Sociobiology 65(1): 10-14 (March, 2018) Special Issue DOI: 10.13102/sociobiology.v65i1.1845

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - TERMITES

Estimating Global Termite Species Richness Using Extrapolation

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Article History

Edited by
Paulo F. Cristaldo, UFS, Brazil
Received 07 July 2017
Initial acceptance 31 July 2017
Final acceptance 29 August 2017
Publication date 30 March 2018

Keywords
Isoptera, diversity, Michaelis-Menten, curve-fitting, maximum likelihood.

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Abstract

Cumulative species description curves since 1758 are given for all termites of the world and for each biogeographical region (Australian, Ethiopian, Nearctic, Neotropical, Oriental, Palearctic, and Papuan). A cumulative description curve is also given for world genera. Estimation by maximum likelihood using the Michaelis-Menten model suggests a maximum of 5366 ± 175 species ($p < 2.2\text{E-}16$) and 704 ± 77 genera ($p < 4.387\text{E-}13$). Model fitting was poor for most individual biogeographical regions, with the exception of the Ethiopian region (estimate = 1295 ± 57 species, $p < 2.2\text{E-}16$). World War I and World War II had marked negative impacts on termite description rates. Data from China was treated separately due to the atypical rate of description of new termites in that country during the last two decades of the 20th century.

Introduction

Wilson (1971) suggested that termite taxonomy was nearly complete almost half a century ago, and that relatively few genera and species remained to be described. Nevertheless, new genera and species continued to be discovered and described in considerable numbers. A partial analysis of termite description rates was presented by Eggleton (1999), covering the second half of the 20th century. Complete description curves have never been published.

It is possible to estimate total species richness using extrapolation based on species accumulation curves (Colwell & Coddington, 1994). For instance, Paxton (1998) estimated the total number of large marine animals using this approach. The major difficulty with this method is to assemble adequate datasets. It requires a nearly complete and accurate taxonomic catalog of the taxon being studied, which takes considerable effort, even for relatively small groups such as termites.

In this paper, complete and accurate cumulative description curves of termite species and genera are presented. Total richness was estimated by maximum likelihood using the Michaelis-Menten model.

Methods

All taxonomic data were extracted from the Termite Database (Constantino, 2016), which is available online since 2002, and has been continuously updated. The current version incorporates taxonomic changes from Krishna et al. (2013) and includes living and fossil termites from all regions of the world, and nomenclatural data from Linnaeus (1758) to the present. The data itself is maintained in a custom relational database using MySQL as the database engine. Data were extrated from the database using SQL queries and PERL scripts, converted to CSV tables, and imported into R software (R Core Team, 2017). Fossil taxa and *nomina dubia* were excluded from the dataset.

Curve fitting was conducted using maximum likelihood with R package *drc* (Ritz et al., 2015) using the Michaelis-Menten model *MM.2()*, and data from 1900 to the present. Description rates from 1758 to 1899 were too low due to the very small number of active taxonomists and were excluded from model fitting (but are presented in the graphs). All graphs were plotted using standard R graphics functions (*plot()*, *lines()*, *points()*).

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

The Michaelis-Menten model is usually represented by the formula $S(n) = S_{max} \cdot n/(B + n)$, where, in this case, $S(n)$ = expected number of species in year n; S_{max} = total number of species (asymptote); B = second parameter of the model (Colwell & Coddington, 1994).

The rationale for the use of this model is that there is a fixed species pool in the planet from which new species can be discovered. Under a relatively constant sampling effort, the rate of new discoveries should decrease as the proportion of known species increases.

Results

The total current numbers are the following (excluding fossils): world total 2951 species (2516 excluding China) and 297 genera (290 excluding China); Australian region 272 spp.; Ethiopian 754 spp.; Nearctic 51 spp.; Neotropical 597 spp.; Oriental 1148 spp. (741 excluding China); Palearctic 169 spp. (126 excluding China); and Papuan 127 spp. A few species occur in more than one region. The current total number of junior subjective synonyms in the species category is 661 (18%), excluding fossils. These are names that were regarded as valid species for some time, have their own types, and can be revalidated. The number of objetive synonyms in the same category is 49; these are nomenclatural synonyms that were never treated as separate species. Another 15 names are classified as *nomina dubia*, with uncertain status; most of these are probably synonyms.

Initial global analyses resulted in poor model fitting. After some testing it became clear that the problematic data were from China (see discussion below). Excluding these data considerably improved model fitting (Fig 1) and resulted in estimates of 5366 ± 175 species ($p < 2.2E-16$, Fig. 1) and 704 ± 77 genera ($p < 4.387E-13$, Fig 2). These results suggest that 2675–3025 species and 337–491 genera remain undescribed.

Curve fitting for separate biogeographical regions was poor in most cases (Fig 3), with the only exception of the Ethiopian region. The S_{max} estimate for this region was 1295 ± 57 species ($p < 2.2E-16$).

World War I (1914–1918) and World War II (1939–1945) had marked negative impacts on termite description rates (Figs 1 and 2).

Discussion

The number of undescribed termite species estimated in this paper is considerably higher than suggested by Wilson (1971). The shape of the species description curve suggests that termite taxonomy is far from complete and that more than half of the species remains undescribed and nameless. This is not surprising considering that the estimated total number of insect species on the planet is nearly 5 million (Mora et al., 2011; Stork et al., 2015), which indicates that approximately 80% of them remain undescribed.

Termite description rates in China, especially from 1980–2000, were very unusual and artificial. Many new "species" were described during a period when the Chinese scientific community was isolated from the rest of the world, with limited access to the literature and collections.

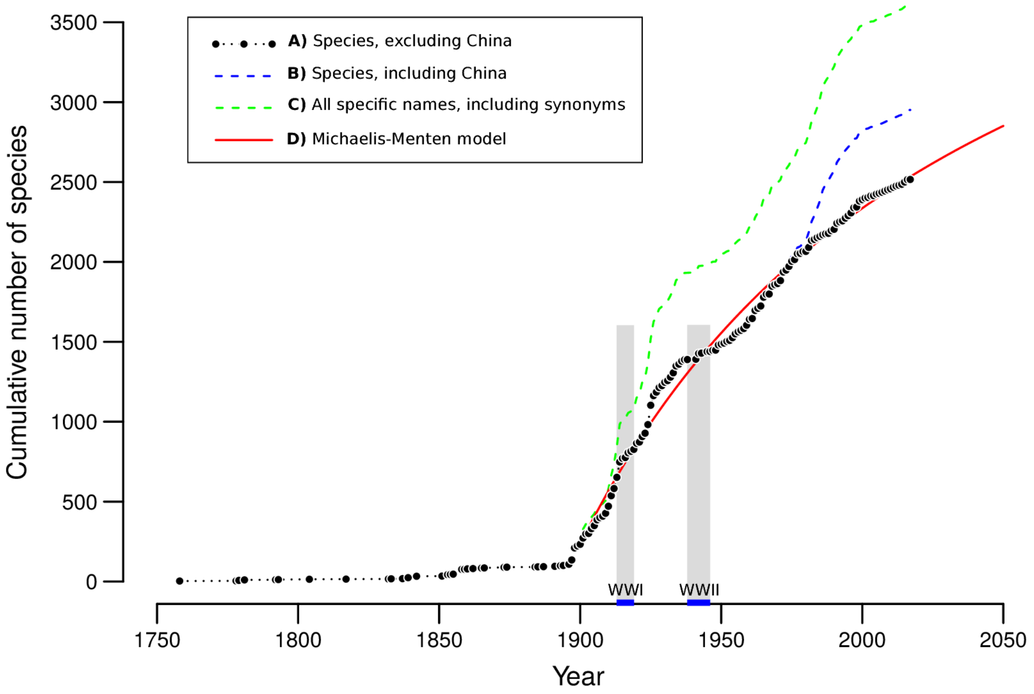

Fig 1. Cumulative number of termite species since Linnaeus (1758). A) number of species, excluding China; B) number of species, including China; C) total number of specific names, including those currently regarded as synonyms; D) Michaelis-Menten model fitted on curve A. WWI: World War I (1914-1918); WWII: World War II (1939-1945).

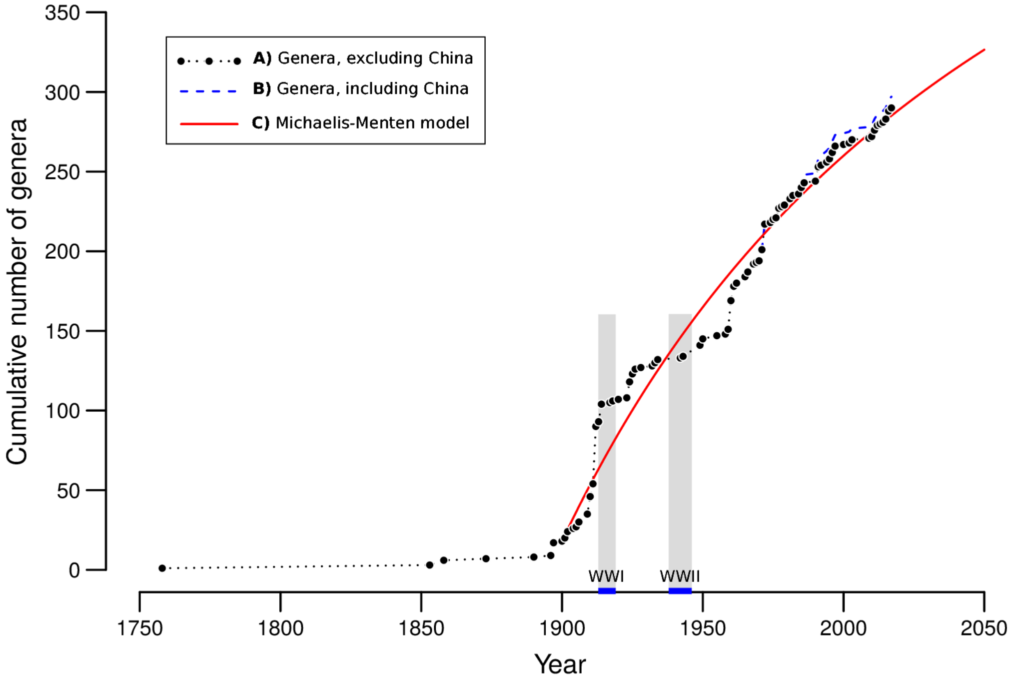

Fig 2. Cumulative number of termite genera since Linnaeus (1758). A) number of genera, excluding China; B) number of genera, including China; C) Michaelis-Menten model fitted on curve A. WWI: World War I (1914-1918); WWII: World War II (1939-1945).

This resulted in artificial taxonomic inflation (Crosland, 1995; Eggleton, 1999), visible as a strong deviation in the species accumulation curve (see Fig 3, Oriental region). They also described several endemic genera such as *Sinonasutitermes* and *Sinocapritermes* which do not seem to be valid. This taxonomic inflation is best illustrated by the number of *Reticulitermes* species in China (117) compared to the entire Nearctic region (6) and to India (5). The most likely explanation for this discrepancy is taxonomic error. This abnormal activity seems to have ceased, but they still need to revise the status of all these names. Most of them will eventually be synonymized, but currently they might be regarded as *nomina dubia*.

The separate cumulative species description curves for the biogeographical regions showed more variation than the global one, and most of them did not fit the Michaelis-Menten model. This variation reflects the number of active taxonomists studying the fauna of each region and also the fact that smaller samples are expected to show more variation than larger ones. For instance, in the Neotropical region the description rate has accelerated in recent years because the number of active taxonomists increased. On the other hand, taxonomic activity has been very low in Australian and Papuan regions in recent decades.

The cumulative description curve of genera also showed more variation than the species one. The delimitation of genera is based on phylogeny, but ranking is arbitrary and subjective, and for this reason we should not expect a perfect correlation between the accumulation curves of genera and species. The average number of species per genus has changed considerably along history. In the classification scheme presented by Desneux (1904), there was an average of about 35 species per genus, while in Snyder's (1949) catalog the average was 14 species per genus, and the current average is about 10 species per genus.

Estimates based on the method used here may be influenced by several factors (May, 1994; Mora *et al.*, 2011) including operational criteria used for species delimitation and changes in taxonomic effort. Incorrect species delimitation may both result in overestimated species richness due to synonyms, or underestimate it due to cryptic (=sibling) species. Molecular data will probably reveal cryptic species (e.g. Hausberger et al., 2011) and increase total richness, but this may be counterbalanced by the discovery of new synonymies, which will reduce the number of valid species in some genera (e.g. *Coptotermes*, see Chouvenc et al., 2016). The number of active taxonomists in each period also affects the rate of new discoveries. We currently do not have a good assessment of the relative importance of these factors, but their net effect is probably small.

Several taxonomic revisions also suggest a large number of undescribed taxa in some groups. The revision of the soldierless termites of Africa (Sands, 1972) resulted in the description of 16 new genera and 51 new species. Before that there were only 9 species, all classified in the genus *Anoplotermes*. Similarly, the revision of the Australian termites of the *Termes*-*Capritermes* group (Miller, 1991) resulted in the recognition of 13 genera (8 new) and 54 species (27 new). In the Neotropical region, a revision of the soldierless genus *Ruptitermes* resulted the recognition of 13 species, 9 of them new (Acioli & Constantino, 2015). There also many undescribed Kalotermitidae. For instance, a revision of *Cryptotermes* from the West Indies (Scheffrahn & Krecek, 1999) listed 17 species, 12 of them new.

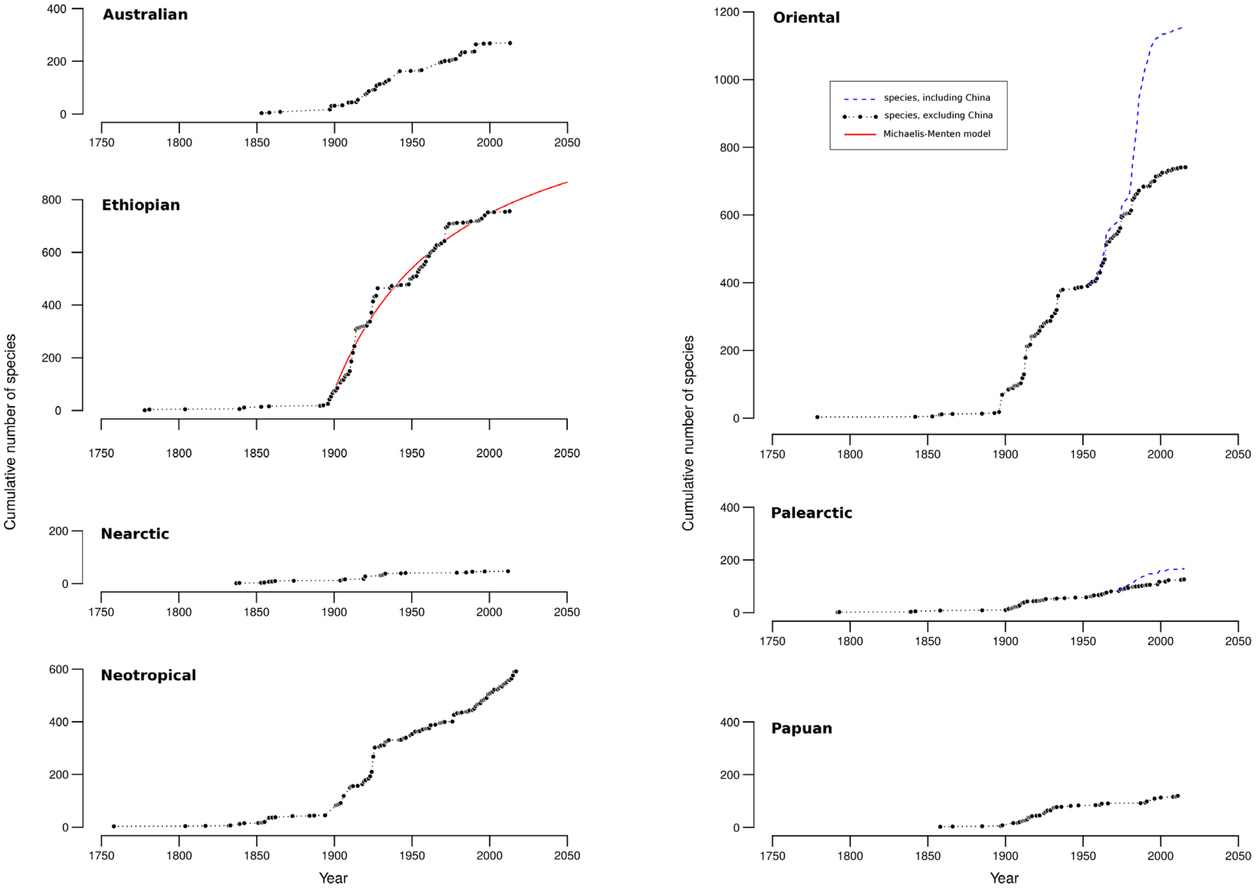

Fig 3. Cumulative number of termite species since Linnaeus (1758) for each biogeographic region: Australian, Ethiopian, Nearctic, Neotropical, Oriental, Palearctic, and Papuan. Data from China is shown as a separate line for the Oriental and Palearctic regions. The Michaelis-Menten model is shown only for the Ethiopian region.

The data presented here suggests that there is still a large number of undescribed termite species. However, this should not be seen as encouragement for the publication of a large number of small and purely descriptive taxonomic papers. Isolate descriptions of new taxa, especially when based on small and incomplete series, are particularly undesirable because they cause fragmentation and are more prone to error. More investment is needed in integrative revisionary taxonomic work based both on traditional and modern methods.

Acknowledgments

This work was supported by the Brazilian National Research Council (CNPq, grants 481360/2013-1 and 311016/2016-2).

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