



Invasive termites and their growing global impact as major urban pests

Thomas Chouvenc

While termites play important ecological roles, a fraction of species have strong invasive capabilities and represent urban pests of economic importance worldwide. Their invasive potential is exacerbated by human activities such as maritime transport, with privately owned boats serving as key vectors for local and global termite dispersal, particularly for *Cryptotermes* and *Coptotermes* pest species. Land establishment by invasive termites can remain undetected for decades, often making eradication attempts too late to succeed. Ultimately, invasive termite species will likely continue to spread at the global scale, and recent new invasive records point toward an underestimation of their actual current invasive status.

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Current Opinion in Insect Science 2025, 69:101368

This review comes from a themed issue on **Pests and Resistance**

Edited by **Warren Booth** and **G. Veera-Singham**

Available online 21 March 2025

<https://doi.org/10.1016/j.cois.2025.101368>

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Introduction

Termites, with over 3000 described species, represent almost a third of the terrestrial arthropod biomass [1–3] and fulfill critical ecological functions by feeding on plant material at different degrees of decomposition [4]. However, a fraction of termite species (<100) have status as structural pests, primarily within the Kalotermitidae ('drywood' termites) and Heterotermitidae ('subterranean' termites) families [1,5•]. As of 2010, the damage to structures resulting from termite infestation and the associated treatment cost and repair was estimated to have an annual economic impact of over \$US 40 B worldwide [6]. The global impact of *Coptotermes formosanus* alone as an invader was since estimated to

range between \$US 20.3 B and \$US 30 B [7,8]. Inevitably, the ongoing spread of some of the most invasive termite pest species will continue to impose a growing economic impact [9].

As eusocial insects, termite colonies have a distinct reproductive division of labor, where a queen and a king often monopolize the reproductive output of the colony, while sterile workers and soldiers focus on resource acquisition and defense of the family unit; however, many termite lineages have complex breeding structures [10]. Once a colony has reached maturity, it produces winged individuals (alates) that disperse over short distances and establish new colonies in favorable nesting sites. While rare, and only for a few termite species, a small group of isolated termites may survive and reproduce as a potentially effective invasive propagule [11]. In addition, for a colony to survive human-mediated dispersal events, it requires a set of traits that varies among invaders [12]. Ultimately, social insect species that possess such invasive potential have a negative impact, both ecological and economic, that can be disproportionate compared to other species [13,14].

For termites specifically, 28 species have been recorded as successful invaders worldwide [15]. Arguably, the propensity of some species to thrive within highly urbanized environments and survive prolonged periods of time on human-made maritime vessels has dramatically accelerated their extensive spread across the world, particularly for *Cryptotermes*, *Incisitermes*, *Coptotermes*, *Reticulitermes* and *Heterotermes* [16–18]. Combined, these five genera represent the bulk of invasive termite species that are the primary cause of structural damage, though some species within other termite genera either have significant pest status restricted within their native area or have relatively lower invasive potential compared to the above genera [15].

In the past five decades, such invasive termite species have not only been recorded in numerous new locations around the world but have also continued to expand their distribution range in locations where they are already established. The predicted dispersal potential [19•] of these invaders raises concerns about their associated economic impact in the near future, which will only increase with their continued spread. Here, I discuss the factors that may heighten the global impact of such invasive termite pest species in the decades to come.

Termite dispersals: past and present

Historical transoceanic dispersals

In a series of recent molecular phylogenetic studies [4,20–22], it was demonstrated that the current distribution of extant termite lineages is, in part, the result of repeated transoceanic dispersal events over the past 40 million years. Entire (or partial) termite colonies infesting a piece of wood may have rafted over oceans after environmentally catastrophic events (landslides into rivers/oceans, tsunamis, cyclones/hurricanes). Therefore, termite dispersals inherently occurred before global urbanization and termites may be predisposed to survive extended dispersal events on floating rafts [4,21,23]. Arguably, while successful transoceanic dispersals over geologic time were critical for the historical biogeography of termite lineages, they were relatively rare [4]. In modern times, fabricated maritime vessels create a situation where boats readily serve as artificial rafts for species with such predispositions, exponentially enhancing their dispersal abilities. Not only is transportation time functionally reduced by modern boats, but critical mass for rafting capacity may have changed from a handful per year (pre-human transportation times) to several millions per year (current times).

Urban adaptation

Termite species that cannot thrive within urbanized environments have little propensity to become structural pests and have little chance of being accidentally picked up and transported away [24]. On the contrary, invasive termite pest species have a peculiar affinity to associate themselves with human activity [1,12], and human population density is a relevant factor in using prediction models to determine future establishment potentials [19•]. In addition, urban microclimates (winter heating, irrigation, urban gardens, air-conditioning, urban tree canopy, etc.) can provide suitable establishment sites for some termite species despite being outside of their expected climatic range [25–28].

Drywood termites within *Cryptotermes* and *Incisitermes* (Kalotermitidae) can establish colonies in single pieces of wood not exposed to water within human goods and structures, such as furniture, which can be readily relocated when a household moves to a new residence [16]. The inherent biology of such species makes them readily capable of hitchhiking on human movement, undetected, and surviving in dry, air-conditioned environments [29–31].

For subterranean termites (Heterotermitidae) such as *Reticulitermes* and *Heterotermes*, their ability to forage in urban environments over long distances underground, with the establishment of secondary reproductives at multiple feeding sites, makes them capable of surviving with continued reproductive capacity even when a portion of the colony is separated and moved to a new

location [32]. Infested landscaping lumber or other large wood items with relatively small portions of a colony can therefore serve as effective propagules across urban environments [11,33,34•].

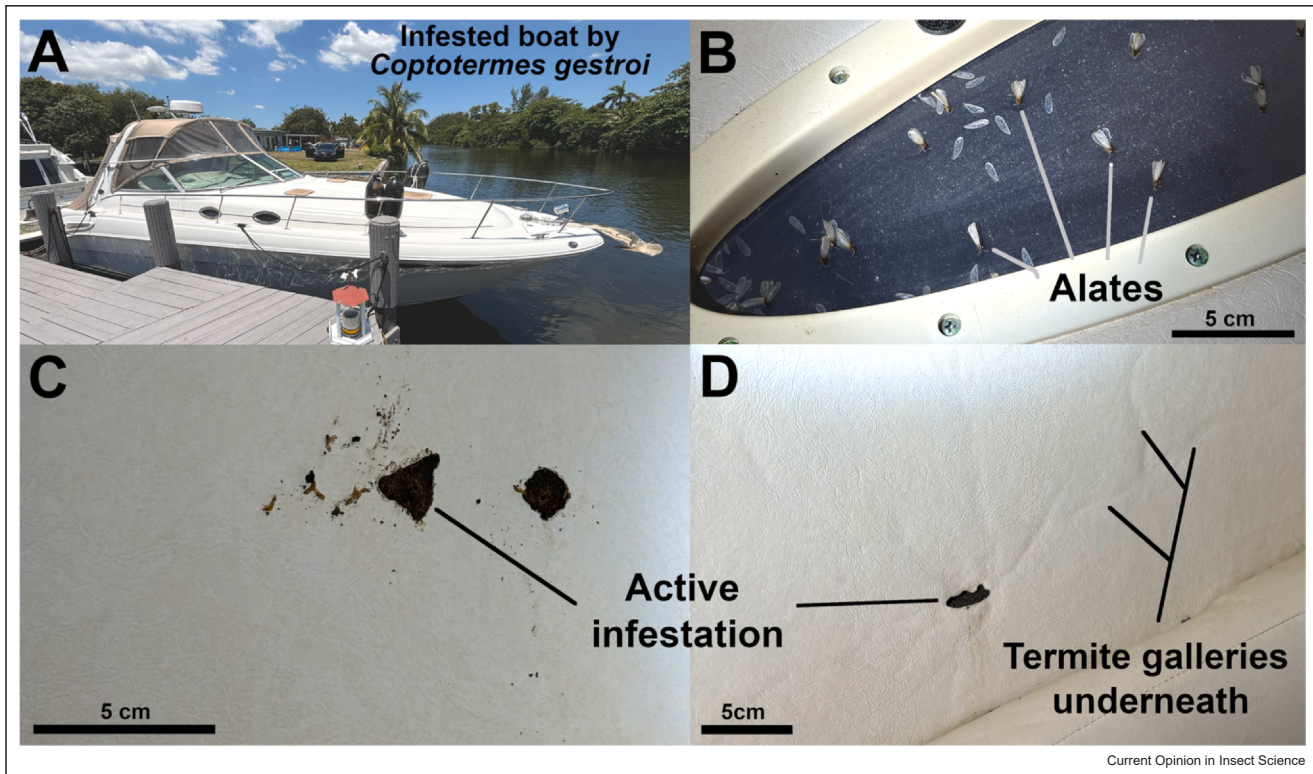
Coptotermes formosanus and *Co. gestroi* both thrive as major invasive structural and arboreal pests in urban and periurban environments [35•], as mature colonies rely on inundative dispersal flights to spread locally [36]. Through sheer numbers (*Coptotermes* synchronized dispersal flight events can involve millions of individuals), incipient colonies can establish at numerous nesting sites [37–39], including within commercial commodities shipments (horticultural trade) and recreational vehicles and boats [17,40•]. As a result, privately owned leisure boats are particularly effective vehicles for over-water dispersal of *Coptotermes* [41,42•] (Figure 1). Furthermore, and critical to their invasive success, the dispersal phenology of *Coptotermes* can minimize the Allee effect even when a single colony is the source of a new invasion from a boat [42•,43•]. Functionally, through a numbers game during inundative dispersal flights, local invasive populations can minimize the risk of a genetic bottleneck and maintain high rates of heterozygosity. By successfully establishing a sufficient number of colonies that cumulatively maintain the initial genetic diversity from the original invasive propagule, the population as a whole can tolerate the weeding out of colonies that would be subjected to the deleterious effect of inbreeding depression [39,43•].

Boat association as the main driver for global spread of termite invaders

It is common to detect new termite introductions at or adjacent to major port cities [18,42•]. The historical transfer of infested military equipment by boats has likely facilitated the spread of termite invaders around coastal military bases in various parts of the world [31,43–45]. Commodity trade and shipping is also a potential invasion route for termites, as infested material is recurrently intercepted at ports of entry [18]. However, the movement of privately owned recreational/leisure boats (yachts, luxury boats, small maritime-capable vessels) is not subjected to rigorous inspections for termite infestation, allowing for boat infestations to perdure for years, arguably making the private recreational boating industry one of the main drivers for the global dispersal of termite invaders (Figure 2).

Cryptotermes and *Coptotermes*, in particular, can readily infest boats during dispersal flight events and complete their life cycle within a handful of years within the boat itself [16,42•]. The growing colony becomes a potential propagule that can spread to various parts of the world and be a source of dispersal flights toward nearby coastal areas, as alates are attracted to urban lights at sunset [36,46]. Once established on land, the termite population grows in density

Figure 1



Example of a small privately owned maritime vessel infested by a *Coptotermes gestroi* colony, moored in a Florida canal. (a) Visual of the boat for scale. (b) Evidence of a recent dispersal flight within the boat. (c) Subterranean termite mud construction showing active infestation of the boat by a colony. (d) Outline of foraging galleries underneath the surface of the cabin material. Image credit: Hoffer Pest Solutions, Inc, with permission.

over decades, increasing the chances of these established termite colonies becoming the source of new boat infestations within local marinas/canals [17]. Such infested boats can then spread the termites further through serial bridgehead introduction events [18,34•,43•]. As a result, with few exceptions, new records of establishment for *Cryptotermes* and *Coptotermes* are first restricted to coastal areas [29,40•], before expanding further inland over time [35•]. Unfortunately, while privately owned boats are now known to be a primary cause for invasive termite dispersal, they remain poorly documented or reported upon discovery [17,42•], leading to a potential gross underestimation of the actual boat infestation rate in most areas at risk.

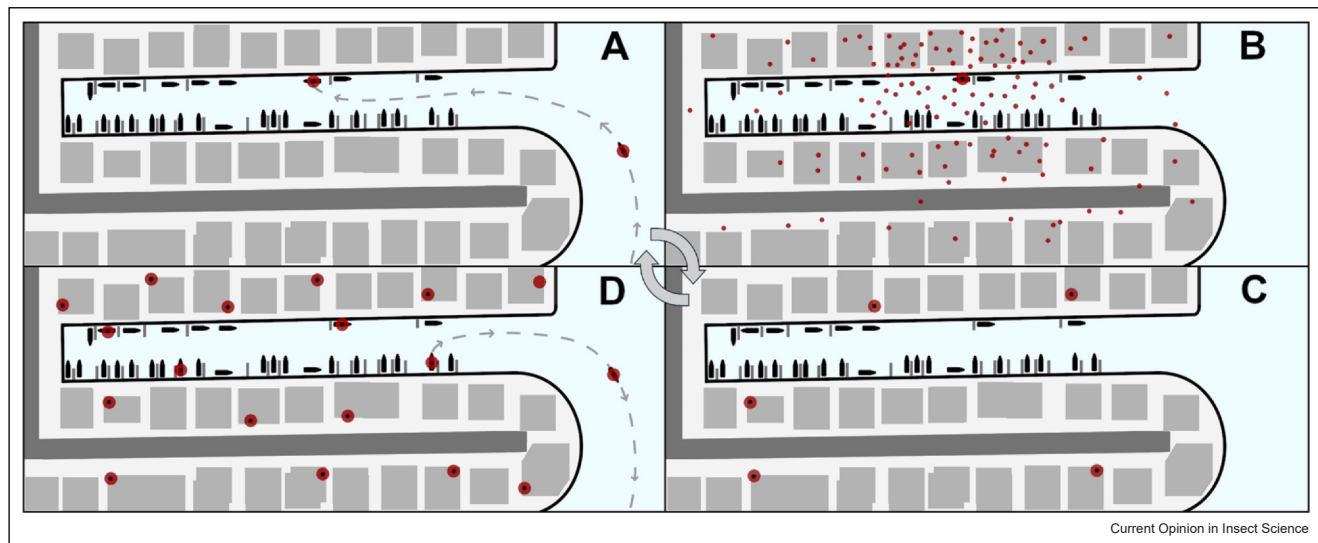
The continuous growth of the global private yacht and leisure boat industry implies an ongoing increase in propagule pressure for termite species that can use such maritime vessels as a gateway to transoceanic dispersals. Many tropical regions around the world are favored destinations for leisure boating activities, and it is therefore expected that *Cr. brevis*, *Co. formosanus*, and *Co. gestroi*, among a few other species, will continue to spread

extensively over time. All three species are solidly established in South Florida, often referred to as the 'yachting capital of the world.' All three species have been extensively established in urban south Florida [47], and privately owned vessels are commonly treated for one of these three species [17,42•]. One may argue that while Florida has long been a disproportionate recipient of invasive social insects [48,49], it is now in a prime position to serve as a bridgehead for enhanced dispersal for all three termite species to the rest of the world. Locations with similar leisure boat activities around the globe are therefore at equal risk of receiving such propagules and ultimately become bridgehead locations themselves (Figure 2).

Detection delay, local awareness, and expectations for eradication programs

There is often an extended interval between the initial time of arrival of a termite invader and the time of discovery of established populations. It often takes years, sometimes decades, before an established species can be noticed and reported. The lag in the detection of

Figure 2



Invasion scenario for *Coptotermes* sp. within a residential area, where boat access is possible via canals connected to the ocean nearby. **(a)** Arrival of an infested boat. **(b)** Dispersal event of alates from the infested boat. **(c)** Initial settlement of a few colonies within the surrounding coastal area, undetected and able to complete their life cycle to maturity. **(d)** Colony density increases over time within the area, including the occurrence of established colonies in locally moored boats. Some of these infested vessels may depart to new destinations and repeat the invasion cycle in a new locality. It may take more than a decade for a locality to switch from being 'recipient' to being 'exporter' of a given invasive termites species.

invasive termites can be especially long for several reasons. First, their cryptic nature makes them difficult to detect until extensive damage is discovered. Second, the life cycle of a termite colony is at least 4–5 years, so to complete dispersal flights and locally establish new colonies at sufficient densities to be detected can take decades. Finally, the initial lack of local expertise with such invaders (identification and control) may further aggravate such delay.

Termite invasions, such as by *Coptotermes*, can be metaphorically compared to extremely slow-motioned and silent hurricanes; they come by sea as a landfall, impacting urbanized coastline areas at first, and then expand further inland, potentially beyond urban areas, raising a wake of structural damage in their path, over several decades. The delay of the impact of invasive termites comes with an absence sense of urgency. Only a few localized communities are impacted at first and by the time the impact becomes noticeable and tangible, it is often too late to contain it. As a result, reactive 'eradication' program initiatives by local administrations usually come with high expectations but are unfortunately often set up far too late for feasible containment or control. It is therefore rather safe to assume that once a termite invader has been established, it is here to stay (and continue to expand its distribution), as is often observed for other invasive social insects [50].

One of the tools to help awareness about the spread of invasive termites and early detection is the establishment of monitoring/identification services in the form of 'citizen science' programs, as offered in Taiwan [51] and in Florida [47], which accelerate the detection of invasive termites beyond their existing documented range. Such programs can help prepare local governments and pest control providers to rapidly adapt and mitigate the evolving termite threat in their local communities.

Invasive termites and hybridization

Since 2010, observations of heterospecific pairing behavior in Florida of *Co. gestroi* and *Co. formosanus* during simultaneous dispersal flights raised concerns about the potential for hybridization between two of the most destructive termite species in the world [37,52,53]. The recent independent discoveries of F1 and F2 *Coptotermes* hybrid alates in Taiwan [54] and F1 alates in Florida [55] demonstrate the possibility of gene flow between the two species in urbanized areas. Hybrid *Coptotermes* temperature tolerance encompasses the range of both parental species [56], suggesting a wide global distribution potential. While the consequences of the discovery of hybrid *Coptotermes* in the field remain to be seen and may be merely a distracting anomaly for the time being, the possibility of greater evolutionary implications in the long term should not be ignored. Through repeated trial-errors of heterospecific mating events, it may only be a matter of time before viable

and fertile hybrid alates establish on a boat and make their way out of Florida or Taiwan [55].

Conclusion

Unequivocally, the ongoing global spread of invasive termite pest species is slowly leading to a partial homogenization of urban termite pests [19•]. While climatic conditions may be a primary restrictive factor for introduced species survival in non-native areas, the ongoing urbanization-associated changes at the local and global scale are conducive to augmented termite damage potential in the near future [19•,57]. The economic impact of invasive termites has been rising over the decades and will continue to intensify as they continue to establish in new locations, via human-mediated transportation, primarily by privately owned leisure boats. However, establishing local awareness programs in areas with known invasive termite pest populations could facilitate early detection of boat infestations and minimize the occurrence of boat-mediated dispersal events.

Once established in new locations, the management of termite pest species can be most challenging. The socio-political context of newly invaded areas varies greatly, and local regulatory agencies may enable or prevent the development of, and access to, management tools [58]. In addition, the inevitable delay of attempted control of termite invaders on impacted communities often comes as ‘too little too late’, making eradication programs unlikely to succeed. The long series of recent establishment records of termite invaders supports that we are only ‘playing catch-up’ with the ongoing reality of global termite dispersal [25,26,28–31,47,59–65]. For many locations around the world, the question is therefore not ‘if’ invasive termites will eventually establish, but rather ‘when’ they will establish — if they have not already.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The author declares that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported in part by United State Department of Agriculture - National Institute of Food and Agriculture (USDA-NIFA) Hatch Project No. FLA-FTL-006285. Thanks to Rudolf Scheffrahn and Johnalyn Gordon for their input on a previous version of this manuscript.

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