

Beyond soldiers: Defensive roles of workers in Neotropical Syntermitinae termites

Edimar Agnaldo Moreira¹

¹ Federal University of Alfenas, Institute of Natural Sciences, Alfenas, Minas Gerais, Brazil

Correspondence: Federal University of Alfenas, Alfenas, Minas Gerais, Brazil. E-mail: edimaragnaldomor@gmail.com

Submitted: July 26, 2026

DOI: 10.14295/bjs.v6i4.967

Accepted: September 05, 2026

URL: <https://doi.org/10.14295/bjs.v6i4.967>

Published: September 08, 2026

Abstract

Termite defence is often described through soldier morphology and secretions, yet colony protection also depends on workers that detect, confront, isolate and repair threats. This review examined the evidence for worker defensive participation in Neotropical Syntermitinae, with emphasis on behavioural, structural and alarm-related functions. A structured public-source literature search was conducted on 25 August 2026 across scholarly web indexing, PubMed, SciELO, Scopus, Web of Science, publisher pages, biological archives, institutional repositories, taxonomic catalogues and backward-forward citation chasing. Searches combined current and historical taxonomic names with terms for workers, defence, aggression, alarm, nest repair, and termite-termite interactions. After eligibility screening, taxonomic harmonisation, duplicate and derivative-report removal, and source verification, 41 curated records were evaluated and 11 independent primary sources directly documented worker participation in defensive contexts. The evidence covered 14 current species in eight genera, but was strongly concentrated in *Cornitermes cumulans* and Brazilian systems. Workers acted as an agonistic caste in nestmate and heterospecific encounters, participated in collective alate protection, contributed to alarm-associated responses, and built or restored barriers after nest damage or competitive tunnel contact. Recent studies on worker head and salivary glands in *C. cumulans* add a mechanistic context, but do not yet demonstrate a defensive chemical function. A single global meta-analysis was not defensible because the available studies reported incompatible response units, including instantaneous aggression counts, survival functions, repair time, binary observations, and qualitative field accounts. The synthesis therefore supports a broader view of Syntermitinae defence in which soldiers remain specialised, but workers provide essential tactical and structural functions. Future experiments should quantify worker-only and worker-soldier responses with shared outcomes, colony-level replication, and openly available summary data.

Keywords: defence, termite behaviour, worker caste, nest repair, Syntermitinae.

Além dos soldados: Papéis defensivos dos operários em cupins Neotropicals Syntermitinae

Resumo

A defesa dos cupins é frequentemente descrita com base na morfologia e nas secreções dos soldados; entretanto, a proteção da colônia também depende dos operários, que detectam, confrontam, isolam e reparam ameaças. Esta revisão examinou as evidências sobre a participação defensiva dos operários em Syntermitinae neotropicais, com ênfase nas funções comportamentais, estruturais e relacionadas a sinais de alarme. Foi realizada uma busca estruturada na literatura de acesso público em 25 de agosto de 2026, abrangendo indexadores acadêmicos na web, PubMed, SciELO, Scopus, Web of Science, páginas de editoras, arquivos biológicos, repositórios institucionais, catálogos taxonômicos e rastreamento retrospectivo e prospectivo de citações. As buscas combinaram nomes taxonômicos atuais e históricos com termos relacionados a operários, defesa, agressividade, alarme, reparo de ninhos e interações entre cupins. Após a triagem de elegibilidade, harmonização taxonômica, remoção de duplicatas e relatos derivados, e verificação das fontes, foram avaliados 41 registros selecionados, dos quais 11 fontes primárias independentes documentaram diretamente a participação de operários em contextos defensivos.

As evidências abrangeram 14 espécies atuais pertencentes a oito gêneros, mas estavam fortemente concentradas em *Cornitermes cumulans* e em sistemas brasileiros. Os operários atuaram como uma casta agonística em encontros com indivíduos da própria colônia e com espécies heteroespecíficas, participaram da proteção coletiva de alados, contribuíram para respostas associadas a sinais de alarme e construíram ou restauraram barreiras após danos ao ninho ou contato com túneis de colônias concorrentes. Estudos recentes sobre a cabeça e as glândulas salivares dos operários de *C. cumulans* acrescentam um contexto mecanístico, mas ainda não demonstram uma função química defensiva. Uma única meta-análise global não foi considerada metodologicamente justificável, uma vez que os estudos disponíveis apresentaram unidades de resposta incompatíveis, incluindo contagens instantâneas de agressividade, funções de sobrevivência, tempo de reparo, observações binárias e relatos qualitativos de campo. Dessa forma, a síntese sustenta uma visão mais ampla da defesa em Syntermitinae, na qual os soldados permanecem especializados, enquanto os operários desempenham funções táticas e estruturais essenciais. Experimentos futuros devem quantificar as respostas exclusivamente de operários e aquelas realizadas por operários em conjunto com soldados, utilizando desfechos padronizados, replicação em nível de colônia e dados-resumo disponibilizados abertamente.

Palavras-chave: defesa, comportamento de cupins, casta operária, reparo de ninho, Syntermitinae.

1. Introduction

Defence in termites is commonly framed as a consequence of soldier specialization. Soldiers possess conspicuous mandibular, frontal-gland, or head-capsule adaptations and are central to many descriptions of colony protection. This emphasis is justified, but it can obscure the distributed character of defence in a colony, where workers are the numerically dominant caste, maintain the nest matrix, interact continuously with brood and reproductives, and are often the first individuals to encounter a disturbance. Across termites, worker participation may include attack, avoidance, alarm, recruitment, sealing, and repair; these actions are not equivalent, but all can alter the outcome of a threat (Sillam-Dussès et al., 2023; Thorne, 1982).

Syntermitinae provides a particularly informative setting in which to revisit worker participation. The subfamily is a Neotropical lineage with substantial morphological and ecological diversity, and recent phylogenetic and taxonomic studies have refined its limits and historical combinations (Hellemans et al., 2024; Rocha et al., 2012; Rocha et al., 2017; Rocha; Canello, 2022). Two studies published in 2026 further refined genus-level phylogeny and added a new Amazonian species, illustrating that the taxonomic frame remains dynamic (Lucena et al., 2026; Pontes-Nogueira et al., 2026). Soldiers in many syntermitines are highly specialised, yet their defensive output is expressed within colonies in which workers can contact intruders, modify nest architecture and coordinate with soldiers. The explanatory question is therefore not whether soldiers defend the colony, but when workers perform independently detectable defensive functions and how their roles vary among threats and taxa.

The available literature gives several reasons to avoid a soldier-only interpretation. In *Cornitermes cumulans*, workers recognize and attack non-nestmates, and aggression is associated with lower survival in mixed groups (Marins; DeSouza, 2008). Workers also participate in responses to nest damage and in the construction of barriers during interspecific tunnel encounters (Cristaldo, 2010; Jost et al., 2012). Field observations indicate collective protection of exposed alates by workers and soldiers in *C. cumulans* and *Silvestritermes euamignathus* (Mill, 1983). These examples represent different ecological problems and cannot be collapsed into a single behavioural endpoint, but together they show that worker participation is neither anecdotal nor restricted to one experimental setting.

A second reason for synthesis is the emergence of mechanistic work on workers. Recent syntheses of Neotropical worker morphology and experimental neuroanatomy in *Procornitermes arauji* likewise emphasize the breadth of worker phenotypes, whereas soldier differentiation is associated with reduced higher-order brain regions (Rocha et al., 2019; Valadares et al., 2023). Morphological studies in *C. cumulans* have described a worker intramandibular gland and caste-specific salivary-gland patterns, generating hypotheses about task specialization, protection and communication (Costa-Leonardo et al., 2025a; Costa-Leonardo et al., 2025b). Such findings should not be treated as evidence that workers use a defensive secretion; however, they make an explicit assessment of the behavioural evidence more timely. The distinction is important because well-documented worker chemical defence occurs in other termite lineages, including *Neocapritermes* and soldierless *Ruptitermes*, but these outgroups cannot be used as direct proof for Syntermitinae (Costa-Leonardo et al., 2019; Costa-Leonardo et al., 2020).

Here, we synthesise direct evidence for defensive roles of workers in Neotropical Syntermitinae. We ask: (i) which worker behaviours or constructions have been observed in a defensive context; (ii) which species, threats

and experimental settings are represented; (iii) whether reported outcomes permit a common quantitative effect size; and (iv) which experimental gaps currently constrain comparative inference. The aim is not to displace soldiers from models of termite defence, but to establish a more complete colony-level account of defensive labour.

2. Materials and Methods

2.1 Review scope and search strategy

The review used a structured evidence-synthesis protocol focused on currently recognised Neotropical Syntermitinae. The search was completed on 25 August 2026 and combined public scholarly web indexing, PubMed, SciELO, Scopus, Web of Science, publisher and archive pages, institutional repositories, the Termite Catalog, and targeted backward-forward citation chasing. Searches were conducted in English, Portuguese, and Spanish. Core strings combined the taxon with worker-related terms and defensive contexts, for example: "Syntermitinae workers defense termite aggression bite alarm", "mandibulate nasute worker defense termite", and Portuguese and Spanish equivalents. Genus- and species-level searches were then applied to current *Syntermitinae* genera, particularly *Cornitermes*, *Procornitermes*, *Silvestritermes*, *Syntermes*, *Embiratermes*, *Curvitermes*, and *Labiotermes*. Historical combinations, including *Armitermes euamignathus* and *Armitermes chagresi*, were retained during retrieval and mapped after screening.

The corpus is reported as a structured, reproducible public-source evidence synthesis, not as a systematic review or a claim of complete export-based coverage from subscription databases. Exact search strings and the screening log were retained in the project spreadsheet. Searches of scholarly web indexes, PubMed, SciELO, publisher and archive pages, repositories, taxonomic catalogues, and backward-forward citation chasing were used to map the available evidence. Because a complete Scopus and Web of Science export-and-deduplication workflow was not undertaken, PRISMA 2020 reporting was not applied. Interpretive literature used to update the Introduction and Discussion was searched to 3 September 2026; broad comparative termite studies that did not provide direct Syntermitinae evidence were excluded from the evidence-map totals.

2.2 Eligibility criteria and taxonomic harmonisation

Records were eligible as direct evidence when they reported field observations, laboratory bioassays, behavioural experiments, theses, dissertations or proceedings involving a current Syntermitinae taxon and directly described or measured a worker response to a predator, intruder, non-nestmate, heterospecific termite, nest breach, competitive tunnel contact or alate exposure. Primary outcomes were worker biting or attack, agonistic contact, threat display, recruitment or alarm, injury or mortality of opponents, and threat-associated barrier construction or repair. Ordinary construction, corpse management, foraging and movement were excluded unless explicitly linked to an immediate threat. Taxonomic names were harmonised using current phylogenetic and taxonomic sources while preserving the source combination in the extraction record (Rocha et al., 2017; Rocha; Canello, 2022).

2.3 Screening, independence and data extraction

For each retained source, we recorded study identity, current and original species names, country or biome when available, defensive context, field or laboratory setting, worker and soldier composition, number of colonies and trials, outcome family, reported quantitative information, and links between potentially duplicate reports. Conference abstracts, theses, and subsequent articles were linked when they appeared to use the same underlying study. The extraction unit was study by current species by defensive context by contrast. A source was retained for quantitative synthesis only when its outcome, comparator, and sampling information could be reconciled with another independent source without redefining the biological response. For clarity, a record was a retrieved bibliographic item, whereas an independent primary source was a non-duplicate source or linked derivative group contributing direct evidence.

2.4 Evidence synthesis and quantitative feasibility

Evidence was first grouped as active mechanical defence, alarm or recruitment, collective protective behaviour, and passive or structural defence. Candidate quantitative effects included log response ratios for compatible continuous outcomes, standardised mean differences for comparable aggression measures, and log risk ratios or

odds ratios for binary outcomes. We did not calculate a pooled effect when studies differed in observation unit, temporal scale, treatment structure, or caste composition. This decision was made a priori to avoid a numerically precise but biologically uninterpretable estimate.

3. Results

3.1 Evidence corpus and taxonomic coverage

The structured public-source search produced a curated corpus of 41 records. After eligibility screening, taxonomic harmonisation, duplicate and derivative-report removal, and source verification, 11 independent primary sources directly documented worker participation in a defensive context (Figure 1; Table 1). The resulting evidence map represented 14 current species in eight genera: *Cornitermes*, *Curvitermes*, *Cyrlillitermes*, *Embiratermes*, *Labiatermes*, *Procornitermes*, *Silvestritermes* and *Syntermites*. *Cornitermes cumulans* was the most frequently represented taxon, appearing in studies of nestmate recognition, stress-modified aggression, nest disturbance, tunnel competition, structural repair and host-inquiline encounters. A recent mixed-caste study of *C. cumulans* and *Curvitermes odontognathus* encounters was retained as contextual evidence but excluded from the direct worker map because survival outcomes could not be attributed to workers independently of the accompanying soldiers (Martins, 2021).

The corpus was geographically concentrated. Most direct studies were conducted in Brazil, frequently in Cerrado-associated systems or in laboratory assays using colonies collected in southeastern or central Brazil. This concentration reflects the history of Syntermitinae research rather than a demonstration that worker defence is restricted to Brazilian taxa. Historical and comparative records broadened taxonomic coverage, but detailed quantitative outcomes remained concentrated in a small number of study systems.

3.2 Forms of worker defensive participation

Active agonism was the most frequently documented function (Figure 2). In worker-only groups of *C. cumulans*, non-nestmates elicited more aggressive contacts than nestmates, and the mixed groups exhibited lower survival, demonstrating that workers can discriminate and impose a direct cost on non-colony individuals (Marins & DeSouza, 2008). Earlier and later sources likewise treated workers as the relevant interacting caste in termite-termite encounters, including *Embiratermes chagresi* and host-inquiline systems involving *Cornitermes* and *Curvitermes* (Clemente et al., 2021; Costa, 2015; Thorne, 1982).

Structural defence was the second recurrent function. Worker activity was associated with nest responses after physical disturbance and with the sealing of competing tunnel networks after contact between *C. cumulans* and *Procornitermes araujo* (Cristaldo, 2010; Jost et al., 2012). Studies of *C. cumulans* mound walls further document rapid repair after experimental or natural damage, linking worker construction to the restoration of a defensive boundary rather than to routine nest building alone (Redford, 1984; Guimarães, 2018).

The retained records also included collective protection and alarm-associated responses. Mill (1983) described workers and soldiers forming protective aggregations around exposed alates of *C. cumulans* and *S. euamignathus*. In a broad comparative study of termite alarm communication, *Labiatermes labralis* showed measurable worker-associated vibroacoustic and disturbance responses (Sillam-Dussès et al., 2023). Moreira (2015) documented species-specific worker attack, threat, and alarm responses in experimental intruder assays across five Syntermitinae species, underscoring that worker participation may vary with both species and opponent identity.

3.3 Quantitative synthesis feasibility

The studies did not yield a common metric for a global pooled analysis. Some reported instantaneous or cumulative aggression counts, some used survival curves or median survival time, others measured repair time or barrier formation, and several were natural-history observations. Caste composition also varied from worker-only arenas to mixed worker-soldier groups. For example, the *C. cumulans* nestmate-recognition assay used five colonies, 15 colony combinations, and repeated observations of 20 workers per arena, whereas the host-inquiline literature reported pair-specific survival outcomes in worker-only encounters across multiple host-inquiline combinations (Clemente et al., 2021; Costa, 2015; Marins & DeSouza, 2008). These designs are informative but are not exchangeable observations. Worker-only host-inquiline assays in the Costa (2015) thesis provide high-value species coverage, but pair-specific sample sizes and effect estimates require further extraction

from figures or underlying data before any species-level effect size is calculated.

3.4 Mechanistic context and evidentiary boundaries

Recent studies of *C. cumulans* workers provide an anatomical basis for future functional tests. A worker intramandibular gland and caste-associated salivary-gland variation have been described, but neither study quantified worker defence during an experimentally defined threat (Costa-Leonardo et al., 2025a; Costa-Leonardo et al., 2025b). Accordingly, these findings were retained as mechanistic context rather than as direct worker-defence effects. No primary record in the retained Syntermitinae corpus demonstrated worker autothysis or a defensive secretion with a confirmed behavioural function. This absence should be interpreted as a research gap, not as evidence that such functions are biologically impossible.

Table 1. Direct primary evidence for worker defensive participation in Neotropical Syntermitinae.

Source	Current taxa	Context	Main worker finding	Quantitative status
Moreira (2015)	<i>C. cumulans</i> ; <i>E. festivellus</i> ; <i>P. araujoi</i> ; <i>S. euamignathus</i> ; <i>S. obtusus</i>	Laboratory intruder assays	Attack, threat and alarm responses; species and opponent variation	Figures and tests available; no directly harmonised effect size
Marins (2007)	<i>C. cumulans</i>	Worker assays under handling stress	Stress modified nestmate and non-nestmate aggression	Thesis tables/figures require final extraction
Marins; DeSouza (2008)	<i>C. cumulans</i>	Worker-only nestmate recognition	Higher aggression and lower survival in non-nestmate groups	Quantitative, but unique outcome scale
Cristaldo (2010)	<i>C. cumulans</i>	Physical nest disturbance	Workers contributed to responses linked to soldier proportion	Quantitative thesis extraction pending
Mill (1983)	<i>C. cumulans</i> ; <i>S. euamignathus</i>	Field observations of alate swarms	Workers and soldiers formed protective cordons	Qualitative/semiquantitative
Thorne (1982)	<i>E. chagresi</i>	Termite-termite encounters	Workers treated as an agonistic caste	Species-specific trial extraction required
Jost et al. (2012)	<i>C. cumulans</i> ; <i>P. araujoi</i>	Competitive tunnel networks	Fighting followed by worker-driven walling-off	Mortality and walling outcomes potentially extractable
Guimaraes (2018)	<i>C. cumulans</i>	Experimental mound-wall damage	Rapid repair of artificial breaches	Repair-time extraction pending
Redford (1984)	<i>C. cumulans</i>	Natural mound damage	Worker repair after predator-associated damage	Field frequencies plus qualitative repair
Sillam-Dussès et al. (2023)	<i>L. labralis</i>	Comparative disturbance assays	Worker-associated vibroacoustic alarm response	Species-level supplemental extraction required
Costa (2015); Clemente et al. (2021)	Eight Syntermitinae species	Worker-only host-inquiline encounters	Survival cost and injury in heterospecific contact	High yield; pair-specific data still need transcription

Source: Authors, 2026.

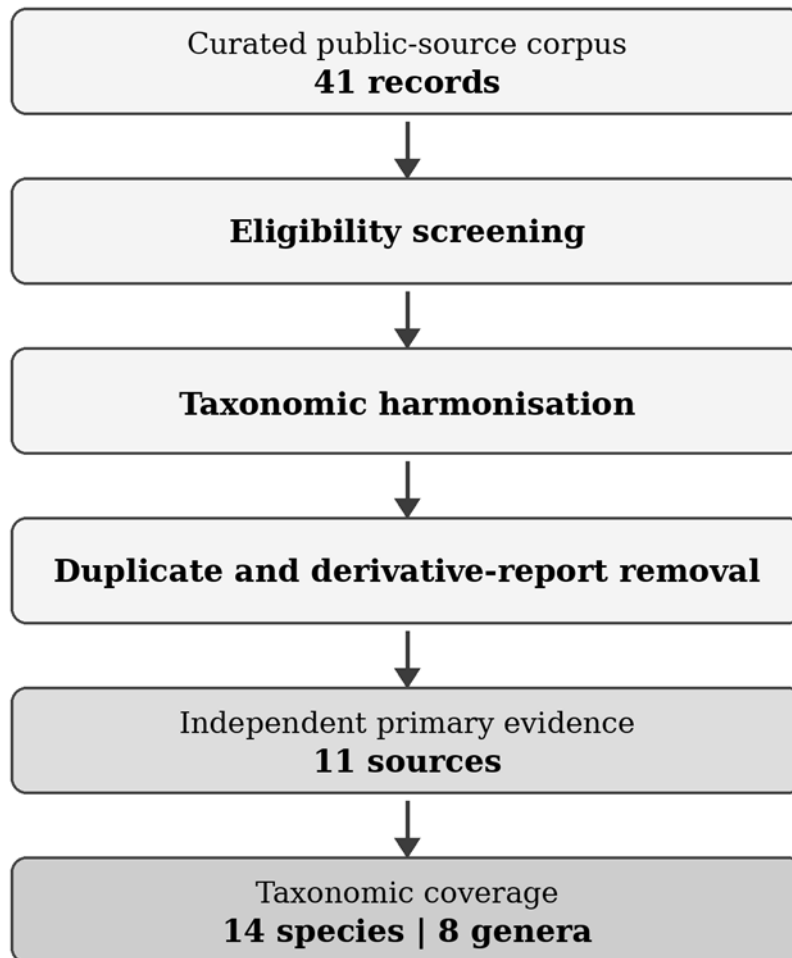


Figure 1. Evidence-corpus workflow and synthesis decision. The 41 records shown comprise the screened corpus used to construct the direct evidence map; only independent primary sources with a directly observed worker-defence context entered the evidence map. Broader comparative studies added solely for interpretation in the Discussion were not included in these totals. Source: Authors, 2026.

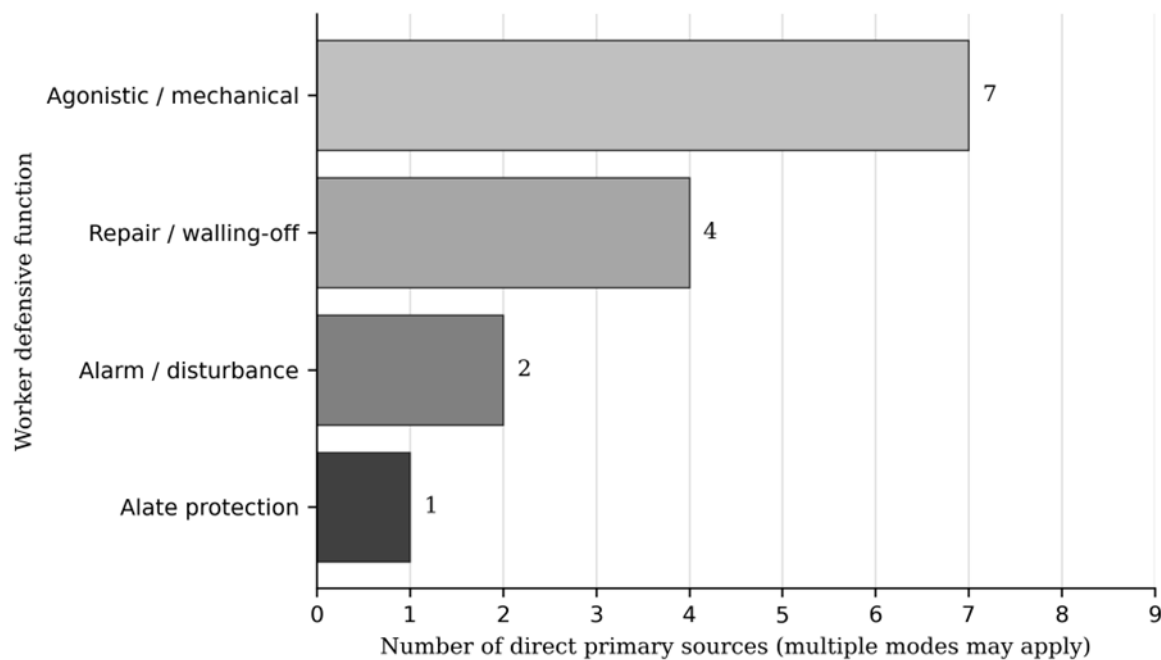


Figure 2. Functional distribution of direct primary sources documenting workers' defensive participation. A source may contribute to more than one functional category. Source: Authors, 2026.

Table 2. Why direct evidence was synthesised by outcome family rather than as a single pooled effect.

Outcome family	Reported units	Representative sources	Reason not pooled
Aggression/attack	Instantaneous or cumulative counts, behavioural scores	Marins (2007); Marins; DeSouza (2008); Moreira (2015)	No common scale, transformation, or variance information across studies
Survival/mortality	Time-to-event models, median survival, proportions	Marins; DeSouza (2008); Costa (2015); Clemente et al. (2021)	Within-study models differ; pair-level sample sizes incomplete in multi-species source
Repair/walling	Latency, wall structure, binary barrier formation	Cristaldo (2010); Jost et al. (2012); Guimaraes (2018)	Threat type and response unit differ
Alarm/protection	Signal timing/rate, presence of protective cordon	Mill (1983); Moreira (2015); Sillam-Dussès et al. (2023)	Mixed qualitative and species-level data; no compatible comparator

Source: Authors, 2026.

4. Discussion

The evidence reviewed here supports a colony-level rather than a soldier-exclusive interpretation of defence in Syntermitinae. Across the retained sources, workers did not merely accompany soldiers: they attacked non-nestmates and heterospecific termites, restored damaged boundaries, isolated competitor tunnels, protected exposed alates and participated in alarm-related responses. These functions are ecologically distinct, but they share a common consequence: workers modify the probability that an intruder reaches a resource, a nest compartment or a vulnerable colony member. The correct conclusion is therefore not that workers replace soldiers, but that defensive performance emerges from interactions among specialised soldiers, abundant workers and nest architecture.

The repeated representation of *C. cumulans* is simultaneously a strength and a limitation. It provides unusually detailed evidence that workers can recognise non-nestmates, impose mortality costs, respond to disturbance and repair protective walls. Yet this concentration makes it unsafe to generalise every mechanism to Syntermitinae as a whole. Several genera are represented only by historical observations, one comparative record, or a single

species-level row within a broader study. Current taxonomy further underscores the need for care: historical *Armitermes* and *Embiratermes* combinations may not correspond to the names used in contemporary phylogenetic work (Rocha; Canello, 2022).

Structural responses deserve particular attention because they connect worker labour to a defensive outcome without requiring workers to inflict injury directly. In mound builders, rapid repair reduces the duration of exposure to predators, desiccation and intruders. In tunnel-network experiments, walling-off can terminate contact after a confrontation and thereby reduce continued losses. These behaviours should be coded as defence only when the threat linkage is explicit; otherwise, routine construction would inflate the apparent evidence base. This distinction provides a practical rule for future syntheses and experimental designs.

A recent field experiment provides a useful comparison for interpreting this structural evidence. In the nasutitermitine *Constrictotermes cyphergaster*, soldiers arrived first at damaged nest walls and were followed by a time-dependent turnover of worker morphotypes; worker recruitment also declined as nest volume increased (Andrade et al., 2024). This species lies outside Syntermitinae and was therefore not added to the direct-evidence corpus. Nevertheless, its results show why a repair assay should not be reduced to a single count of workers: arrival order, worker phenotype, nest size, breach dimensions, and closure time can each change the inferred defensive role. Equivalent measurements are needed for *C. cumulans* and other Syntermitinae mound builders.

Alarm-associated records likewise require a colony-level interpretation. The comparative study that included *Labiotermes labralis* found that workers and soldiers mostly share a vibroacoustic repertoire, while soil-feeding *Labiotermes* lacked a detectable alarm-pheromone channel; worker participation in alarm can therefore be informative even when it is expressed through vibration rather than a worker secretion (Sillam-Dussès et al., 2023). Experimental work in other termite lineages strengthens the need to control social composition. Worker vibroacoustic responses to breach-like stimuli varied with species and with soldier presence or soldier extracts (Janowiecki et al., 2024), whereas worker attack against ants in *Reticulitermes chinensis* depended on queen presence rather than soldier presence (Li et al., 2026). These outgroup studies do not establish the same mechanisms in Syntermitinae, but they make a clear prediction: worker defence should be measured in caste- and royal-composition treatments rather than inferred from mixed groups alone.

The recent morphology of worker head and salivary glands in *C. cumulans* is promising, but it should be interpreted at the appropriate evidentiary level. Gland structure, polyethism and a plausible protective role do not identify a secreted compound, its release context or its behavioural effect. This is especially important because worker chemical defence is well demonstrated in other termite lineages, where workers may release toxic secretions or use autothytic mechanisms (Costa-Leonardo et al., 2019; Costa-Leonardo et al., 2020). A functional demonstration for Syntermitinae will require chemical characterization coupled to caste-resolved behavioural and survival assays. The worker-gland studies should therefore be treated as a mechanistic hypothesis generator, not as retrospective confirmation of defensive chemical function.

Nest architecture is also a plausible source of heterogeneity. Across termite species, worker movement is strongly associated with nesting strategy: foragers moved more and sustained locomotion longer than one-piece nesters in standardized arenas (Kikuchi et al., 2025). That study did not test defensive performance and cannot be used to infer a Syntermitinae effect. It does, however, provide an ecological rationale for recording nest type, foraging exposure, and structural access points alongside behaviour. Such variables may determine which workers first encounter a breach or opponent and whether an observed response is attack, alarm transmission, escape, or boundary repair. More broadly, a phylogenetic comparison found lower soldier investment in strong-point than in counter-attack strategies and an association between defence and foraging strategy (Satoh et al., 2026). Because that analysis operated at the genus level and focused on soldiers, it provides a comparative prediction rather than direct evidence for Syntermitinae workers.

The failure to calculate a global pooled effect is a result of the review, not a failure of the literature. A pooled mean would have mixed the frequency of bites, a survival-model coefficient, a repair delay, the occurrence of walling, and a field observation of alate protection. Such a number would conceal exactly the biological diversity that the review aims to explain. The appropriate next step is a set of outcome-specific meta-analyses once new studies report compatible effect estimates. Candidate subsets include worker aggression toward nestmates versus non-nestmates, survival in standardised heterospecific encounters and repair latency after standardised breaches.

Future work should use factorial designs that separate worker-only, soldier-only and mixed-caste responses while keeping colony identity explicit as a replicate. When feasible, queen- or royal-presence treatments should be incorporated because social composition can modify worker attack and alarm responses in other termite lineages. The same threat should be presented across species with predefined observation windows, response definitions,

and accessible mean, variance, and sample-size data. Behavioural endpoints should be complemented by opponent injury, survival, arrival order at the breach, and post-threat barrier formation. For chemical hypotheses, head-region extracts or identified compounds should be tested against solvent controls and independently scored for worker and soldier responses. These design features would convert the present evidence map into a data set suitable for comparative inference.

5. Conclusions

Workers make direct, repeated and ecologically diverse contributions to defence in Neotropical Syntermitinae. They function as agonistic responders, builders of protective barriers, participants in collective protection and components of alarm-associated responses. The existing evidence is taxonomically concentrated and methodologically heterogeneous, so it supports a structured synthesis rather than a global meta-analysis. A worker-inclusive framework better captures how Syntermitinae colonies defend their members and nest resources, while identifying the experimental standardisation needed for a future quantitative meta-analysis.

6. Acknowledgments

The author thanks the curators of public repositories, journals, and taxonomic resources that made the underlying literature traceable and accessible.

7. Authors' Contributions

Edimar Agnaldo Moreira: conceptualization, methodology, investigation, data curation, formal analysis, visualization, writing – original draft, writing – review & editing, and publication.

8. Conflicts of Interest

No conflicts of interest.

9. Ethics Approval

Not applicable. This study synthesised published and repository-accessible literature and did not involve new collection of animals or human participants.

10. Artificial Intelligence Statement: Declaration of Generative AI and AI-Assisted Technologies in the Writing Process

OpenAI ChatGPT was used to support English-language editing, organization of the literature-extraction database, and preliminary structuring of tables and figure concepts. No scientific data were generated or altered by AI. The author critically reviewed, verified, and approved all text, data, references, tables, figures, and interpretations and assumes full responsibility for the accuracy and integrity of the manuscript. AI tools are not authors and do not assume any responsibility for the content.

11. References

- Andrade, M. R. L., Eloi, I., de Oliveira, M. H., & Bezerra-Gusmão, M. A. (2024). Dynamics of dimorphic workers of *Constrictotermes cyphergaster* (Blattodea: Termitidae) during nest repair. *Journal of Insect Science*, 24(1), 1. <https://doi.org/10.1093/jisesa/iead118>
- Clemente, L. O., Constantino, R., Costa, D. A., & DeSouza, O. (2021). The role of mandible morphology in termite inquilinism. *Entomologia Experimentalis et Applicata*, 169(12), 1103-1112. <https://doi.org/10.1111/eea.13103>
- Costa, D. A. (2015). Custos do encontro entre cupins inquilinos e hospedeiros (Blattodea: Isoptera). PhD thesis. Universidade Federal de Viçosa, Viçosa, Brazil.
- Costa-Leonardo, A. M., da Silva, I. B., Janei, V., Esteves, F. G., dos Santos-Pinto, J. R. A., & Palma, M. S. (2019). Worker defensive behavior associated with toxins in the Neotropical termite *Neocapritermes*

- braziliensis* (Blattaria, Isoptera, Termitidae, Termitinae). *Journal of Chemical Ecology*, 45(9), 755-767. <https://doi.org/10.1007/s10886-019-01098-w>
- Costa-Leonardo, A. M., Janei, V., Bacci, L. M. G., & da Silva, I. B. (2025a). Morphology of the head-associated exocrine glands in *Cornitermes cumulans* with the description of a novel gland for the worker caste. *Tissue and Cell*, 93, 102688. <https://doi.org/10.1016/j.tice.2024.102688>
- Costa-Leonardo, A. M., Janei, V., & da Silva, I. B. (2025b). Salivary glands associated with polyethism in the termite *Cornitermes cumulans* (Isoptera, Termitidae, Syntermitinae). *Zoomorphology*, 144(3), 53. <https://doi.org/10.1007/s00435-025-00740-4>
- Costa-Leonardo, A. M., da Silva, I. B., Poiani, S. B., dos Santos-Pinto, J. R. A., Esteves, F. G., da Silva, L. H. B., & Palma, M. S. (2020). Proteomic components provide insights into the defensive secretion in termite workers of the soldierless genus *Ruptitermes*. *Journal of Proteomics*, 213, 103622. <https://doi.org/10.1016/j.jprot.2019.103622>
- Cristaldo, P. F. (2010). Mecanismos de defesa em ninhos de cupins (Insecta: Isoptera). MSc thesis. Universidade Federal de Viçosa, Viçosa, Brazil.
- Guimarães, M. P. M. (2018). A manutenção da muralha: o investimento diferencial no reparo de danos em paredes de cupinzeiros. MSc thesis. Universidade Federal de Viçosa, Viçosa, Brazil.
- Hellemans, S., Rocha, M. M., Wang, M., Romero Arias, J., Aanen, D. K., Bagnères, A.-G., Buček, A., Carrijo, T. F., Chouvenec, T., Cuezco, C., Constantini, J. P., Constantino, R., Dedeine, F., Deligne, J., Eggleton, P., Evans, T. A., Hanus, R., Harrison, M. C., Harry, M., Josens, G., Jouault, C., Kalleshwaraswamy, C. M., Kaymak, E., Korb, J., Lee, C.-Y., Legendre, F., Li, H.-F., Lo, N., Lu, T., Matsuura, K., Maekawa, K., McMahon, D. P., Mizumoto, N., Oliveira, D. E., Poulsen, M., Sillam-Dussès, D., Su, N.-Y., Tokuda, G., Vargo, E. L., Ware, J. L., Šobotník, J., Scheffrahn, R. H., Canello, E., Roisin, Y., Engel, M. S., & Bourguignon, T. (2024). Genomic data provide insights into the classification of extant termites. *Nature Communications*, 15(1), 6724. <https://doi.org/10.1038/s41467-024-51028-y>
- Janowiecki, M. A., Jandák, V., Brothánek, M., Jiříček, O., Vargo, E. L., & Šobotník, J. (2024). Effect of soldiers on vibroacoustic alarm response in workers of subterranean termites (Blattodea: Rhinotermitidae). *Insectes Sociaux*, 71(1), 75-83. <https://doi.org/10.1007/s00040-023-00945-0>
- Jost, C., Haifig, I., de Camargo-Dietrich, C. R. R., & Costa-Leonardo, A. M. (2012). A comparative tunnelling network approach to assess interspecific competition effects in termites. *Insectes Sociaux*, 59(3), 369-379. <https://doi.org/10.1007/s00040-012-0229-7>
- Kikuchi, K., Bourguignon, T., & Mizumoto, N. (2025). Nesting strategy reflects individual worker movement in termites. *Movement Ecology*, 13(1), 88. <https://doi.org/10.1186/s40462-025-00612-y>
- Li, X.-Y., Wang, H., Khan, Z., Xiao, Y.-L., & Dong, Y.-N. (2026). Defensive behavior of termite workers depends on the queen rather than soldiers in *Reticulitermes chinensis* (Blattodea: Heterotermitidae). *Insectes Sociaux*. <https://doi.org/10.1007/s00040-026-01125-6>
- Lucena, E. F. de, Cysneiros, G., Figueiredo, R. E. C. R. de, Rocha, M. M. da, Haugaasen, T., Peres, C. A., & Vasconcellos, A. (2026). *Mapinguaritermes marizalensis*, a new species of Syntermitinae (Blattodea, Termitidae) from Brazilian Amazon. *Zootaxa*, 5814(4), 498-512. <https://doi.org/10.11646/zootaxa.5814.4.3>
- Marins, A. (2007). Agressividade em *Cornitermes cumulans* (Kollar) (Insecta: Isoptera) submetidos a estresse. MSc thesis. Universidade Federal de Viçosa, Viçosa, Brazil.
- Marins, A., & DeSouza, O. (2008). Nestmate recognition in *Cornitermes cumulans* termites (Insecta: Isoptera). *Sociobiology*, 51(1), 1-9.
- Martins, E. G. (2021). Habituation facilitates host-inquiline cohabitation in termites. MSc thesis. Universidade Federal de Viçosa, Viçosa, Brazil. <https://doi.org/10.47328/ufvbbt.2021.031>
- Mill, A. E. (1983). Observations on Brazilian termite alate swarms and some structures used in the dispersal of reproductives (Isoptera: Termitidae). *Journal of Natural History*, 17(3), 309-320. <https://doi.org/10.1080/00222938300770231>
- Moreira, E. A. (2015). Glândula frontal dos soldados de Syntermitinae (Termitidae): uma abordagem ultraestrutural e comportamental dessa nova subfamília de cupins. MSc thesis. Universidade Federal de Alfenas, Alfenas, Brasil.
- Pontes-Nogueira, M., Aguilera, S. M., Palma-Onetto, V., Wang, M., Hellemans, S., Scheffrahn, R. H., Canello,

- E. M., Bourguignon, T., & Carrijo, T. F. (2026). Phylogeny and biogeography of the termite genus *Labiotermes* Holmgren, 1912 (Isoptera, Syntermitinae) suggests predominant sympatric speciation. *Journal of Biogeography*, 53(1), e70124. <https://doi.org/10.1111/jbi.70124>
- Redford, K. H. (1984). The termitaria of *Cornitermes cumulans* (Isoptera, Termitidae) and their role in determining a potential keystone species. *Biotropica*, 16(2), 112-119. <https://doi.org/10.2307/2387842>
- Rocha, M. M., Canello, E. M., & Carrijo, T. F. (2012). Neotropical termites: revision of *Armitermes* Wasmann (Isoptera, Termitidae, Syntermitinae) and phylogeny of the Syntermitinae. *Systematic Entomology*, 37(4), 793-827. <https://doi.org/10.1111/j.1365-3113.2012.00645.x>
- Rocha, M. M., Morales-Corrêa e Castro, A. C., Cuezco, C., & Canello, E. M. (2017). Phylogenetic reconstruction of Syntermitinae (Isoptera, Termitidae) based on morphological and molecular data. *PLoS ONE*, 12(3), e0174366. <https://doi.org/10.1371/journal.pone.0174366>
- Rocha, M. M., Cuezco, C., Constantini, J. P., Oliveira, D. E., Santos, R. G., Carrijo, T. F., & Canello, E. M. (2019). Overview of the morphology of Neotropical termite workers: history and practice. *Sociobiology*, 66(1), 1-32. <https://doi.org/10.13102/sociobiology.v66i1.2067>
- Rocha, M. M., & Canello, E. M. (2022). Updated taxonomy of Syntermitinae (Blattodea: Isoptera, Termitidae), with the description of three new genera. *Zootaxa*, 5138(4), 445-463. <https://doi.org/10.11646/zootaxa.5138.4.6>
- Satoh, A., Planas-Sitjà, I., Cronin, A. L., & Mizumoto, N. (2026). Variation in soldier investment is linked to the evolution of termite soldier defense strategies. *Evolutionary Ecology*, 40(2), 21. <https://doi.org/10.1007/s10682-026-10386-3>
- Sillam-Dussès, D., Jandák, V., Stiblik, P., Delattre, O., Chouvenc, T., Balvín, O., Cvačka, J., Soulet, D., Synek, J., Brothánek, M., Jiříček, O., Engel, M. S., Bourguignon, T., & Šobotník, J. (2023). Alarm communication predates eusociality in termites. *Communications Biology*, 6(1), 83. <https://doi.org/10.1038/s42003-023-04438-5>
- Thorne, B. L. (1982). Termite-termite interactions: workers as an agonistic caste. *Psyche: A Journal of Entomology*, 89(1-2), 133-150. <https://doi.org/10.1155/1982/86584>
- Valadares, L., da Silva, I. B., Costa-Leonardo, A. M., & Sandoz, J.-C. (2023). Differentiation of workers into soldiers is associated with a size reduction of higher-order brain centers in the Neotropical termite *Procornitermes araujoii*. *Scientific Reports*, 13(1), 18279. <https://doi.org/10.1038/s41598-023-45221-0>

Funding

Not applicable. No external funding was received specifically for this literature synthesis.

Institutional Review Board Statement

Not applicable. This review did not involve human participants or newly collected animals.

Informed Consent Statement

Not applicable.

Copyrights

Copyright for this article is retained by the author(s), with first publication rights granted to the journal.

This is an open-access article distributed under the terms and conditions of the Creative Commons Attribution license (<http://creativecommons.org/licenses/by/4.0/>).