



SHORT NOTE

Taxonomic Partition Suggests a High Degree of Coevolution Between Termites and Their Termitophiles

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Abstract

Termites have a tight interaction with their social parasitic Corotocini beetles. This association is thought to be mainly host-specific, despite some host-switch events. By analyzing the taxonomic partition between species and genera of Corotocini, we propose the hypothesis that the main driver of the diversity of these termitophiles is coevolution.

The complexity and diversity of life rely strongly on the interactions of the organisms and the specializations that result from such interactions (Thompson, 1994). Indeed, some interactions are so robust that at some point a phylogenetic step on one side, is closely followed by a phylogenetic step on the other side, and vice versa: a phenomenon called coevolution (Janzen, 1980). This process leads to tangled trees, and relations worthy of investigation. An interesting case, yet poorly explored, is that of the association between termites and other organisms, the termitophily.

The rove beetles of the subfamily Aleocharinae, comprising the most diverse group of the family Staphylinidae (Irmeler et al., 2018), is also the group that most evolved towards the termitophilic habit (Parker et al., 2018), resulting in a variety of termitophilous lineages with seemingly

parasitic habits and extravagant adaptations (Seevers, 1957). Within Aleocharinae, the most specialized and diverse group is the tribe Corotocini (Jacobson et al., 1986), which represents a mostly Pantropical group with a total of 214 physogastric species sorted into 64 genera (Eloi et al., 2020).

Scenarios of the relationship and diversification of parasites and hosts are constructed by historical events occurring along with the coevolutionary processes. These events are not always quite apparent and require investigation to ensure their presence during the codiversifications. They are often a mixture of cospeciation, host-switching, independent speciation, and lineage sorting (Page, 2003). The common line of thought is that the current Corotocini assemblages are the result of the inheritance of ancestral associations, especially cospeciation and independent speciation, rather than frequent



host transfers (Jacobson et al., 1986). But within the tribe, we observe some host-relationship disjunctions, sometimes even between different termite subfamilies, suggesting that host-switching could very well be a reality for the tribe. Here, we sought to contribute to the solution of this problem by analyzing the degree of taxonomic partition of these termitophiles. We expected the existence of two alternative scenarios: (i) the diversity of Corotocini is the outcome of specialization processes in synchrony with their hosts, resulting in species arising from the same ancestral lineages; or (ii) the diversity of Corotocini is mainly the result of Corotocini lineages in constantly host-switching along the coevolutionary process, resulting in species arising from independent lineages.

In order to test it, we sampled from the literature which termite species had Corotocini tenants associated with their nests and the number of different genera and species of beetles associated with each host (Data available at <https://doi.org/10.5281/zenodo.4568772>). Then, we fitted a log-log linear model with the number of genera (G) per host species as a response to the number of species (S) per host species and used the regression to compute the scaling coefficient (slope). This model linearization derives from the allometric power scaling (Pagel & Harvey, 1989) and was used by Enquist et al. (2002), to test for biomass partitioning in tree assemblages and by Mouillot and Poulin (2004), to test for macroecological patterns in the partitioning of parasite assemblages. Here we follow the latter in our logic: a slope that is closer to zero indicates that S grows faster than G, therefore suggesting that several species belong to the same genera, indicating that they share a common lineage (scenario I), while a slope that is really close to one, would indicate a similar growth rate between G and S, suggesting that each species had an independent origin, and therefore that host-switching is probably the main driver of diversification (scenario II).

The regression (Fig 1) pointed out that the number of genera is moderately modulated by the number of species found in association with a host species ($R^2 = 0.53$; $P < 0.001$), and the computed power function for species is low ($G = S^{0.45}$ (ci = 0.38 – 0.52)), indicating the existence of high levels of endemism in these beetle assemblages as a function of their specific hosts and highlighting that they are likely the result of cladogenesis within the same branches (see Mouillot & Poulin (2004) for comparison between parasites populations).

Our data suggest that the majority of the hosts are known to harbor only one species of termitophile, that was generally attributed to an individual genus. But 21.7% of the data is made of host species that house congeners. Not coincidentally, this is the situation of the termites that are traditional biological models, such as *Nasutitermes corniger* (Motschulsky, 1855) and *Constrictotermes cyphergaster* (Silvestri, 1901), and of organisms that were well sampled over the years, such as the case of the *Termitogaster* species associated to *Nasutitermes* spp. or the genera of termitophiles associated with *Trinervitermes* spp. Similar scenarios are

likely to increase in frequency as we acquire more information about other termite species and their termitophiles. In general, our results suggest that the composition of the termitophilic assemblages is likely the result of codiversification with specific host lineages throughout evolution rather than host-switching, with the latter possibly occurring with some periodicity (reflected by the moderate coefficient of determination $R^2 = 0.53$). The common thought is that the relationship between termites and aleocharines started about 99mya, soon after the arising of eusociality in modern termites (Cai et al., 2017a; 2017b). Since the rise of the first termitophiles, several lineages of Aleocharinae evolved the same lifestyle (Seevers, 1957), indicating a clear case of evolvability towards termitophily, and we suggest that the results found in Corotocini could potentially be generalized for other taxa of termitophilous Aleocharinae, since termitophilous beetles accompanied termites throughout the major events in their evolutionary history, such as the development of truly sterile functional castes, the beginning of fungal culture, the colonization of the world, and the emergence of the higher termites and their niche occupation (Bourguignon et al., 2014). During this millennial symbiosis, the termitophiles turned out to become extremely specialized, and have accumulated adaptations according to their hosts' ecology, rather than a generalized "way of living". We indeed often observe traits that hint at niche specialization within Corotocini, demanded from these close interactions, reflected in extravagant strategies to reproduction (Oliveira et al., 2018) and specific ways to acquire food from their hosts.

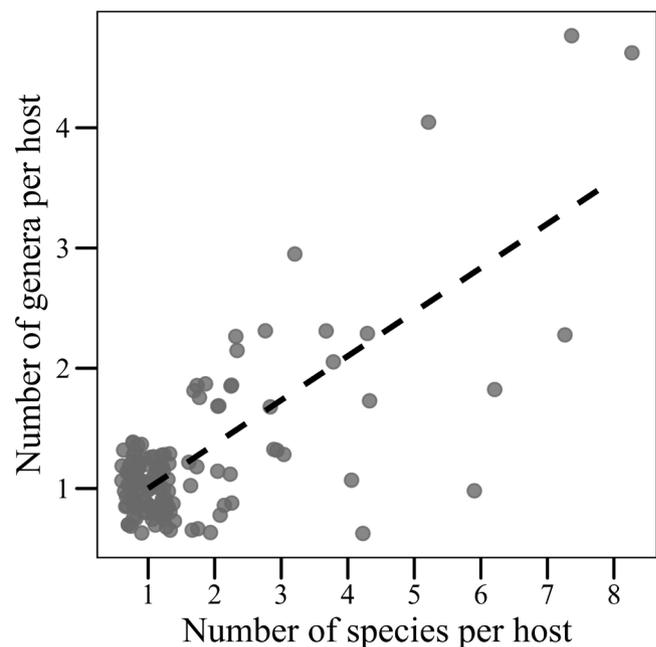


Fig 1. Scatter plot between the number of genera and the number of species per host for 214 species of Corotocini beetles. The tendency line was estimated using the least square linear regression. The data points were jittered due to superposition.

Despite the degree of synchrony between termites and their associates, we must highlight that the making of specific inferences regarding specific coevolutionary processes requires more robust methods, and needs at least phylogenetic topologies for which coevolution is hypothesized. However, they demand much more time and resources, which make them less pragmatic. The method we applied is useful in the process of raising hypotheses (Gotelli, 2002), and the results can be tested in conjunction with future studies on coevolution. Thus, this study shows that the biodiversity of Corotocini is likely the result of an old association plus niche specialization, pointing to a testable scenario, usually through cophylogeny (Page, 2003).

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Authors' Contribution

All authors contributed equally.

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