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Ecology of termites from the genus *Nasutitermes* (Termitidae: Nasutitermitinae) and potential for science-based development of sustainable pest management programs

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Key Message

- We reviewed the taxonomic status of *Nasutitermes*, which is currently the most diverse termite genus, has a particularly complex taxonomic history, and includes some major pest species.
- We performed a comparative literature analysis, especially concerning the type-species *N. corniger*, while filtering available information concerning its biology through the prism of termite control.
- We critically examined the existing management of *N. corniger* (synthetic chemical products, botanical insecticides towards various targets, and biological control) to lead to the development of innovative management tools and strategies.

Author Contribution Statement

IB conceived the first draft. RC wrote the taxonomic history part and corrected biological part. EH, AR and NA corrected and greatly contributed to the pest management part. MF made all the drawings of *N. corniger*'s colony. All authors read, corrected and approved the manuscript.

Abstract

The genus *Nasutitermes* is among the most abundant wood-feeding Termitidae and an extremely diverse and heterogeneous group in terms of its biogeography and morphology. Despite the major role of several *Nasutitermes* species as structural pests, the phylogenetic status of this genus is still unclear, alongside with a confused taxonomy and species identification remaining difficult. The first aim of this review was thus to gather and discuss studies concerning the taxonomic status of the genus *Nasutitermes*, in order to clarify this crucial point. Then, our goal was to gain new insights into the management of *N. corniger*, considered to be the most economically detrimental pest of this genus in South America and a *Nasutitermes* model species, while filtering available information concerning its biology through the prism of termite control, as well as critically examine the existing methods. We indeed strongly believe that increasing our knowledge of this species' biological strategies is the key to progress in the challenging question of their sustainable management.

Keywords: Taxonomic history, *Nasutitermes corniger*, Termitidae, sustainable management, IPM, antimicrobial and insecticidal botanical extracts.

1. Introduction

The species causing the most considerable damage to tropical agriculture belong to four of the eight subfamilies of higher termites (Termitidae), and Nasutitermitinae is one of them (Rouland-Lefèvre 2011; Krishna et al. 2013). The genus *Nasutitermes* is among the most abundant wood-feeding Nasutitermitinae in the tropics and several *Nasutitermes* species are important structural pests (Constantino 2002; Fontes and Milano 2002). This genus comprises a diverse and heterogeneus group of species (Miura et al, 2000). The distributional patterns of *Nasutitermes* species were probably shaped by environmental conditions and historical factors, such as continental drift, orogeny, and Quaternary climatic variations (Miura et al, 2000).

As currently defined, *Nasutitermes* does not comprise a monophyletic group of species (Eggleton 2001; Inward et al. 2007; Roy et al. 2014), its taxonomy is confused, and accurate species identification is very difficult. Many nasute species that do not belong to the *Nasutitermes* clade remain nested within *Nasutitermes*, generating taxonomic confusion, while misidentifications and nomenclatural errors are frequent (Gush et al. 1985; Traniello et al. 1985; Constantino 2000; 2002; Scheffrahn et al. 2002; Scheffrahn et al. 2005a; Scheffrahn et al. 2005b). A comprehensive taxonomic revision of the genus is highly necessary, but has never been attempted due to the enormous difficulties involved.

However, despite this heterogeneity, some aspects, such as nest building (Thorne et al. 1996; Fuller and Postava-Davignon 2014), soldiers' defense strategies (Prestwich 1979) and hindgut microbiome role in symbiosis (Brune 2014), are well known for several *Nasutitermes* species. Yet, this information could be more clearly highlighted and discussed in the perspective of pest management to exploit at its most and face the growing importance of *Nasutitermes* pest species. These termites live in a large range of habitats in urban, anthropized, disturbed and natural environments, in dry as well as in moist conditions and at elevations of up to 1000 m (Scheffrahn et al. 2005a; Bustamante and Martius 1998; Dunn and Messier 1999, Vasconcellos and Moura 2010, Mello et al. 2014, Lima et al. 2013). This versatility, alongside with changes in urban soil occupation in the last few decades, leads to an increasing infestation in large buildings which are full of structural voids, narrow fissures and wood (Fontes and Milano 2002).

In this paper, we thus gathered and commented studies on taxonomic history and current status of genus *Nasutitermes*, in order to clarify this crucial point. Indeed, taxonomy provides an essential framework, as no effective and sustainable management can be set up without precisely identifying and describing the intended species.

We also aimed to gain new insights into the biology of *N. corniger* as a *Nasutitermes* model species, in the perspective of improving termite control. Better insights into these aspects would indeed contribute to the development of more adapted and efficient control methods, as highlighted by Scharf (2015) in a recent review.

Eventually, we critically examined the existing management methods against *N. corniger* and lastly underlined the fact that termites are also beneficial, playing a key role in the wood decomposition process.

2. Taxonomic history of genus *Nasutitermes* Dudley, 1890

Nasutitermes has a complex taxonomic history and many of the species currently included in this genus have been classified in other termite genera, while several species previously included in *Nasutitermes* have been transferred to other genera.

Our current taxonomic system begins with Linnaeus (1758), who described a single termite genus, *Termes*, which means termite in Latin. All termite species were classified in genus *Termes* for nearly a century after Linnaeus. In 1781 the British naturalist Henry Smeathman, described *Nasutitermes arborum* (as *Termes arborum*) from Sierra Leone, Africa, which was the first species of *Nasutitermes* to be formally named. Smeathman (1781) also presented information on its biology, nests, and damage to houses.

Termite classification started to change in the second half of the 19th century, when the German entomologist H.A. Hagen was the main authority on termite taxonomy. Hagen's (1858) monograph on world termites listed seven species of *Nasutitermes*, all of them included in the subgenus *Termes* (*Eutermes*) Heer, 1849. *Eutermes* was defined based on wing venation and in Hagen scheme it included a heterogeneous group of species, currently classified in several distinct genera.

The concept of "*Eutermes*" was restricted by Brauer (1868) to include only the termite species with a nasute soldier. Müller (1873), Froggatt (1897), and Silvestri (1903) adopted Brauer's definition and also raised *Eutermes* to the status of a genus. During that period, "*Eutermes*" was equivalent to our current definition of the subfamily Nasutitermitinae, and included all known species of *Nasutitermes*.

After the discovery of many new termite species with nasute soldiers, Holmgren (1910, 1912) subdivided the genus *Eutermes* into several subgenera. In Holmgren's system, subgenus *Eutermes* (*Eutermes*) was approximately equivalent to our current definition of genus *Nasutitermes*.

The name *Nasutitermes* itself appears for the first time in a paper about termites of Panama (Dudley 1890). Because Dudley did not provide a formal taxonomic description and did not include any species in the new genus, several authors overlooked the new name. It is important to note that formal international rules of nomenclature did not exist in 1890 (the first edition of the Code was published in 1905). Despite its limitations, Dudley's description satisfies the rules of nomenclature established in the first edition of the Code, and is therefore an available name.

Banks (1918) revealed a major problem with the previous use of the name "*Eutermes*": its type-species, *Eutermes debilis*, a fossil, was identified as a species of *Microcerotermes*, a genus with mandibulate soldiers not related to the nasutes. In the same paper, Banks adopted the name *Nasutitermes* Dudley, 1890 for the termites with nasute soldiers. The status of the name *Eutermes* is still considered uncertain and it has not been used for living termites. However, many species currently placed in *Nasutitermes* appeared in the literature under the name "*Eutermes*" for a couple of decades, including the important monographs published by Holmgren (1909, 1910, 1912).

The name *Nasutitermes* was widely adopted after 1918. Initially, it included all species with nasute soldiers (= subfamily Nasutitermitinae), and was later subdivided into several new subgenera and genera. Snyder's (1949) world catalog of termites lists about 400 species of nasute termites, classified into 25 different genera; among them, 190 species were listed under the genus *Nasutitermes*.

Today, *Nasutitermes* is the most diverse termite genus, with 254 valid species (Krishna et al. 2013, updated). It is present in all biogeographical regions, distributed as follows: Oriental 114, Neotropical 78, Papuan 20, Ethiopian 19, Australian 19, Palearctic 14, and Nearctic 01. As shown in Figure 1, new species of *Nasutitermes* have been discovered continually since the end of the 19th century. Variation in the description rate is related to the number of active termite taxonomists, which was larger during the first half of the 20th century. The total number of species is likely to increase in the future.

The species currently included in genus *Nasutitermes* do not form a monophyletic group (Inward et al. 2007). Some are quite distinct from the type species (*N. corniger*) and were included in *Nasutitermes* when this genus comprised most Nasutitermitinae. The reexamination of the status of these species has resulted in changes in the classification, with the description of new genera and reassignment of some species to other known genera of

Nasutitermitinae. For instance, several species previously included in *Nasutitermes* were transferred to *Cortaritermes* by Mathews (1977), Fontes (1998), and Cuezzo et al. (2015). The name *Nasutitermes*, however, will always be associated with its type-species, *N. corniger*.

3. *Nasutitermes corniger* (Motschulsky, 1855) as a model species

Nasutitermes corniger is a neotropical species which occurs natively from southern Mexico to northern Argentina and in the Caribbean islands, and it is an invasive species in the Bahamas, Florida and New Guinea (Figure 2) (Scheffrahn et al. 2005a; Evans et al. 2013). In the latter area, it may have been introduced accidentally due to human transport (Scheffrahn et al. 2005b). It is widely distributed in the neotropics, with high adaptability to a wide range of habitats (Scheffrahn et al. 2002). *Nasutitermes corniger* is the most important pest species of this genus in the New World (Constantino 2002; Fontes and Milano 2002) and its biology is relatively well-known.

3.1 Biology, ecology, and behavior of *Nasutitermes corniger*

Apterous line: tasks and morphological polyethism

Nasutitermes corniger is a social insect that has colonies that can contain up to 900,000 individuals (Dunn and Messier 1999; Thorne 1984). A colony is composed of workers, soldiers, and imagoes. In Termitidae, this structure originates from a common first stage of development, from which an apterous and an imaginal concurrently emerge. The imaginal line leads to the reproductive caste. From the apterous line the worker caste appears, followed by soldiers (Figure 3) (Lima et al. 2013).

Workers are primarily responsible for foraging, constructing and repairing the nest; carrying eggs and nursing; and feeding and grooming immature stages, soldiers, and reproductives as well as participating in defensive activities with soldiers (Thorne 1984). Soldiers are a defensive caste responsible for guarding the colony (Traniello 1981; Gazal et al. 2012; Verma et al. 2009). They also organize foraging by exploring new wood sources (Traniello 1981) and by regulating foraging activity. During nest defense, soldiers squirt from their nasus a sticky, odoriferous, irritating secretion to distances of more than three times their body length (Traniello 1981; McMahan 1982). All sterile forms (workers and soldiers) are blind and lucifugous (Thorne 1983; Scheffrahn et al. 2005a; Verma et al. 2009). These termite castes are 4 to 6 mm long, pale and soft bodied (Figure 4); mature in one year; and can live up to 5 years (Verma et al. 2009). As is typical for the genus *Nasutitermes*, workers show sexual dimorphism, with females conspicuously larger than males (Lima et al. 2013; Scheffrahn et al. 2005a; Jones 1980). Soldiers represent between 5 and 20% of a colony (Dunn and Messier 1999; Thorne 1984). They are characterized by reduced mandibles and a modified cephalic projection (the nasus), giving its name to the genus (Thorne 1984). Both soldiers and workers are completely sterile, with vestigial reproductive organs.

In a recent study, Lima et al. (2013) studied caste polymorphism of *N. corniger* apterous line using morphometric and discriminant analysis. Based on the comparison of the length of the antenna, thorax and metatibia, they highlighted two morphological types in presoldiers and soldiers, and two lines of development for workers. These elements demonstrate that morphological studies of *N. corniger* still remain crucial to increase the knowledge of the caste system in this species. Coupled with analytical and statistical tools, they can still lead to new discoveries. In addition to the rigorous determination of morphological types, these elements contribute to improving the understanding of individuals' interactions inside the colony. Lima et al. (2013) emphasized the fact that knowing whether the different morphological types perform different tasks would help in understanding the behavioral dynamics in termites' societies. Former studies have, for example, shown that the behavior of each caste is significantly different during nest repair and nest expansion (McMahan 1970). Moreover, molecular approaches also offer promise for deciphering cryptic aspects of caste biology, potentially leading to insights for new control technologies (Scharf et al., 2015).

Nymphal line: Description of the reproductive strategies

Imagoes are of three types: primary reproductives (queens and kings), alates, and adultoids (Thorne 1984). They have fully developed eyes and are winged and pigmented (Scheffrahn et al. 2005a; Verma et al. 2009; Thorne 1983). The primary reproductives are the imagoes that initiated the colony after the dispersal flight. Alates are produced seasonally and leave the nest after spending 5 to 8 months within the parental colony, while adultoids are replacement reproductives derived from alates that did not disperse (Thorne 1983).

Ergatoids are worker-like neotenic reproductives derived from immatures of the neuter line. They have two additional molts compared to worker's development. They are wingless, blind and are at the bottom of the fecundity hierarchy (Figure 3) (Thorne 1984).

Mature colonies of *N. corniger* release large numbers of alates during massive crepuscular nuptial flights (35% of the colony biomass and 5000 to 25000 individuals on average), usually after rain (Thorne 1983). Royal couples are formed, find moist places with wood food, shed their wings, and remain together throughout the life cycle of the colony. Queens have a physogastric abdomen (due to ovariole growth), are capable of laying approximately 3000 eggs per day, and can live up to 25 years (Scheffrahn et al. 2005a). The eggs are yellow to white and incubate for 50 to 60 days before hatching (Verma et al. 2009).

Colonies of *N. corniger* have the largest number of primary queens per colony and the highest proportion of polygynous colonies, as 20 to 25% of mature colonies are headed by multiple unrelated primary reproductives (Thorne 1984; Atkinson and Adams 1997; Hartke and Rosengaus 2013). The tolerance of several queens in polygynous nests was hypothesized to be due to the high individual cost of intensively laying at high rates, and this phenomenon is apparently inversely related to the mean weight of queens (Adams and Atkinson 2008). However, a study performed by Hartke and Rosengaus regarding the cost of pleometrosis compared with colony foundation by monogamous pairs demonstrated that this strategy is disadvantageous for the colony's fitness (Hartke and Rosengaus 2013). Thus, mature polygamous nests of *N. corniger* may not be established via pleometrosis, but may imply other phenomena, such as the coalescence of young monogamous colonies. In fact, polygyny in *N. corniger*, as in the case of other Isoptera and some Hymenoptera, is not accompanied by nepotism because no data showed that workers care for their mothers more than the other queens (Atkinson et al. 2008). Likewise, experimental young colonies easily merged under laboratory conditions (Hartke and Rosengaus 2013). These results highlight the fact that further studies may be useful to understand the exact process as well as the ecological advantages of this phenomenon of colony fusion. Alongside its feeding habits and the aspects related to nesting, these reproduction mechanisms may play a part in the species' success in colonizing space, thus making *N. corniger* a major urban pest (Mello et al. 2014).

Role of the nest: from structural protection to immunity enhancement

Nests of *N. corniger* (Figure 5) are constructed on trees, bases of trunks, in secluded places of buildings or, less often, on the open soil (Scheffrahn et al. 2005a). These nests are single or polycalic, from ovoid to conical in form, with dimensions ranging up to 90 cm in height and 40 cm in width (Dunn and Messier 1999; McMahan 1982; Levings and Adams

1984; Scheffrahn et al. 1990). The nests have three parts: a superficial area with a thin skin of carton, which can exclude predators and prevent desiccation and flooding conditions (McMahan 1982; Fuller and Postava-Davignon, 2014); a middle part consisting of interconnecting galleries and chambers made of hard and dense carton (McMahan 1982); and a queen chamber located near the center of the nest (Thorne 1980). Additionally, carton-covered tunnels radiate from the nest and provide protection to termites during foraging (Levings and Adams 1984). This particular organization represents a challenge in termite management, because nests are often distant from infestation sites and are so structurally sound, *Nasutitermes* control can thus often be difficult (Fontes and Milano 2002; Gazal et al. 2012).

The stercoral carton used by termite workers during foraging, constructing or repairing processes is a black substance mainly composed of masticated wood and feces, cemented with salivary secretions (Postava-Davignon 2010; Traniello 1981; McMahan 1982). In addition, some other chemical or biological substances can also be incorporated inside this material. For example, β(1,3)-glucanase activity was recently discovered in the *N. corniger* nest carton due to the presence of the native tGNBP-2 protein. By cleaving and releasing pathogenic components, it participates in the colony’s immunological defense system against infections (Bulmer et al. 2004; 2009). Also, preliminary results obtained on *N. acajutlae* highlighted that, in general, fewer bacteria and fungi were observed inside the nests compared to the soil and trails (Postava-Davignon 2010). Thus, *Nasutitermes* nests are effective structures that allow the insects to survive in their environment, and antimicrobial defense integrated in the structure can help termites to enhance their immunity. This perfectly exemplifies the richness of defense strategies among insect colonies. Based on this information, Bulmer et al. (2009) developed a glycomimetic molecule blocking tGNBP-2 using rational design, which increases infection and death rate of exposed termites and can be used as an alternative control method.

This work clearly demonstrated that understanding termite biology is key to their sustainable management, as well as the resolution of product engineering and development issues.

Pheromone biology: communication, recruitment, modulation

Chemical odor trails are produced by the sternal gland (Stuart 1963). This gland is located on the fifth abdominal sternite and is composed of modified epidermal cells (Traniello and Busher 1985). Soldiers' sternal glands are smaller, on average, than workers'. These sternal pheromones are implicated in several aspects of the colony life. When nest defense is necessary, soldiers release a secretion from their nasus, which contains a mixture of terpenoids and elicits alarm and defensive recruitment (Thorne 1984; Roisin et al. 1990). Pheromones also communicate information about the presence and location of food, are used to recruit more soldiers and workers, and can modulate caste differentiation, either positively or negatively (Traniello and Busher 1985; Scharf 2015).

Recruitment was formerly proposed to depend on the quantitative production of the pheromone (Traniello and Busher 1985). In fact, it was effectively measured that the worker/soldier concentration ratio was 0.2 times for compounds concentrated in *N. corniger* (Arab et al. 2006). Moreover, behavioral evidence for species, colony, and caste specificity of the trail pheromone were also presented (Dunn and Messier 1999; Arab et al. 2006). In particular, Arab et al. (2006) described that both *N. corniger* workers and soldiers preferred the trails made by conspecific soldiers over those from workers. Extracts from the same species, and more particularly from the same colony, were also demonstrated to be preferred (Arab et al. 2006). Dunn and Messier (1999) highlighted that soldiers are able to discriminate their own colony members from conspecific neighbors and strangers; therefore, they behave more aggressively toward neighbors, with which they are competing for resources and territory, compared to strangers.

If quantitative differences between soldiers' and workers' trail pheromones can help to regulate the foraging behavior of these termites, the chemical composition of the sternal gland secretions should also be taken into account. For example, chemical analysis identified neocembrene, dodecatrienol and trinervitatriene in the pheromone trail, with a ratio of dodecatrienol/neocembrene of 1:25 and a ratio of trinervitatriene/neocembrene of 1:2 in the sternal glands of *N. corniger*'s workers (Sillam-Dussès et al. 2010). Monocyclic 14-membered ring diterpene cembrene-A is also a common constituent of this trail and is a short-term alarm capable of orienting soldiers to an area of disturbance (Hall and Traniello 1985). Moreover, some other parameters may play an important role in trail following. For example, a study performed by Gazal et al. highlighted the significant effect of feces on the trail (Gazal et al. 2014). Chemical analyses on the feces' composition, and behavioral studies implicating the identified compounds, may lead to valuable information that could help to improve the understanding of trail following mechanisms. This could be of importance to develop attractant or repulsive products in the context of an integrated pest management procedure. In addition to their crucial role for recruitment, chemical trails also probably exhibit antimicrobial activities and might be involved in the control of nest microbial competitors (Rosengaus et al. 2000). According to these results, studying the influence of the morphological type on potential specificity induction in trail preference could also lead to interesting results, besides contributing to the understanding of the social function of each morphological type inside a colony. Eventually, as primer pheromones from soldiers and other castes may also regulate caste homeostasis (Scharf et al., 2015), studying these compounds and their associated biology could potentially lead to insights for new control technologies.

Food selection: a complex process

Nasutitermes corniger feeds on dry, wet, or partially decomposed wood (He et al. 2013). It has the ability to consume a large variety of wood, such as dead twigs and branches in trees, tree stumps, wood debris on the ground and structural wood, including framing, plywood, pressboard, hardwood handles, wooden artwork, fences and paper and derivatives in laboratory conditions (Scheffrahn et al. 2005a). However, the exact stimuli implicated in the finding and selection of food by *N. corniger* is still under evaluation.

Nasutitermes corniger was first described as having no significant consumption preference among different wood species, but with a strong preference for decayed over fresh wood (Bustamante and Martius 1998). However, further contradictory studies demonstrated a significant species preference under laboratory conditions (Gazal et al. 2010). Yet, consistent with the results obtained by Bustamante and Martius (1998), the choice was not shown to exclusively depend on the density. Concerning the stage of decay of the wood, a more recent study conducted by Gazal et al. (2012) confirmed the results of Bustamante and Martius. Whatever the tested species, decayed wood always recruited more individuals than undecayed wood in standard foraging arenas. The next step was to investigate whether the choice of the source of wood was attributed to physical or chemical factors. This work thus demonstrated the crucial role of the secondary metabolites produced during wood degradation in the choice of a food substrate by comparing impregnation of a neutral (filter paper) and of wood (fresh or decayed) substrate with weathered or unweathered *Eucalyptus grandis* wood extracts (Gazal et al. 2014).

Following these results, further studies should be performed on the identification and origin of the compounds linked to wood degradation and to investigate their action on wood's physicochemical properties. It may also be interesting to investigate the effect of weathered and unweathered extracts on a neutral wood substrate from which secondary metabolites would have been removed or on non-durable wood, such as *Pinus* sp. According to some authors, the preference for decayed wood could be due to several factors. Decomposition may lead to an increase of nutrient availability and a facilitation of mastication during the process and the depolymerization of cellulose, making wood fibers easier to remove and compounds more degradable. Moreover, it is possible that wood degradation releases allelochemicals that influence the foraging behavior or trigger trail following. Decomposition is also associated with the presence of microorganisms, notably fungi, which are potential additional sources of nitrogen and vitamins for the termites (Vasconcellos and Moura 2010; Gazal et al. 2012; Gazal et al. 2014). In addition to improve the ecological and biological knowledge of the species, understanding the mechanisms of termites' food selection would play a central role in developing new techniques to control *N. corniger* in case of infestation, such as substrates for insecticide-impregnated baits, or prevent *N. corniger* colonization of buildings by orienting technological choices.

Symbiosis and mutualism

The insect gut is divided into three regions: the stomodeum (foregut), the mesenteron (midgut), and the proctodeum (hindgut). The foregut includes the crop, a food-storage organ. In termites, the hindgut is enlarged and subdivided into five segments (P1-P5). The crop is slightly acidic, whereas the hindgut is moderately alkaline, with anaerobic conditions (Bignell and Anderson 1980). In the third hindgut segment (P3 or paunch), a bacterial community has developed that confers certain important benefits to the termite. In fact, in the case of *N. corniger,* such as other higher termites (Termitidae), digestive enzymes are encoded both by the termite genome itself and by these symbiotic bacteria, as these species do not possess hindgut flagellate protozoa, contrary to lower termites for which these organisms are the sources of cellulases and hemicellulases (Warnecke et al. 2007). However, this microbiome appears to play a far more complex role than only being related to cellulose degradation, as in nitrogen fixation (Prestwich and Bentley 1981; Tayasu et al. 1994). In the case of an arboreal species close to *N. corniger*, a metagenomic analysis of the hindgut-associated microbial community highlighted the presence of bacterial genes for cellulose and xylan hydrolysis and also provided information about the possible functional role of this community concerning free H_2 generation and CO_2-reductive acetogenesis, alongside the identification of genes associated with nitrogen fixation (Warnecke et al. 2007). Metaproteome analysis of this community revealed the presence of proteins of known enzymatic functions in the case of *N. corniger*, thus permitting the reconstruction of the enzymatic pathways concerning transport, glucan binding, sugar fermentation, hydrogen metabolism, amino acid synthesis, and nitrogen fixation and assimilation (Burnum et al. 2010). These findings are complementary to the results previously obtained by Warnecke et al. (2007), although from all the isolated known proteins no enzyme involved in cellulose degradation could be observed. This may be due to methodic limitations, or because the cellulose native degradation may occur elsewhere than inside the termite hindgut.

Spirochetes, mostly from the *Treponema* genus, and Fibrobacteres, alongside an undetermined phylum (TG3), were the most abundant phyla of these *N. corniger* microbial symbionts and were established to be fiber-associated bacterial communities that significantly contribute to the cellulotic activity (He et al. 2013; Warnecke et al. 2007; Mikaelyan et al. 2014). Warnecke et al. (2007) also demonstrated that gene modules coding for iron-only hydrogenase were bound to the genus *Treponema*, as well as maker genes linked to the acetogenesis pathway, and this process apparently dominates in *Nasutitermes* by Spirochaetes. In the actinobacterial community, well known for its role in organic matter decomposition, such as cellulose, five families (*Propionibacteriaceae*, *Streptomycetaceae*, *Cellulomonodaceae*, *Corynebacteriaceae* and *Rubrobacteraceae)* were identified for *N. corniger*, regardless of the geographical origin or feeding behavior (Lefebvre et al. 2009).

Regarding the apparent role of microbial symbionts concerning cellulose digestion and other essential metabolic functions, disrupting this effective equilibrium would be important in the continuous search for insecticidal products. In fact, it was demonstrated that modifying the carbon source allocated to the higher termite *N. takasagoenis* led to marked changes in the bacterial community structure, thus highlighting the delicateness of this relationship (Miyata et al. 2007). Moreover, in the case of an integrated pest management strategy, searching for products that exhibit antimicrobial activity seems to be a promising perspective (Shelton and Grace 2003).

Concurrent to this crucial symbiosis, other types of associations can be observed in termites' societies. In particular, ants could be associated with facultative or opportunistic mutualism where these insects use part of the termite nest, prey on live or dead workers, provide the termites with nitrogen nutrients and assist in nest protection. The frequency of *N. corniger* association with ant species depends, in particular, on the cost-benefit balance linked to predation risk. A Brazilian study demonstrated that Formicidae species richness in *Nasutitermes*' nests (*N. corniger* and *N. ephratae*) was significantly higher in abandoned nests, in 48 species, compared to active or decadent nests, in 6 and 8 species (Santos et al. 2010). In the latter case, *Crematogaster acuta* (Fabricius) and *Ectatomma tuberculatum* (Olivier) were the most frequent species observed. *Monacis bispinosa* (Olivier), which is highly susceptible to the soldier frontal gland mixture and which do not prey on live termites, was the most frequently found species in common ants / *N. corniger* nests in Venezuela (Jaffe et al. 1995). *Crematogaster brevispinosa* (Mayr), an arboreal ant, has been observed in association with *N. corniger* in Brazil, sharing the same nest even if a physical barrier is built between the two communities. The participation of ants in nest protection and nutritional substrate supply thus appears to be another factor contributing to the success of *N. corniger* colonization.

3.2 Pest management

Synthetic chemical products, as active substances inhibiting wood degradation by termites and microorganisms, can be applied through soil, wood treatment, or chemical fumigations, before or after infestation (Paiva et al. 2011) (Table 1). Excellent reviews or technical reports, such as those by Schultz et al. (2007; 2008) concerning wood preservation, Verma et al. (2009) on the biological control of termites, or the expert group on termite biology and management of the United Nations Environment Program (UNEP 2000), have taken an inventory of the different strategies, depending on the geographical zone. Despite the perceived efficiency of all of these substances, we cannot ignore the constraints on use, environmental risk, human health and toxicity to non-target organisms (Pluke et al. 1999; Clausen and Yang 2007; Santana et al. 2010; Scheffrahn and Scherer 2013; Scheffrahn et al. 2014). However, the efficacy of the different strategies mentioned above is mainly evaluated against subterranean termite species. Despite their recognized status as a significant urban pest, few references specifically mention arboreal termites, particularly *Nasutitermes* spp. This observation can be explained by several factors. First, damages caused by subterranean termites are less predictable, and preventive treatments must therefore be very efficient and are crucially needed. In fact, in regard to physical management, the easily detected *N. corniger* nests are often simply collected, broken and/or burnt (UNEP 2000; Pluke et al. 1999), whereas barriers often containing insecticides must be used as a management strategy for subterranean termites (Verma et al. 2009; UNEP 2000; Paiva et al. 2011). A second factor to be taken into account is the fact that *Nasutitermes* species mostly impact Central and South America, alongside other tropical zones of the globe, such as Southeast Asia and Australia, while the main commercial markets related to insecticidal products are located in the Northern hemisphere, mostly concerned with subterranean termites (Constantino et al. 2002;

UNEP 2000; Miura et al. 2000). For example, in 2008, North America represented 60% of the total market for wood preserving biocides and Europe and Asia/Oceania represented 20% each (Schultz et al. 2008).

However, products for wood protection commercially available in the market must be active against a wide range of organisms, from decaying fungi to various xylophagous insects (Schultz et al. 2007). Even if species specificities exist, the insecticidal products mainly tested on subterranean termites (which target the workers caste) are thus also efficient towards arboreal termites, such as *N. corniger*. In the following sections, we thus focused as much as possible on environmentally low-risk management strategies, presenting examples specifically concerning *N. corniger* but also some references concerning *Nasutitermes* sp. and sometimes about other termites species when needed.

Botanical insecticides: antitermitic extracts and compounds

Numerous laboratory studies target the evaluation of botanical extracts and natural compounds against termites. Even if they mostly address the activity of these products against subterranean species, some interesting results can be cited concerning *Nasutitermes* spp. and, more particularly *N. corniger*.

One strategy for finding new specific termiticidal compounds from botanical sources is called "bioinspiration," which aims to understand the functional role of secondary metabolites in living organisms, thus gaining inspiration from the abilities of plants or microorganisms to produce adapted bioactive molecules under specific environmental conditions (Rodrigues et al. 2010; Basset et al. 2012; Houël et al. 2015). In particular, one source for these antitermitic natural compounds are woods naturally resistant to biodegradation, which is closely linked to the accumulation of extractives typically in the heartwood (Taylor et al. 2002; Ragon et al. 2008; Kampe and Magel 2013). Results concerning wood extracts activity against *N. corniger* or *Nasutitermes* sp. (Peres Filho et al. 2006; Barbosa et al. 2007; Sá et al. 2008; 2009; Santana et al. 2010; Boulogne et al. 2011; Rodrigues et al. 2011; Rodrigues et al. 2010) are summed up in Table 2.

The research for natural extracts for wood protection contemplates various modes of action such as elicitors, regulators, inhibitors, enzymes, or repellents for pest control. In fact, specific defense mechanisms were evidenced in plant seeds and roots, which are essential for the propagation and survival of the species. Lectins, for example, which are toxic proteins widely distributed among plants, are supposedly involved in defense mechanisms against phytophagous predators (Carlini and Grossi 2002). These compounds, isolated from various sources, were extensively studied for their insecticidal activity, *N. corniger* being among the selected targets (Sá et al. 2008; Silva et al. 2009; Napoleão et al. 2011; Paiva et al. 2011; Souza et al. 2011). These proteins play a role in cell agglutination by carbohydrate recognition and could therefore act by binding to glycoproteins present in the insect's digestive tract (Sá et al. 2008). They were demonstrated to be able to disrupt enzymes' activities from the gut of termites (Lima et al. 2014). These molecules are now the basis of commercial formulations currently developed against termites (Paiva et al. 2011). Eventually, some well-known insecticidal compounds from plant extracts are active as biocides, strong repellants or antifeedants against several species, including subterranean termites (Sharma et al. 1991; Grace and Yates 1992; Serit et al. 1992; Ivbijaro 1993; Delate and Grace 1995; Chuanchuan et al. 1998; UNEP 2000; YunLing et al. 2009; Tahiri et al. 2011; Sharma et al. 2011; Himmi et al. 2013; Boulogne et al. In prep.) (Table 2).

Concurrently to the evaluation of extracts' biological activity, several reviews have been reported in natural products for wood protection (Singh and Singh 2012; Verma et al. 2009; Yang 2009; Mai et al. 2004; Kirker et al. 2013; González-Laredo et al. 2015). These reports discuss the development of botanical pesticides against subterranean termites, with in particular results concerning *Nasutitermes* wood decay control. Some extracts could be employed unadjuvanted as wood protectants, as reported in an African study, about the effective extracts of *Erythrophleum suaveolens* (Guill. & Perr.) Brenan (Fabaceae), *Azadirachta indica* A. Juss. (Meliaceae) and *Chromolaena odorata* (L.) King & Rob. (Asteraceae) in improving the durability of *Antiaris toxicaria* Lesch. (Moraceae) wood, exposed to decay for five years (Antwi-Boasiako and Damoah, 2010). In another study, *Cryptomeria japonica* (Thunb. ex L. f.) D. Don (Cupressaceae) wood treated with essential oils, showed strong activity against subterranean termites, in a three weeks test (Kartal *et al*., 2006). Turner and Conradie have also demonstrated the enhanced termitic resistance of *Pinus patula* Schltdl. & Cham. (Pinaceae) treated with extracts from four African durable species - *Breonadia salicina* (Vahl) Hepper & Wood (Rubiaceae), *Spirostachys Africana* Sond. (Euphorbiaceae), *Ptaeroxylon obliquum* (Thunb.) Radlk. (Rutaceae) and *Syncarpia glomulifera* (Sm.) Nied. (Myrtaceae)- in a two years test (Turner and Conradie, 1995).

Another way to employ botanical pesticides is to combine natural products to other protectants compounds, such as described in a 2007 study, where 0.5 percent thujaplicin was used in several multicomponent biocide systems with borate and carbon-based biocides. Noticeable results were obtained for protecting wood from mold, decay, and termite damage (Clausen and Yang 2007).

Despite all these advances, until now there has been no available chemical formulation containing these compounds for wood treatment against termites. Moreover, although they present a repulsive effect against *N. corniger*, their effects are not persistent and they did not lead to any contact toxicity (Paes et al. 2010).

Botanical insecticides: antimicrobial extracts and compounds

In most previously cited studies, the authors chose to use bioassays using the whole insect as a target, thus highlighting potent extracts or molecules. However, another process could be used to precisely search for compounds or extracts acting on a selected mechanism of action, as exemplified by Bulmer et al. (2009) with the glycomimetic molecule D-δ-gluconolactone, as above cited in this review. Thus, in-depth studies of *N. corniger* biology could be helpful for the discovery of targeted alternatives to non-specific pesticides.

Another specific approach based on natural processes is searching for phytochemicals targeting termites bacterial gut community. Even if some publications describe antimicrobial activities of compounds isolated from *Nasutitermes* sp. (Zhao et al. 2004; Siderhurst et al. 2005; Coutinho et al. 2009; Coutinho et al. 2010; Nirma et al. 2013), few articles describe the search for antibacterial products according to the perspective of an integrated pest management strategy against *Nasutitermes* species. However, a recent study showed that botanical lectins had an antibacterial effect on symbiotic bacteria from the gut of *N. corniger* (Napoleão et al. 2011). This approach could be of valuable interest, as similar results have also been achieved with other termite species (Table 2) (Maistrello et al. 2001; Maistrello et al. 2003; Ahmed et al. 2006; Doolittle et al. 2007).

Other biopesticides

Other strategy for finding new termiticidal compounds from other sources is considering soil actinomycetes fermentation products. These naturally occurring compounds were discovered from *Streptomyces* sp. culture broths. Some studies dealt with control of termites with these pesticides. Indeed, Chen et al. (2015) found that avermectin (abamectin and ivermectin) has optimal insecticidal properties to manage the subterranean termite *Reticulitermes speratus*. This strategy could be tested in the control of *Nasutitermes* but it has to be taken into account that these compounds have a large range of action and thus potentially noticeable impact in the field, being used in particular as an agent against worms, ticks, flies and other insects in veterinary applications (Duke et al. 2010).

Biological control of termites: entomopathogens and natural enemies

Nematodes, bacteria, and fungi have several interesting properties for the biological control of termites (Verma et al. 2009; Paiva et al. 2011). In recent years, the number of publications concerning the biological control of termites has increased dramatically (Chouvenc et al. 2011). In a critical review based on the study of 227 publications in which 427 bioassays were reported, Chouvenc et al. (2011) showed that these strategies were largely unsuccessful. Even if numerous examples of bacterial and nematode control can be found in the recent literature, mostly concerning subterranean termites (Grewal et al. 1999; Mo et al. 2006; Devi et al. 2007; Verma et al. 2009; Chouvenc et al. 2011), the authors raise questions about the fact that the described protocols may encounter poor biological relevancy, that the obtained data may often be improperly and overly optimistically interpreted, and that field bioassays often lack (Chouvenc et al. 2011). Other reasons that potentially explain this lacking of success may be linked to the remarkable way that termites have evolved to resist diseases due to biochemical and immunological strategies (Meikle et al. 2005), as also exemplified earlier in this review.

Among the few successes, biological control using fungi against *Nasutitermes* sp. (Table 2) should be mentioned (Ensaf et al. 2006; Chouvenc et al. 2011; Salas-Acuña 2012). A commercial formulation using the generalist enthomopathogenic fungus *Metarhizium anisopliae* (formerly flavoviride) (Metsch.) Sorokin (Bioblast^{TM}, Ecoscience Co.) was developed, but was unfortunately removed from the market in the early 2000s due to insufficient results (Verma et al. 2009; Chouvenc et al. 2011). The pathogenicity of the fungus is dependent on various factors, such as its capacity for germination and penetration on and through the cuticle as well as the insect's immune system to prevent fungus growth (Verma et al. 2009). A perspective to improve the efficacy of this enthomopathogen would therefore be to collect strains directly from native infected termites to improve the probability of isolating fungi having circumvented termites' adaptation strategies and natural defenses (Meikle et al. 2005). The challenge in termites' biological control is thus to develop more biologically relevant models, promote interdisciplinarity to finalize and conduct the assays, and add field and technology transfer studies (Chouvenc et al. 2011). As described earlier in their review, Chouvenc et al. (2011) also clearly appeal to an increase in research concerning termites' biology to find ways for pathogens to bypass termites' defense mechanisms.

In addition to entomopathogens, other biological control agents may involve some predators like ants, such as *Camponotus abdominalis,* one of the most aggressive species of this fierce natural enemy of termites (UNEP 2000). Another well-known predator of *N. corniger* is the hemipteran *Salyavata variegata* nymph (Reduviidae), which captures termite workers with the help of traps made of empty carcasses of previous prey and carton crumbs (McMahan 1982). However, the investigation of natural predators as control agents did not reveal any commercial potential (Chouvenc et al. 2011).

3.3 Not only a pest!

As with other termite species, *N. corniger* is a decomposer insect that plays a fundamental role in the decomposition process and nutrient cycling by aerating the soil, recycling plant matter and fixing nitrogen (Vasconcellos and Moura 2010). The presence of these insects also indicates the good health of an ecosystem, and they can be considered as bioindicators of its actual function (Täyasu et al. 1994; Paiva et al. 2011). Moreover, the presence of termites has a positive impact on biodiversity, termitariophile organisms, or insects depending on the nest structure for shelter, food or reproduction, thus being maintained in the environment (Jaffe et al. 1995; Santos et al. 2010). Eventually, arboreal nests may also provide homes for other animals, such as birds and bats (Postava-Davignon et al. 2010).

Concurrently with playing a role in dynamic environmental processes, *N. corniger* can also provide services to mankind, acting as a source of active secondary metabolites, particularly antimicrobial compounds. Inspired from its traditional use as a medicine in Northeastern Brazil, aqueous extracts from *N. corniger* were studied and shown to exhibit low antimicrobial activity against *Escherichia coli* aminoglycoside-resistant strains, but presented interesting synergist activities with antibiotics (Coutinho et al. 2009; 2010). Extracts from *N. corniger* could therefore be used as sources of compounds to bypass bacterial resistance mechanisms. Other results highlighted antibacterial (Zhao et al. 2004) or antifungal (Bulmer and Crozier 2004) activities for compounds isolated from *Nasutitermes* species. Eventually, active compounds can also be obtained through termites' symbionts, such as the antifungal compounds tyroscherin and N-methyltyroscherin, isolated from *Pseudallescheria boydii*, a saprophytic fungus frequently found in soil and water, but that was isolated in this case from *Nasutitermes* sp. (Nirma et al. 2013). In addition to appealing to the preservation and the pharmacochemical study of this species, these examples highlight the fact that improving the knowledge of termites, and more particularly *N. corniger* biology, could lead to a marked improvement, not only in the pest management field but also in the continuous search for new antimicrobial compounds.

4. Conclusion

Nasutitermes is the most species-rich termite genus, with a complex taxonomic history, and a growing number of known species present in all biogeographical regions. *Nasutitermes corniger*, which is the type-species of the genus, is an urban and agricultural pest, and also an invasive species, with a remarkable ability to adapt to a variety of habitats and food sources. Controversially, ecological and human health problems potentially arising from the use of synthetic chemical substances, particularly if the label guidelines are not strictly followed, are the limiting factor for their use. However, the extensive use of botanical or biological insecticides remains up to date unconclusive because of their ineffectiveness or their poor durability in external wood exposure cases. In the continuous effort to develop safe and effective methods for conehead termite management, we therefore believe that a paradigm shift is necessary and that sustained efforts must be performed in the field of termite biology. Alongside an increase in field bioassays, improvement in this knowledge is the key to more elaborate pertinent models and integrated strategies, targeting both the insect and its symbionts.

Eventually, integrated management rather than eradication is necessary in the native zones of occurrence of this termite. Although it is considered to be a pest, the termite is clearly an essential component of ecosystems as well as a potential source of valuable compounds that could contribute to the improvement of human health. Thus, the perspective remains open concerning *Nasutitermes* species study and management, and exciting discoveries are still to be made.

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Figure 1: Cumulative number of valid species of *Nasutitermes* since 1758.

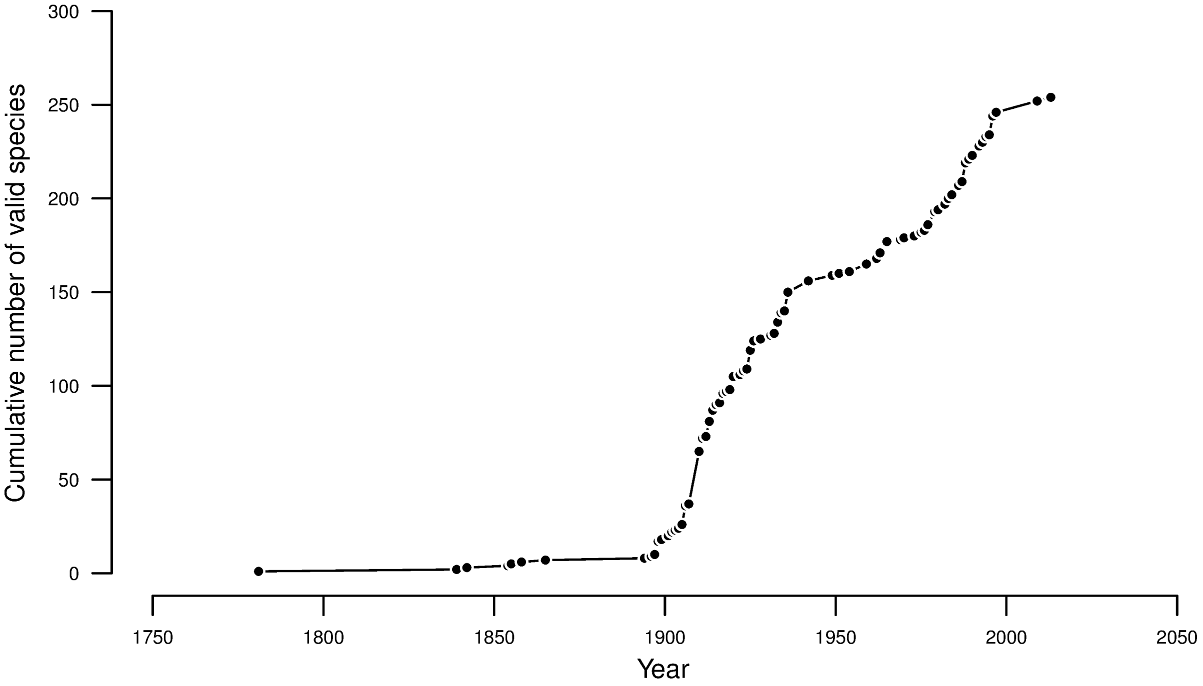

Figure 2: Geographical distribution of *Nasutitermes corniger*. This termite is native of Central and South America and the Caribbean islands, and is invasive in the Bahamas, Florida and New Guinea (according to Scheffrahn et al. and Evans et al.).[7,9]

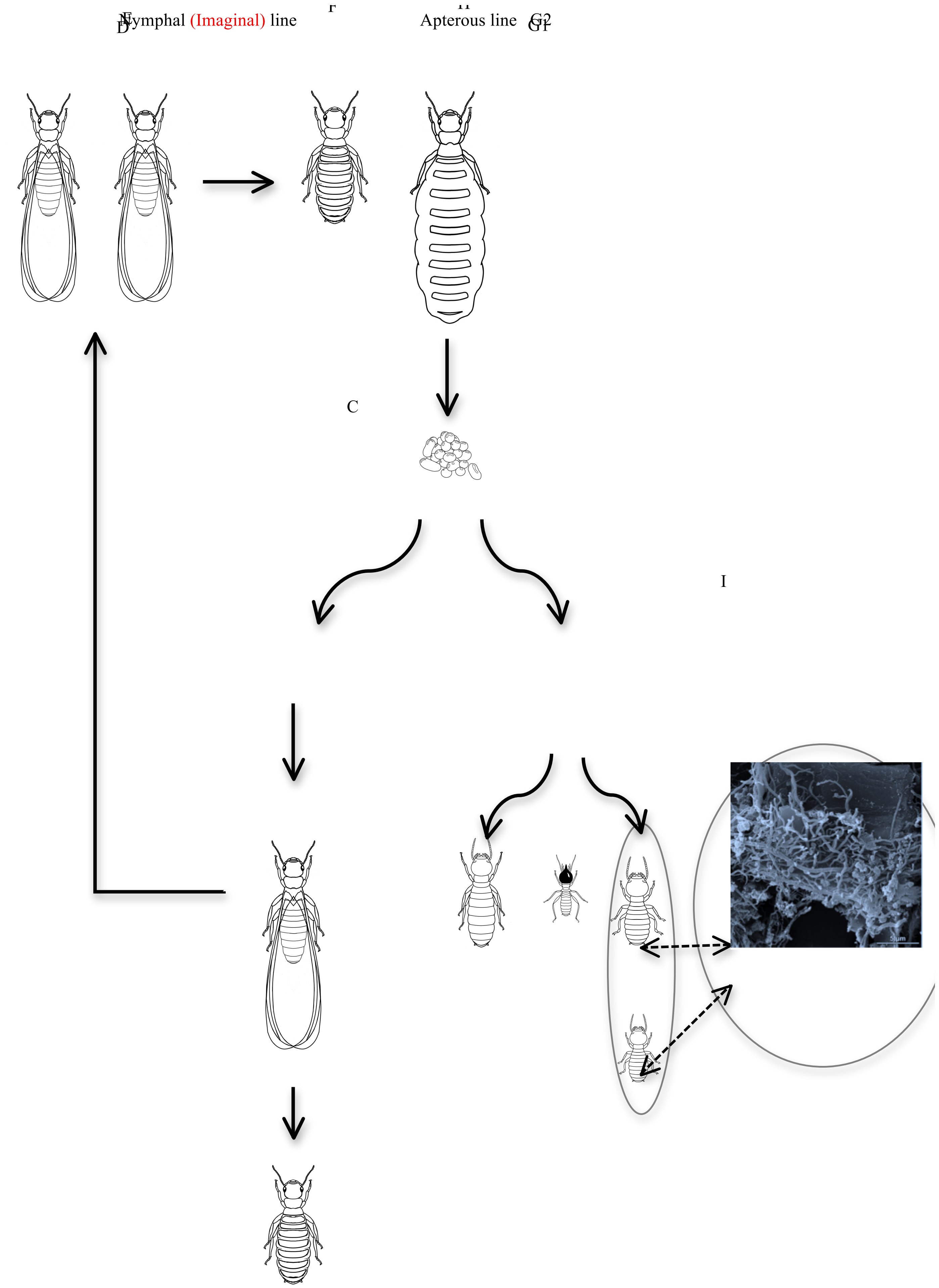

Figure 3: *Nasutitermes corniger*'s colony with the king (A), queen (B), eggs (C), alate (D), adultoid (E), ergatoid (F), large (G1) and small (G2) workers, soldier (H), and gut's microbiome (photo according to Mikaelyan et al. 2014) (I).

Dotted arrows indicate symbiotic relationships. Gray circles indicate targets of all pest management strategies found in the literature.

Figure 4: Soldier (left) and major worker (right) of *Nasutitermes corniger*, same magnification. © Copyright 2016 R. Constantino.

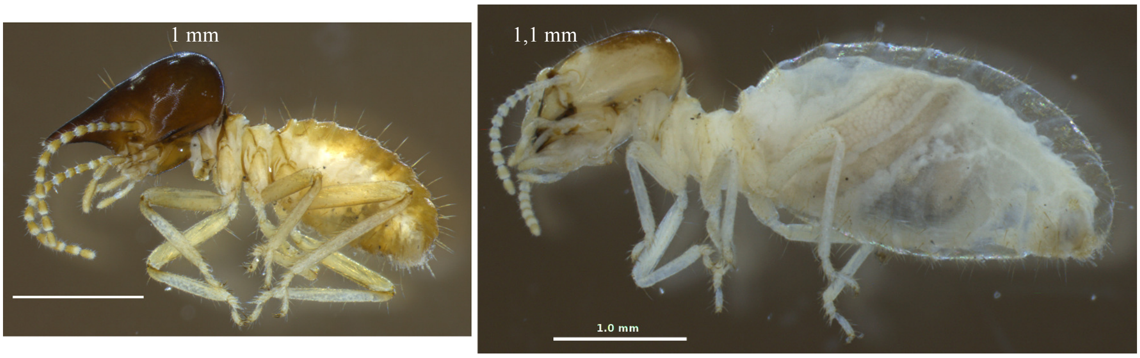

Figure 5: Arboreal nest of *Nasutitermes corniger* on a cacao tree. © Copyright 2016 R. Constantino.

Table 1: Examples of the synthetic chemical products used for termite management.

Classes	Active compounds	References
Arsenic derivatives	Chromated copper arsenate (CCA) Arsenic trioxide Calcium arsenate	Schultz et al. 2007 Verma et al. 2009; UNEP 2000; Santana et al. 2010
Copper derivatives	Alkaline copper quat (ACQ) Copper azole Copper naphthenate	UNEP 2000; Schultz et al. 2007
Zinc derivatives	Zinc napthenate	UNEP 2000; Schultz et al. 2007
Borate formulations	Disodium octaborate tetrahydrate (DOT)	UNEP 2000; Schultz et al. 2007; Clausen and Yang 2007
Pyrethroids	Permethrin	UNEP 2000; Schultz et al. 2007
Neonicotinoids	Imidacloprid Thiamethoxan	Schultz et al. 2007; Scheffrahn et al. 2014
Phenylpyrazoles	Fipronil, Chlorfenapyr	Verma et al. 2009; UNEP 2000; Scheffrahn et al. 2014, Santana et al. 2010
Pyrethroid ethers	Silafluofen	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Organophosphate compounds	Chlorpyrifos Fenitrothion Phenthoate Triazophos	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Organochlorate compounds	Chlorothalonil	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Benzoylureas	Chlorfluazuron Diflubenzuron Hexaflumuron Triflumuron	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Anthralinic diamides	Chlorantraniliprole	Verma et al. 2009; UNEP 2000; Santana et al. 2010; Scheffrahn and Scherer 2013
Aminohydrazones	Hydramethylnon	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Spinosoids	Spinosad	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Sulfonamides	Sulfluramid	Verma et al. 2009; UNEP 2000; Santana et al. 2010
Organic and inorganic gas	Carbon dioxide Methyl bromide Phosphine Sulfuryl fluoride	Verma et al. 2009; UNEP 2000; Santana et al. 2010; Scheffrahn et al. 2014

Table 2: Sustainable management with antitermitic and antimicrobial botanicals and with entomopathogens.

Termite	Plant (Family)/part of plant or Entomopathogens (Family)	Activity	Active extracts / compounds	References
		Antitermitic botanicals		
N. corniger	*Diospyros dichroa* Sandw. (Ebenaceae)	Repellent activity (> 90%) at 3.2 µg/mm^2 (40 mg/ml)	Wood ethyl acetate extract	Pers. results based on Ganapaty et al 2004, Rodrigues 2010, and Boulogne et al 2011 previous works
N. corniger	*Lonchocarpus chrysophyllus Kleinhoonte (Fabaceae)*	Repellent activity (> 90%) at 3.2 µg/mm^2 (40 mg/ml)	Bark ethyl acetate and petroleum ether extracts	Pers. results (Boulogne et al. *in prep*)
N. corniger	*Myracrodruon urundeuva* Allemão (Anacardiaceae)/ heartwood	No repellent activity Contact toxicity (LC_{50}=0.248 mg/mL for workers and 0.199 mg/mL for soldiers)	Lectins	Sá et al. 2008
N. corniger	*M yracrodruon urundeuva* Allemão (Anacardiaceae)/ heartwood and bark	No contact toxicity Repellent activity	Crude methanolic extract	Sá et al. 2009
N. corniger	*Anadenanthera colubrina* (Vell.) Brenan (Fabaceae)/ heartwood	Contact toxicity (LC_{50} = 7.3 mg/mL for ethyl acetate extract , LC_{50} =67.4 mg/mL for cyclohexane extract after 4 days)	Cyclohexane and ethyl acetate extracts	Santana et al. 2010
N. corniger	*Hymenaea stigonocarpa* Hayne (Fabaceae)/ heartwood	Contact toxicity (LC_{50}=11.9 mg/mL after 4 days)	Cyclohexane extract	Santana et al. 2010
N. corniger	*Bowdichia virgilioides* Kunth, (Fabaceae)/ heartwood	Contact toxicity (LC_{50}=7.2 mg/mL after 4 days)	Alkaloidal extract	Santana et al. 2010
N. corniger	*Bowdichia virgilioides* Kunth, (Fabaceae)/ heartwood	Toxic (LC_{50}=12.2 mg/mL after 4 days) and repellent activities	Cyclohexane extract	Santana et al. 2010
N. macrocephalus	*Sextonia rubra* (Mez) Van der Werff (Lauraceae)/ heartwood	Contact toxicity (LC_{100}<1.9 µg/mm^2 after 72h)	Ethyl-acetate extract/ rubrynolide	Rodrigues et al. 2011
***Nasutitermes* sp**	*Bagassa guianensis* Aubl. (Moraceae), *Erisma uncinatum* Warm. (Vochysiaceae), *Buchenavia parvifolia* Ducke (Combretaceae), *Dinizia excelsa* Ducke (Fabaceae) *Pouteria guianensis* Aubl. (Sapotaceae)/ wood	Wood impregnation conferred durability to *Cecropia* sp. (Urticaceae) and *Simarouba amara* Aubl. (Simaroubaceae) woods		Barbosa et al. 2007; Peres Filho et al. 2006
N. macrocephalus	*Diospyros dichroa* Sandw. (Ebenaceae)/ wood	Contact toxicity (LC_{100}<1.9 µg/mm^2 and 5.6 µg/mm^2 after 72h)	Methanolic extract and Ethyl acetate extract.	Harun and Labosky 1985; Rodrigues 2010
N. corniger	*Bauhinia monandra* Kurz (Fabaceae)/ roots	Contact toxicity (LC_{50}= 0.09 mg/mL for workers and 0.395 for soldiers after 12 days)	Lectins	Souza et al. 2011
N. corniger	*Opuntia ficus-indica* (L.) Mill. (Cactaceae)/ cladodes	Contact toxicity (LC_{50}=0.116 mg/mL for workers and 1.5 for soldiers)	Lectins	Paiva et al. 2011
N. corniger	*Moringa oleifera* Lam. (Moringaceae)/ seeds	No repellent activity Contact toxicity at 1.0 and 1.5 mg/mL	Lectins	Paiva et al. 2011
N. corniger	*Myracrodruon urundeuva* Allemão (Anacardiaceae)/ leaves	Contact toxicity (LC_{50}=0.374 to 0.974 mg/ml on workers and 0.432 to 0.787 mg/ml on soldiers)	Lectins	Napoleão et al. 2011
N. corniger	*Cladonia verticillaris*	Contact toxicity	Lectins	Silva et al. 2009

	(Cladoniaceae) / lichen	(LC$_{50}$= 0.196 mg/mL on workers and 0.5 mg/mL on soldiers after 10 days)		
N. corniger	*Microgramma vaccinifolia* (Langsd. & Fisch.) Copel. (Polypodiaceae)/ rhizome	Contact toxicity Ability to disrupt trypsin-like protease, acid phosphatase, and cellulase activities in termite's gut	Lectins	Lima et al. 2014
***Coptotermes formosanus*, *Coptotermes gestroi*, *Reticulitermes speratus*, *Macrotermes bellicosus*, *Macrotermes nigeriensis*, *Odontotermes obesus*,**	*Azadirachta indica* A. Juss. (Meliaceae) *Ricinus communis* L. (Euphorbiaceae)	Contact toxicity , metabolic poison, repellent or antifeedant activities		Sharma et al. 1991; Grace and Yates 1992; Serit et al. 1992; Ivbijaro et al. 1993; Delate and Grace 1995; Chuanchuan et al. 1998; UNEP 2000; Yunling et al. 2009; Sharma et al. 2011; Tahiri et al. 2011; Himmi et al. 2013
Antimicrobial botanicals				
N. corniger	*Myracrodruon urundeuva* Allemão (Anacardiaceae)/ bark, heartwood and leaf	Antibacterial activity on gut's symbiotic bacteria (MIC from 62.5 to 250 mg/mL)	Lectins	Napoleão et al. 2011
Microtermes obesi	*Withania somnifera* (L.) Dunal (Solanaceae), *Croton tiglium* L. (Euphorbiaceae) and *Hygrophila auriculata* Schumach.) Heine (Acanthaceae) */* seeds and leaves	Reduction of colonies number of bacterial symbionts		Ahmed et al. 2006
Coptotermes formosanus	*Chrysopogon zizanioides (L.) Roberty (syn.Vetiveria zizanioides* (L.) Nash) (Poaceae)	Reduction number of hindgut flagellate species (more specially *Pseudotrichonympha grassii*, an important cellulolytic flagellate protist)	Oil/ Nootkatone	Maistrello et al. 2003; 2011
Coptotermes formosanus	*Azadirachta indica* A. Juss. (Meliaceae)	Reduction of population of *P. grassii* and *Spirochaetes*	Azadirachtin	Doolittle et al. 2007
Entomopatogens				
***Nasutitermes* sp.**	*Termitaria coronata* (Deuteromycetes, Termitariales)			Ensaf et al. 2006
***N. corniger* and *Nasutitermes* sp.**	*Metarhizium* sp			Chouvenc et al. 2011; Salas-Acuña 2012