

Biogeography history, morphological variation of *Macrotermes gilvus* and patterns of interaction specificity with its fungal symbiont, *Termitomyces sp.* in Southeast Asia

by

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Abstract

The Southeast Asia Sunda archipelago harbours a rich biodiversity with a substantial proportion of endemic species. Various environmental forces were identified to drastically influence the evolutionary history of these species including tectonic movements, glacial cycles, climatic changes and volcanic activities. *Macrotermes gilvus* (Hagen), an indigenous subterranean and fungus-growing termite species of Southeast Asia is well suited to investigate the relative impact of these forces in shaping the natural distribution of this species across Southeast Asia. This paper summarizes the biogeography history, morphological variation, and fungal symbiont interaction specificity of *M. gilvus* which may serve as a model of generalisation for early terrestrial dispersal pattern across Southeast Asia and additionally provide an insight into the termite-symbiont mutualism in a complex insular environment of Southeast Asia.

Key words: termite, biogeography, Southeast Asia, dispersal

Introduction

Island archipelagos render dynamic ecosystems for the study of biological diversifications and have been the subject of many foundational works in the field of evolution and biogeography (Darwin 1859, MacArthur and Wilson 1967). The present distribution of plants and animal in Southeast Asia may owe much more to the last one million years or so in the Pleistocene epoch than the preceding 30 million years (Hall 1998). The significance of the periodic land connections to the evolution of the Sunda shelf fauna has been well demonstrated for some animal groups such as non-volant mammals, shrews, bats, water snakes and frogs (Heaney 1986, Ruedi 1996, Schmitt et al. 1995, Inger and Voris 2000), but remains to be investigated in a phylogeographical framework for the most diverse group of soil organism – the termites.

Termites are excellent indicators of biogeographic and evolutionary studies due to their wide functionality in native habitats and sensitivity to landscape disturbances reflective of historical patterns (Jones and Eggleton 2000, Gathorne-Hardy et al. 2002). *Macrotermes gilvus*, an indigenous fungus-growing termite of Southeast Asia offers great potential in understanding the phylogeographic history of regional fauna. This species is endemic and ubiquitous in distribution throughout Southeast Asia from Indochina to Malayan peninsula, Sumatra, Java, Borneo and the Philippines (Roonwal 1970). It is a poor disperser and transoceanic dispersal is improbable in this species (Neoh and Lee 2009). Therefore, the genetic signature from this species should reflect a historical vicariance rather than contemporary gene flows between different regions of Southeast Asia. This species cultivates fungal symbiont which gives additional perspective in understanding the termite-symbiont mutualism specificity in an insular environment such Southeast Asia.

Phylogeography becomes useful as a conceptual umbrella to weigh relative merits of oft-competing vicariance and dispersalist scenarios invoked to account for the origins of spatially disjunct taxa (Ronquist 1997). Vicariance is considered when related populations became detached as the continuous ranges of ancestral forms were sundered by environmental forces (Myers and Giller 1988). Alternatively, dispersal is important to phylogeography through rare long-distance movements which often implicates the colonization of new habitats such as oceanic islands (Briggs 1974, Freeland 2005). Knowledge on these historical processes is of utmost importance in understanding the natural history or evolutionary processes that shaped the spatial structure of local taxa.

This paper summarizes the natural history of *M. gilvus* by investigating its biogeography, morphological variation and pattern of interaction specificity with its fungal symbiont *Termitomyces sp.* across Southeast Asia by means of a phylogeographic approach.

Biogeography History of *M. gilvus*

The consistency of results between the mitochondrial DNA and microsatellites markers suggest that the phylogeographic pattern of *M. gilvus* was most likely relics from Pleistocene environmental changes. Even at microsatellite loci, contemporary processes seemed not to influence the historical processes that shaped the phylogeographic structure of this species. Most genetic differentiation was associated with Pleistocene geographical division, which remains distinct despite temporary connections. Gene flow between geographical groups was rare. An obvious exception to this is a strong genetic propinquity between Malayan peninsula and North Sumatra populations despite the presence of a formidable physiographic barrier – the straits of Malacca separating the two regions. This either suggests ongoing gene flow and/or a recent dispersal event in order to explain the narrow time factor suggested by the lack of distinct genetic differentiation. Unexpectedly, a significant genetic divergence was observed within populations on Borneo and Sumatra that can be best explained by multiple, independent dispersal events rather than vicariance. There was no direct connectivity inferred between Borneo and Sumatra. This finding is of paramount importance as it elucidates the position of Java as a central biogeographical link connecting the two major islands. Phylogeographic analysis also suggests a likelihood of *M. gilvus* introduction into the Philippines and/or northern Borneo from mainland Indochina.

The range expansion of *M. gilvus* was detected during the early Pleistocene, spreading out of Indochina towards Java and the Philippines reaching the modern distribution across Southeast Asia by the end of late Pleistocene.

Morphological Variations

Morphological variation in *M. gilvus* was highly concordant to the phylogeographic structure inferred by molecular data. Specifically, the genetic subdivision observed in Sumatra and Borneo was consistent with the significant morphological sub-structure displayed by discriminant function analysis. Moreover, the close genetic association between Malayan Peninsula, Singapore and North Sumatra was well supported by the morphological similarity between their soldier castes. Similarly, the inferred migratory route between Indochina and Java based on the mtDNA data was supported by the morphological similarity observed between the two regions. The Philippines termites stood out by being the smallest in size. By contrast, Riau and West Sumatra were among the largest, particularly in head size and tibial length. It is worth noting that the termites of Thailand were intermediate in size when compared to the rest of the geographical groups in the discriminant dimensions, suggesting a potential ancestral phenotype. Overall, present data displayed a clear correlation between genetic data and morphometric similarity on a large spatial scale, an indication that morphology matches genetics. Therefore, it can be hypothesized that the morphometric variation of *M. gilvus* across Southeast Asia was a result of geological evolution rather than a case of phenotypic plasticity. Nevertheless, on a small spatial scale in Java, previous records of various morphological forms or variants of *M. gilvus* can be relegated as a single geographical race most likely due to nutritional phenotypic plasticity.

Termite-Symbiont Mutualism

There are at least three genetically distinct types of fungal symbiont associated with this fungus-growing termite. The host termite was found to be promiscuous in symbiont acquisition. In turn, the symbionts were specific to the host. Such interaction may benefit the host by increasing chances of the foraging termites to pick up viable spores from the environment during colony establishment. Divergence dating demonstrated that the fungal symbiont co-diversified with host, *M. gilvus* during its initial radiation in Southeast Asia. Investigation of the host-symbiont interaction specificity revealed that the geographical variation of the fungal symbiont in relation to the host termite was not exclusive. On the one hand, the fungal distribution shows no support for the genetic subdivision of *M. gilvus* in Borneo, since only a single *Termitomyces* type was found (type A). On the other hand, the patchy distribution of type C in North Sumatra and type B in Riau/West Sumatra displayed excellent support for the termite subdivision in Sumatra. This means that genetic differentiation in the host termite may not necessarily reflect the genetic differentiation of the fungal symbiont.

Conclusion

Given the complexity of the natural history of Southeast Asia, there is no single force which single-handedly shapes the phylogeographic signature of *M. gilvus* in the region. In general, phenotypic variations were in accord with genotypic differentiation in *M. gilvus*. The divergence time suggests a co-diversification between the host, *M. gilvus* and its fungal symbiont, *Termitomyces* sp. however, the relationship was not completely exclusive. The natural history of *M. gilvus* has shed light on the early dispersal pattern of terrestrial fauna across Southeast Asia and additionally gives insight on the host-symbiont mutualism scenario in the frequently changing environment of Southeast Asia.

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