

A diverse group of arthropods is strictly associated with ants (Hölldobler & Wilson 1990). They benefit from the resources provided by their host and the homeostatic nest conditions. Myrmecophiles are confined to ant nests, but differ in degree of host specificity. While some species are restricted to one ant species or narrowly related species, others occur with different ant taxa and few even show no preference at all (Hölldobler & Wilson 1990). Myrmecophiles live thus in small, spatially distinct and stable patches (= ant nests of associated host ant taxa) susceptible to colonization surrounded by a large landscape matrix unsuitable for colonization. Hence, the populations of myrmecophiles can be expected to be organized as metapopulations (sensu Hanski & Gilpin 1991) wherein local dynamics in the ant nest interact with dispersal among the ant nest patches. When multiple myrmecophile species live in the same set of distinct ant nests, their community can be described as a community of metapopulations or a metacommunity (Hanski & Gilpin 1991). Metapopulation theory has proven to be a successful concept to study fragmented populations connected through dispersal. A key prediction of metapopulation theory is that populations in small and isolated patches are more likely to get extinct because of smaller carrying capacities and smaller odds to get rescued by new colonisations. Consequently, those patches support fewer species at the metacommunity level. Local environmental characteristics of the patch have been demonstrated as a third factor to affect patch occupation probability in metapopulations (Chisholm, Lindo, & Gonzalez 2011; Jeffries 2005; Ranius 2000; Thomas et al. 2001).

Because of their hidden life style, the distribution and abundance of myrmecophiles are unclear and likely underestimated. In this study, we investigate which (metapopulation) processes structure myrmecophiles associated with European red wood ants (*Formica rufa* group). Red wood ants are dominant and aggressive arthropod predators in European woodlands (Laakso & Setälä 2000; Hawes, Stewart, & Evans 2002; Skinner 1980). Still, many arthropods managed to evade ant aggression and live successfully in or around their nest mounds in one of the largest associations of arthropods including Coleoptera, Hymenoptera, Diptera, Lepidoptera, Heteroptera, Isopoda, Collembola, Acari and Araneae (Parmentier, Dekoninck, & Wenseleers 2014).

Two red wood ant species, *Formica rufa* and *Formica polyctena*, co-occur in western Flanders, Belgium (Dekoninck et al. 2010). Their populations are isolated units due to forest fragmentation. They vary considerably in size, but the majority of the populations is relatively small. Nest mounds differ in local ecological characteristics, size and relative position to other mounds of the site. Nests persist likely by budding or by accepting related new queens (pers. observations). Those distinct and small red wood ant sites are thus ideal subjects to test factors classically structuring the dynamics and affecting the composition and richness of metapopulations and metacommunities.

Studies in large forest complexes in Finland by Päivinen, Ahlroth, Kaitala, and Suhonen (2004) and Härkönen and Sorvari (2014) demonstrated that isolation of mounds of the red wood ants *F. aquilonia* and *F. polyctena* negatively affected the diversity of myrmecophiles. Lower beetle diversity was also demonstrated in smaller mounds (Päivinen et al. 2004). These findings agree thus with metapopulation theory. Yet, it is not understood whether the same processes structure myrmecophile metacommunities in highly fragmented and impoverished, small, red wood ant sites. Moreover, it remains unknown whether local patch (i.e. mound) characteristics and factors at a larger spatial scale affect myrmecophile metacommunities. Therefore, we want to test in-depth potential factors structuring the myrmecophile metacommunity in fragmented red wood ant sites. More specifically, we assess the effect of site, isolation and multiple mound characteristics (size, pH, moisture, host ant) on: (a) myrmecophile metacommunity composition and (b) myrmecophile species richness.

Materials and methods

Study area

The study area is situated in northwest Belgium (province: Western Flanders) (Fig. 1). This is a highly urbanized region with only few fragmented woodland patches remaining. Two red wood ant species, *Formica rufa* Linnaeus, 1761 and