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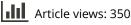
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West Indian drywood termite, *Cryptotermes brevis*, in Australia: current understanding, ongoing issues, and future needs

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ABSTRACT

West Indian drywood termite, *Cryptotermes brevis*, is an invasive pest of particular importance due to its global distribution, cryptic lifecycle, potential to spread and economic impact. The species has been under a Queensland Government-funded prevention and control program since its detection in the 1960s, but this program ceased in 2021. It is now increasingly important to develop alternative methods for managing this pest and slowing its spread. This review synthesises information on *C. brevis*, its commercial impact, and the unique factors contributing to its global spread. We highlight areas where information on the species is lacking and identify corresponding research needed to fill these gaps. Results from these future research efforts may help improve the management of this termite in terms of improved detection and spot-control of colonies and creating a better understanding of at-risk timber species.

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KEYWORDS drywood termite; eradication; fumigation; history; Queensland; control

Introduction

West Indian drywood termite, Cryptotermes brevis (Walker) (Blattodea: Kalotermitidae), is a significant economic pest that infests structural timber and sheltered wood, including framing, cladding, flooring and furniture (Scheffrahn et al. 2009). It is one of the world's most destructive termites, feeding on sound dry wood while living inside it; it is very cryptic and has small colony sizes. The species can produce secondary reproductives (neotenics) frequently, allowing colonies to survive without a primary king and queen (McDonald et al. 2022a). The ability to attack very dry, solid timber also means that colonies nest in structurally strong material that creates protection from most predators. Like some other termite species, C. brevis is invasive, being transported to new locations in furniture, wooden articles, pallets, dunnage, sailboats, and ships and planes (Scheffrahn et al. 2009; Evans et al. 2013). Currently, C. brevis is the most widely distributed drywood termite and is found in Australia, North America, Central America, the Caribbean, South America, many Atlantic islands, and Africa (Evans et al. 2013). In Australia, the first occurrences of C. brevis were in Sydney, New South Wales, in the 1940s, but those colonies were rapidly identified and destroyed. Later, in the 1960s, established infestations were confirmed in Queensland. The species has now been present in Queensland for decades, and it has been managed by a Queensland Government prevention and control program under the Diseases in Timber Act 1975 until 2016 and then under the Biosecurity Act 2014 (Peters 1990a; McDonald et al. 2022a). However, the control measures deployed failed to eradicate the pest in the state, with the termite now firmly established and new infestations common (Evans 2010); nevertheless, the measures have succeeded in limiting the spread of the pest.

Here, we review current knowledge of *C. brevis* biology, history and management in Australia, identify knowledge gaps, and make recommendations for research on the species in light of a recent shift in responsibility in the control of *C. brevis* from government to property owners and pest controllers (PPM 2021; Horwood et al. 2022).

Economic importance

Despite the economic importance of C. brevis, few reports highlight the economic damage it causes around the world. In 2005, the species was calculated to be responsible for around USD 120 million (AUD 170 million) of the USD 300 million annual cost of drywood termites in the United States of America (Nunes et al. 2005). South Africa has long had mandates requiring the treatment of all susceptible wood in termite-infested regions and restrictions on timber movement, causing high annual costs (Coaton 1948; Coaton and Sheasby 1979). The islands of the Azores, Portugal, have been considerably affected by the pest; little effort was made on those islands to eradicate the termite after its introduction (Borges et al. 2014). The termites are now widespread there, costing the government an estimated EUR 51 million (AUD 75 million) to treat infested buildings and up to EUR 175 million to reconstruct the same structures (Guerreiro et al. 2014). In Queensland, more than 890 buildings and other wooden materials have been fumigated under the governmentfunded prevention and control program since its inception in 1968. In 2007, C. brevis control efforts in Queensland were estimated to have cost more than AUD 4.2 million (Peters and Fitzgerald 2007), which, with an ongoing annual cost of around AUD 500 000 (Horwood 2008), suggests that more than AUD 10 million has been spent on control to date. With the cessation of the program in 2021, appropriate and effective management strategies are now needed to prevent the further spread of the pest and reduce its financial impacts.

Biology of Cryptotermes brevis

The biology of insect pests can be exploited for their management – knowledge about a pest's life cycle, behaviour, mating systems, feeding habits and environmental requirements can assist in developing control strategies. This section highlights aspects of the biology of *C. brevis* that affect its detection, monitoring and management.

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Like other subterranean and drywood termites, C. brevis has a typical termite life history (Figure 1) and symbiosis with various bacteria and protists (Desai et al. 2010). However, unlike subterranean termites, C. brevis has a relatively simple form of eusocial organisation (Korb 2008). Colonies are essentially small and exist entirely within drywood excavations lacking the elaborate nest architecture seen in most subterranean termite colonies (Noirot and Darlington 2000; Grace et al. 2009). There is a system of caste differentiation but no true workers and few soldiers per colony (Korb 2008). Soldiers have a phragmotic head, with the front heavily sclerotised and used as a plug to block access to the gallery system; undifferentiated worker-like individuals (pseudergates) are also present in the colony (Ewart 2020). Pseudergates, soldiers and reproductives all have specific roles in caste systems, but class developmental routes and ensuing potential vary among termite groups. The developmental pathway of C. brevis demonstrates multiple morphologically distinct moults (Cesar et al. 2019; Ewart 2020). Embryonic development is well known (Kawanishi 1975), but knowledge about embryonic moults is lacking (Korb and Hartfelder 2008; Ewart 2020).

Like most other wood-dwelling termites, *C. brevis* shows high developmental plasticity, with progressive, regressive and stationary moults allowing reversible morphological change into any phenotype in response to ecological and social cues (Korb 2015; Cesar et al. 2019). This flexible type of development is called the linear developmental pathway (Figure 1) (Oguchi et al. 2021), in which all workers are ontogenetically totipotent immatures. Larvae develop into pseudergates, a transitional class that functions as workers but with the potential to develop further (Hartke and Baer 2011).

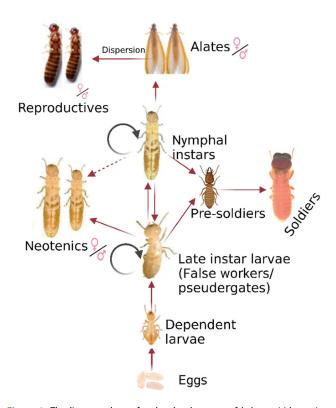


Figure 1. The linear pathway for the development of kalotermitid termites, including *Cryptotermes brevis*. Solid forward arrows: progressive moults; solid backwards arrows: regressive moults; dashed arrows: potential progressive moults in some species; circular arrows: remain in the same stage by doing stationary moults (not all pseudergates or false workers moult into subsequent developmental stages)

These pseudergates can undergo further moults to become soldiers, sexual alates or even neotenic reproductives given suitable genetic, maternal and environmental factors. Neotenic individuals aid colony health by producing offspring at low rates in a natal colony (Vargo 2019). This development is regulated by pheromonal release from the queen and allows the colony to adapt to changes such as the death of the primary reproductive (Weil et al. 2009). Even the most morphologically distinct class, the soldiers, can undergo regressive moults to become sexually reproductive (Abe 1987) and thereby ensure a colony's survival.

New colonies are formed by alates (winged reproductives) or secondary reproductives. Alates develop about one month before flight and are drawn to short-wavelength visible light, preferring wavelengths in the white, blue and green spectra (Ferreira and Scheffrahn 2011). Alates can fly less than 100 m (Ferreira et al. 2012). Although flights typically take place in spring and autumn, they are largely determined by environmental factors such as local and temporal variation in temperature and humidity and therefore can also occur at other times (Ferreira and Scheffrahn 2011; Tong et al. 2017; Ewart 2020). Minnick (1973) reported that C. brevis is crepuscular; in South Florida, however, flight periods are common in the middle of the night when it is very dark (Ferreira and Scheffrahn 2011; Ewart 2020). Alates after wing loss seek darkness, using beetle exit holes, drilled or broken timbers and unsecured joints between timber pieces as entry points (Ewart 2020). They can burrow directly into the wood; however, this energy-intensive process may put them at greater risk of being eaten by predators (Minnick 1973; Ewart 2020). According to McMahan (1962), females typically lay five or more eggs, which can take up to 70 days to hatch, depending on temperature and food availability. Soldiers start appearing after the colony has been established for 2-3 years. Alates are not formed until the colony is fully developed, which takes around five years (Ewart 2020). Pseudergates can also become sexually mature and reproduce without leaving the nest or flying (neotenic replacement reproductives) (Lenz et al. 1982; Cesar et al. 2019). Neotenics have recently been found to produce intersex individuals, the importance of which is not understood (Laranjo and Costa-Leonardo 2017). Under optimal conditions, colonies can increase to a few hundred within five years. However, because individual pieces of wood may house multiple colonies, the overall number of termites in a structure can be significant (Gay and Watson 1982; Grace et al. 2009). In contrast to subterranean termites, which produce liquid faeces, C. brevis and other drywood termites produce dry faecal pellets. These are removed from galleries through 'kick holes'; the presence of pellets is typically the first indication of C. brevis and other drywood termite infestations (Grace and Yamamoto 2009; McDonald et al. 2022a).

Due to several physiological and behavioural adaptations, including their concealment in timber except during alate dispersal, *C. brevis*, like other drywood termites, can be challenging to detect and treat in infested structures (Lewis 2003), particularly with their slow colony growth and the scattering of small colonies throughout a building (Grace et al. 2009). *C. brevis* can withstand desiccation, stay away from light, and tolerate temperature extremes (Williams 1976; Steward 1981). A previous study reported the lethal upper limit for the species at 51.3°C (Woodrow and Grace 1998b), and other studies showed that 10 min at 48°C and 3 min at 50°C are lethal (McDonald et al. 2022a). Sub-lethal high temperatures significantly affect colony life and can lead to more conversion of pseudergates to reproductives (Steward 1983a).

The preferred moisture range of C. brevis is 76-89% relative humidity (RH) (Collins 1969; Minnick, Kerr et al. 1973; Steward 1983b; Collins et al. 1997; Zukowski and Su 2017), although it is adapted to reproduce guickly in dry and warm conditions and does not normally live outside protected structures (Steward 1983b). Pseudergates live longer at high humidity (87-98% RH) but sometimes show temporary symptoms of water poisoning (Minnick, Kerr et al. 1973). Cryptotermes brevis feeds on wood with lower moisture contents (7-12%), and its preferred feeding strategy indicates that the species has adapted well to various cellulosic food sources, such as hardwoods and softwoods (Minnick, Wilkinson et al. 1973). It can vary its feeding rate depending on temperature and RH and can survive without food for several months. These adaptive abilities may help explain the success of the species as an economic pest in warmer climates such as Queensland and the southern United States and invasions into locations with low temperatures and humidity, such as Germany (Berlin) (Becker and Kny 1977).

Distribution

The origin and distribution of C. brevis have been reviewed previously (Scheffrahn et al. 2009; Evans et al. 2013). Briefly, C. brevis was described in 1853 by Francis Walker from specimens collected in Jamaica (Edwards and Mill 1986) (hence the common name). Although the termite is established on every island in the West Indies, no reproducing populations have been observed in the wild, so it is unlikely to have originated there (Scheffrahn and Su 2014). Instead, this species is believed to have evolved in the coastal regions of Peru and Chile (Scheffrahn et al. 2009), where several colonies have been collected from decaying trees. Although the species is likely to have originated in that region, its ecological requirements make it ideally suited to human-facilitated spread to structures far beyond its original limited range. The global spread of C. brevis (Figure 2) progressed rapidly, with establishments seen throughout the West Indies before the species was found in the United States. The first report of the termite in the United States was in Key West, Florida, in 1919,

although it is suspected to have been present before then, and the species has since spread to cities on the coast of the Gulf of Mexico, with large populations found in New Orleans, Galveston and Corpus Christi (Scheffrahn and Su 2002). The increased global movement of susceptible ships facilitated more termite transport, and reports of infestations on other continents began in Africa around the start of the twentieth century (Coaton 1948), Europe around mid-century (Martínez 1957), and Australia in the 1940s (Peters 1990a). The only continent with a suitable tropical climate where the termite has not been reported is Asia (Figure 2), with the exception of Hong Kong (Light and Zimmerman 1936) - although, in this case, identification was unclear and more recent reports found no evidence of C. brevis in that city (Scheffrahn et al. 2009). Endemic populations of C. cynocephalus (Light), C. dudleyi (Banks) and C. domesticus (Haviland) are suspected to competitively occupy the same niche, which may have prevented the establishment of the species in Asia (Guerreiro et al. 2014).

Cryptotermes brevis in Australia

The history of C. brevis as an introduced invasive pest in Australia is well recorded, and the history of detection, identification and distribution of the pest in Queensland and its treatment has been reviewed previously. Briefly, the first occurrences of C. brevis were in Sydney, New South Wales, in 1946, but the colonies were rapidly identified and destroyed, preventing establishment (Eldridge and Simpson 1987). In 1966, termites collected in Maryborough, Queensland, two years previously were identified as C. brevis (Heather 1971). At that point, the species was already established, and damage to structures was widespread. A survey was performed to delimit the scale of the problem, initially revealing 26 buildings infested with the termite (Heather 1971), and 49 buildings were fumigated within ten years (Peters 1990a). The delayed identification precluded any attempt to trace the source of the importation. Similar damage was reported in the Brisbane area in 1973, leading to a survey of the termite in 1977. The extent of damage and the fact that infested buildings had been constructed during the Second World War led to the conclusion that the pest had most likely been present since the 1940s in both locations

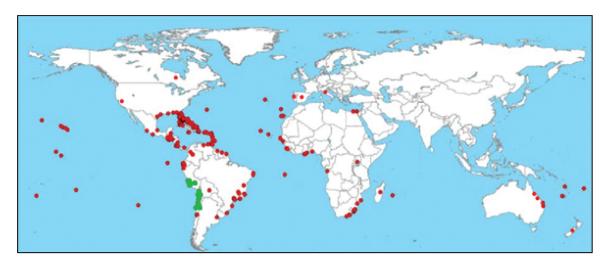


Figure 2. Global reported distribution of Cryptotermes brevis. Green indicates the purported native range; red indicates the introduced range. Modified from Scheffrahn et al. (2009), updated data: CABI (2022)

(Peters 1990a). It was believed that C. brevis was introduced to Australia through the entry of wooden supplies during the war and then spread unchecked for many years. Afterwards, several border and post-quarantine detections of C. brevis in infested wood and wood products were also observed in Australia (Scheffrahn and Crowe 2011; Horwood et al. 2022). For example, there were 64 border and post-guarantine detections of C. brevis between 2003 and 2016, with most interceptions (38) associated with wood (Horwood et al. 2022). Transport of C. brevis in recreational vessels and boats is also suspected of bringing the pest to Australia. Scheffrahn and Crowe (2011) reported eight shipborne detections between 1989 and 2009 in ports in Queensland. A yacht carrying C. brevis was recently found at a port in New Zealand, where it was treated effectively using lethal heat treatment (MPI 2022).

Commonwealth assistance was sought to aid eradication efforts of the termite in Australia. This was granted in 1973, but, due to an adverse public reaction and the belief that the termite was contained to Maryborough, large-scale 'security fumigations' did not go ahead (Peters 1990a). The Queensland Government then established initiatives to help manage the pest, including ongoing surveillance and an obligation under the *Diseases in Timber Act 1975* (Eldridge and Simpson 1987) for the public and pest-control officers to report confirmed infestation cases to the state. Active eradication attempts, primarily via the fumigation of infested structures, have been undertaken since 1976 (Horwood 2008).

Currently, C. brevis is established in many regions of Queensland, including suburbs in greater Brisbane and in many other Queensland cities and towns. Based on reports and confirmations of detections made by the Queensland Department of Agriculture and Fisheries (DAF) since 2011, C. brevis has been detected in Southeast Queensland, Central Queensland, North Queensland, Mackay–Whitsunday and Wide Bay Burnett. DAF receives 3-4 reports per month of detections from pest inspectors and homeowners (Horwood et al. 2022). The Queensland Government was responsible for the management of this pest under its prevention and control program, but the program ended in 2021 when the state moved to a community-based management approach; the species remains a notifiable pest under the Biosecurity Act 2014 (Queensland Government 2021). Currently, a two-year transitional plan aims to increase public awareness of the pest, improve detection techniques through research, and train pest controllers to detect and treat infestations more effectively. Previous cases have shown that the termite will migrate and infestations will occur in previously unaffected areas, with the potential for it to become established in other Australian states.

Feeding behaviour and timber susceptibility

In contrast to subterranean termites, *C. brevis* is a single-piece nester and does not relocate its nests. Therefore, the selection of sites by reproductives to start new colonies and the selection of food are both critical. Conspecific interactions and the development of secondary reproductives in *C. brevis* are influenced by food type and size (Lenz et al. 1982; Korb 2006). *Cryptotermes brevis* prefers to colonise small pieces of wood (Evans et al. 2011). The quality and moisture content of food, temperature and humidity all affect the quantity of food consumed by *C. brevis* (Wolcott 1957). In optimal conditions, a single termite can eat up to 0.15 mg of wood day⁻¹ (Grace

and Yamamoto 2009). Several previous studies have reported the food preference of C. brevis, which can attack various softwood and hardwood species (Wolcott 1924, 1946, 1957; Appendix Table 1). However, natural variability between pieces of wood can significantly affect feeding rates (Horwood 2008). Cryptotermes brevis prefers the sapwood of both hardwood and softwood species, especially those protected from rain, such as in construction and furniture. Unlike most subterranean termites, which exclusively gnaw on the softer wood fibres found between grains, C. brevis leaves galleries that do not match the wood's grain because they also eat across it (Coaton 1948). Drywood termites create tunnels in the wood that are clean and smooth compared with subterranean termites (Figure 3). A piece of wood typically becomes more susceptible to C. brevis with age (Ewart 2020), consistent with hoop pine timber (Araucaria cunninghamii (Mudie)) infestations now prevalent in Queensland, suggesting that other timber constructions will likely become more susceptible over time.

Wood extractives (chemicals produced as plantspecialised metabolites) and wood anatomy are important factors influencing resistance to drywood and subterranean termites (Wolcott 1951, 1957; Scheffrahn and Rust 1983; Arango et al. 2006; Cosme et al. 2018). Different wood species have different levels of defence, which also vary depending on a tree's age, vigour, stand type (e.g. secondary growth vs old growth), silvicultural practice, location and environmental conditions (Taylor et al. 2002). In addition to extractives, other factors contributing to wood resistance to termites include wood hardness, density and specific gravity (Arango et al. 2006) – that is, the relative density of the material at a given moisture content. Wood species with a higher specific gravity appear more resistant to termite attack (Esenther 1977), with harder and denser woods more resistant to C. brevis colonisation (Cosme et al. 2018). In contrast, Wolcott (1951) reported that neither the hardness nor the high lignin content of wood determines its resistance to drywood termites. Similarly, Peralta et al. (2004) indicated no relationship between wood density and subterranean termite resistance. Mass loss of wood caused by termite feeding has been found to be inversely correlated with the specific gravity of hardwood species and positively related with the specific gravity of softwood species (Arango et al. 2006). Cosme (2020) found that wood extractives in tropical wood species are not important for C. brevis resistance, in contrast to previous studies reporting that immunity to drywood termites in wood is due to the presence of certain specific chemical constituents (Wolcott 1951, 1957). Hence, the natural durability of wood against xylophagous pests such as C. brevis is a complex phenomenon that may vary between species, and no single wood characteristic defines susceptibility (Nascimento et al. 2013).

The species-level susceptibility of woods to *C. brevis* has been addressed in other countries (Wolcott 1946, 1957; Minnick, Wilkinson et al. 1973; Cosme et al. 2018; Appendix Table 1) in the context of the available timber, but there is little information on the susceptibility of most native species and common construction timbers in Australia. Hoop pine is a well-known host of *C. brevis* in Australia (Peters 1990a), and serious damage can occur in Queensland houses constructed with this timber. Hardwoods such as maples (*Flindersia* spp.), red cedar (*Toona australis* (Roem.)) and silky oak (*Grevillea robusta* (Cunn. Ex R. Br.)) are also hosts (Peters et al. 1996). There are indications that *C. brevis* can readily consume pines

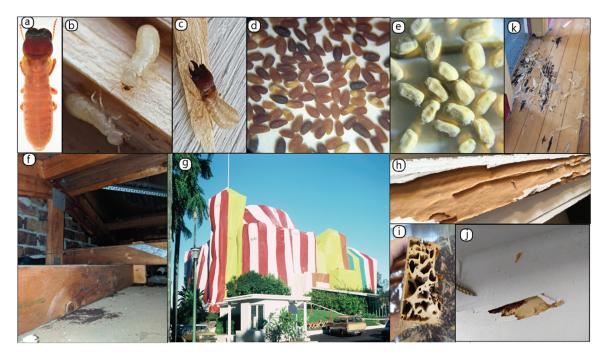


Figure 3. Examples of drywood termite castes, frass, fumigation and damage: *Cryptotermes brevis* soldiers (a); *C. brevis* pseudergates (b); soldier of native drywood termite, *C. primus* (c); *C. brevis* frass (d); *C. primus* frass (e) (typically, *C. brevis* frass is larger and more pointed, and the soldier head capsule more rugose than that of *C. primus*); piles of *C. brevis* frass in roof cavity (f); *C. brevis*-infested building cover with tarpaulins for fumigation (g); feeding pattern of *C. brevis* (h,i) see across and along grain feeding in Figure 3h; examples of termite damage in wall (j) and floor boards (k). Photos: DAF a–h, j, k; Scott Kleinschmidt i

such as *Pinus radiata* (D.Don), *Pinus elliottii* var. *elliottii* (Engelm.) and its hybrids, engineered wood products manufactured from these softwood species, and some *Eucalyptus* species, all of which are common commercial timbers in Australia (Appendix Table 1). However, experimental evidence of susceptibility and its underlying mechanisms is lacking for commercially important Australian wood species.

Identification and detection in structures

Infestations of C. brevis are often difficult to discern from other, less harmful endemic termites. Several factors are used to distinguish the species, although it often takes a trained specialist to confirm a specimen. Soldiers are commonly used for identification because they show most variation with related termite species (Krishna et al. 2013); for example, C. brevis heads have more wrinkles than the native Australian drywood termite C. primus (Peters et al. 1996) (see Figure 3). Another way to identify a termite species is through wing venation (Scheffrahn and Su 1994; Engel et al. 2011), but this requires the collection of alates, which only develop at certain times of the year and disperse before rapidly losing their wings; therefore, any chance of observing them is restricted to a few days per year. Drywood termites are also often identified by their distinctive faecal pellets (frass), with their hexagonal shape and lack of moisture (Bobadilla et al. 2020).

As for other drywood termites, *C. brevis* is commonly detected through visual searches and by probing wood for evidence of termite faecal pellets, discarded alate wings and damaged wood (Lewis 2003). The shape of faecal pellets produced by drywood termites is species-specific (Figure 3). The number of faecal pellets coming from a kick hole can be used to estimate the population size of a colony and to

¹https://termatrac.com/t3i-all-sensor

monitor termite activity after chemical treatment (Lewis 2003): C. brevis produces 0.7-1 pellet termite⁻¹ day⁻¹ (Grace and Yamamoto 2009). However, it is challenging to discern whether pellets have come from active termites or been displaced by other means such as ant activity. The appearance of blistering or peeling of thin surface wood and paint are indications of wood infestations. Additionally, tapping timber with a hard object can expose extensive hollowing of damaged timber, although this is less effective during an early infestation because of the lack of, or only slight resonance difference between, damaged and sound wood (Hadlington 1996; Ewart 2020). Common inspection sites for drywood termites in structures include flooring, wall panelling, trusses, attics, moulding and furniture. During visual searches, pest inspectors commonly use a large screwdriver or awl to probe wood, aided by a strong torch (Lewis 2003).

Several other detection methods and tools are used to detect drywood termites, including C. brevis, worldwide. Examples of these are the Termatrac[™] T3i, optical borescopes, canines, thermal imaging cameras, electronic stethoscopes, laser, and acoustic emissions (Lewis 2003; Zahid et al. 2012). The Termatrac[™], a non-invasive termite radar detector,¹ successfully detected C. brevis in naturally and artificially infested wood in laboratory tests. Factors such as wood density, grain orientation and detection depth, however, affected the detection ability of the device (McDonald et al. 2022b), and device movement during use and vibration within a structure or outside can affect results under field conditions. Similarly, thermal imaging cameras are not very successful in detecting drywood termites because the small colonies generate minimal metabolic heat. Lewis (2003), Zahid et al. (2012) and Lewis and Forschler (2014) reviewed drywood-termite detection methods and their accuracy, advantages and disadvantages.

Control methods

Controlling existing infestations in houses

Although attempting to eradicate a well-established invasion of *C. brevis* from a country is considered futile (Borges et al. 2014), several methods for controlling *C. brevis* in structures have been explored (e.g. Lewis and Haverty 1996; Woodrow and Grace 1998a, 2005; Grace et al. 2002; Lewis 2003; Guerreiro 2009; Borges et al. 2014). Each has merits and limitations in given circumstances, which are well documented (Lewis 2003; Lewis and Forschler 2014; Table 1).

The most effective method is whole-structure fumigation, which many consider the only truly effective way to remove widespread or discrete C. brevis infestations from a structure (Scheffrahn et al. 2006). In this method, the whole structure is sealed using tarpaulins, and toxic fumigant is pumped into the building at a specific concentration and for a specific time to ensure the destruction of termite colonies present in the wood. However, sometimes it is challenging to ensure good quality control and assess the efficacy of fumigants, especially in large structures (Peters 1990b). The most commonly used fumigant is sulphuryl fluoride, which causes high termite mortality rates (Osbrink et al. 1987); historically, methyl bromide was also used before being phased out under an international treaty due to its ozone-depleting properties and other disadvantages (Peters 1990b). Whole-house fumigation was used to treat C. brevis infestations in Queensland at the

government's expense. Initially, the government also covered the cost of alternative housing for displaced residents, but later only the expenditure of fumigation was compensated (Peters 1990b). Contracts for fumigation, requiring preparation, coordination, compassion and attention to detail, were provided to licensed fumigators. Standards were upheld by strict regulations and government control. Peters (1990b) provided details of the procedure, schedule, duties of the contractor, specifications for equipment and the safety precautions needed in Queensland for residential fumigations of *C. brevis*.

A total of 898 fumigations were carried out in Queensland between 1968 and 2021 to eradicate *C. brevis* under the state's prevention and control program (B. Hassan, pers. comm., Nov 2022; Figure 4). Fumigations were conducted on 872 houses or buildings, and the remaining 26 were performed on infested furniture and other wooden articles. Seventy-nine structures were re-fumigated in Queensland between 1968 and 2021 (Figure 4), and six buildings in the greater Brisbane region received three fumigation treatments. Most (633) of the fumigations were carried out in greater Brisbane in 119 suburbs, followed by the Wide Bay region (246); the fewest fumigations (19) were in North and Central Queensland.

Another option for whole-house treatment is the use of lethal high temperature, in which the building is sealed (as for fumigation) and circulating hot air is pumped in (Ewart 2020).

Table 1. Summary of benefits and costs of the treatment options available to Cryptotermes brevis infestations (arrow directions depict increase or decrease in factor

Treatment	Effectiveness	Cost	Effort	Damage	Reference
Fumigation				Ļ	Scheffrahn et al. 2006
Heat treatment	i	Ť	▲	Á	Gordon et al. 2021
Spot treatment: chemical	Ļ	i	Į.	Į.	Rust & Venturina 2008
Spot treatment: heat	Ļ	↓	↓	Á	Gordon et al. 2021
Spot treatment: microwave/electricity/freezing	Ļ	, i	Ļ		Lewis & Haverty 1996
Trapping	, i	, i	†	Į.	Ferreira et al. 2013
Replace damaged wood	≜	†	Ť	≜	Nunes et al. 2005

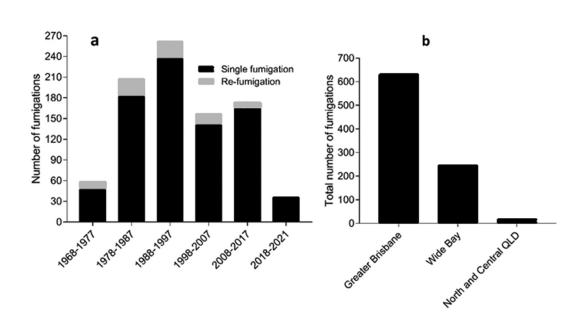


Figure 4. The number of fumigations conducted in Queensland to eradicate *Cryptotermes brevis* under the West Indian drywood termite Prevention and Control Program (1968–2021). (a) The number of single and re-fumigations, per decade starting from 1968 to 2017 and the last three years 2018–2021 (total length of each bar indicates the total number of fumigations). (b) Geographical distribution of structures where *C. brevis* was reported and fumigated in different Queensland regions

The practicalities of heat treatment to whole structures is complicated, however. The size and variability of the wood in a house make it challenging to achieve an appropriate core temperature in all wood structures to kill the termites without heating smaller units too high, causing structural damage. Heat treatment is usually restricted to smaller items and rooms where temperature can be monitored effectively (Gordon et al. 2021). Cryptotermes brevis can be killed by exposure to high temperatures, with a lethal wood core temperature of 54.4°C (Woodrow and Grace 1998b). The lethal temperature for C. brevis is 50–55°C, depending on exposure time (McDonald et al. 2022a). Treating C. brevis using lethal temperatures in whole-house treatment is a wellestablished practice in the United States; it could replace fumigants in Queensland but requires a unique skill set and training. Therefore, to develop the lethal heating method, research and training is advisable for the Queensland pest industry to ensure effectiveness and no off-target impacts. Work is ongoing to enhance heat treatments to reduce reliance on fumigation in Queensland. The major obstacle to this technique is the inability to prevent pockets of sub-lethal temperatures in hard-to-heat areas and pockets of increased heat that damage the structure (Perry and Choe 2020). Recent work has been done to remove these heat sinks in houses by specifically applying the heated air to isolated pockets, such as cabinets (Tay and James 2021).

Spot treatments can be effective in removing localised termite infestations if applied correctly. These will only work when each colony is located and treated directly for the entirety of its excavations. A range of chemicals are lethal to C. brevis, including disodium octaborate tetrahydrate, p-limonene, thiamethoxam, imidacloprid and fipronil (Woodrow and Grace 2005; Woodrow et al. 2006; Rust and Venturina 2008). The use of insecticides has issues of efficacy due to the inherent need for physical contact with the chemical. Because the species spends most of its life within the nest, insecticides must be applied directly into the galleries. This can be done by drilling into the wood and injecting the chemical (Gordon et al. 2021), which requires accurate knowledge of colony locations to ensure complete coverage. Alternatively, the chemicals can be applied to the whole wood surface and absorbed (Adame 1961), but this is only appropriate for more-permeable wood species (Kolin and Stevanovic Janezic 1996). Treatment with borate solution has been shown to prevent colony establishment by alates (Gillenwaters et al. 2018). Due to the various issues associated with them, including potential negative environmental impacts, insecticides are recommended only for small-scale infestations. Pest inspectors may prefer foam formulations due to their better placement in termite galleries, but the availability of these registered formulations is not always apparent. Foam and liquid formulations containing imidacloprid, fipronil or permethrin are registered for C. brevis in Australia, but there is no history of their use for this purpose in the country. Work is ongoing to test the effectiveness of various registered insecticides against C. brevis. A registration process is underway for another product, 'Pestigas' pyrethrin insecticide, for use against C. brevis. This mixture of natural pyrethrin in a carbon dioxide gas carrier is registered in Australia for use against many insect pests.

Alternative non-chemical spot treatments investigated include electrocution, microwave and liquid nitrogen (Lewis and Haverty 1996). These have proved less effective than chemicals and increase the risk that treatment will damage the wood.

Many insect management plans involve trapping during dispersal to prevent spread, and reproductive alates of C. brevis can be trapped effectively (Ferreira et al. 2013). Alates are positively phototactic when leaving the nest during swarming events (Ferreira and Scheffrahn 2011), and the effectiveness of traps can be increased by adding a strong light source to attract the reproductives (Ferreira et al. 2012). The alates fly only infrequently during the year, however, and disperse in all directions (Ferreira 2008), making it unlikely that all individuals will be trapped by this method and therefore new colonies could still form. Many colony members remain in the original timber host, and more alates will eventually be produced, further reducing the viability of trapping. Trapping can be used to monitor rather than control infestations. Light traps and wooden baits with light sources can be used in areas with suspected infestations to confirm the presence of C. brevis alates, and they can be deployed in areas surrounding established colonies to monitor spread (Borges et al. 2014).

Preventing infestations

Control measures are often ineffective in eradicating established infestations or costly to perform; therefore, a more efficient way to combat the pest is to prevent initial invasion. Removing susceptible habitats or making them less attractive can prevent colony formation. Because C. brevis lives in dry timber, usually in houses, this material would be the target for prevention improvements. Different woods have different resistances to termite attack (Wolcott 1946, 1957; Cosme et al. 2018), and termites are less successful in infesting timbers of higher wood hardness and density (Cosme et al. 2018). This knowledge can inform future building decisions – for example, the use of softer, less dense woods will mean that structures are more susceptible to termite attack and will propagate infestations. Judicious wood selection may aid prevention in future construction, but innovations are needed to increase prevention in existing structures. 'Termite shields' comprise the use of resistant metal or plastic to form a barrier and thereby prevent establishment (Sperling 1967). Such physical prevention can be effective but is also costly and time-consuming to install over large areas; thus, chemical defences have been explored with more useful realworld applications. Chemical elements lethal to the termites can be applied to wood, either in solution or as a powder. Proposed chemicals include silica gel powder, which causes desiccation by adsorbing to the insects' cuticular wax layer, and Tim-Bor[®], an insecticide that acts as a lethal metabolic toxin when ingested (Gillenwaters et al. 2018). Both material choice and treatment can control the termite effectively but their use is limited due to the high cost of application to many structures. Exposed unfinished wood is uncommon in modern construction in Australia, and locating timber framing within cavity walls may make it harder for termites to find susceptible host materials. There may be some repellency due to the extensive use of anti-termite sheet treatments with pyrethroid in the base of outside walls. It is also possible that the increased use of softwoods other than hoop pine, such as radiata pine, with potentially improved termite resistance, will contribute to a marginally decreased long-term

risk. However, it should not be assumed that there will be fewer successful infestations because there is less hoop pine.

Further research into natural alternatives for treating wood to confer termite resistance is also underway. Gonçalves et al. (2021) investigated the change in resistance of particleboards to *C. brevis* with the incorporation of agricultural byproducts such as macadamia nut carpel, eucalypt sawdust and coffee husk during construction. These treatments demonstrated good resistance to *C. brevis* attack, suggesting they may be developed into cheap and readily available control measures in the future. New composite materials are also being developed with the potential for inherent resistance to termites. A 50/50 polypropylene–wood composite demonstrated significantly increased resistance to *C. brevis* colonisation in a recent study (Gonçalves et al. 2021).

The Queensland Government is informing the public, the pest management industry and all timber allied industries about the cessation of the West Indies Drywood Termite Prevention and Control Program (as of 15 January 2021) (Queensland Government 2021) and the implications of this for the future management of C. brevis. The aim is to educate property owners, including residents, businesses, non-profit organisations and local governments, on the available treatment options for C. brevis and measures to reduce the spread of the pest. This information is being disseminated, for example, via the Business Queensland website,² social media platforms, face-to-face forums, emails and printed material. The key message is that although treatment is now the responsibility of property owners, C. brevis is still a notifiable pest under the Biosecurity Act 2014 and any known or suspected infestations must be reported to the DAF within 24 hours. In addition, those in possession of C. brevis-infested material must not exacerbate the spread of the pest, for example through the non-secured disposal of infested material or the movement of infested furniture from one property to another.

Preventing invasions into Australia

Preventing the establishment of additional populations of C. brevis in Australia is essential, and the species is still listed as one of Australia's 'national priority plant pests' (DAWE 2019). The risk of additional arrivals has grown with increasing globalised trade and travel (Hulme 2009). The primary sources of exotic pest importation are cargo ships (Scheffrahn & Crowe 2011) and imported goods (Schofield and Chesmore 2008; Skarpaas and Økland 2009). Restrictions are in place to control the importation of wooden articles and international standards for wood packing materials to reduce the likelihood of additional arrivals (DAFF 2022). These include mandatory declarations of goods, the use of approved treatments on articles, and inspections by border control personnel. Inspection of incoming materials provides an opportunity to gain information on potential termite importation pathways, and this can be used to direct measures to prevent the pest in the future. Historically, all imported goods at risk of drywoodtermite infestations were fumigated with methyl bromide or sulphuryl fluoride (Wylie and Yule 1977). More innovative, sustainable methods have been developed as countries attempt to rely less on costly and sometimes damaging

chemical solutions. These include the use of trained termitesniffer dogs, acoustic signal monitoring on wood, x-ray and thermal imaging, and visual inspection by trained inspectors (Lewis 2003; Sutherland et al. 2014). Although *C. brevis* is wellestablished in Queensland, it is thought that the employment of these biosecurity strategies aimed at preventing additional arrivals, in addition to an aggressive fumigation program, is the principal reason why the infestation rate remains low (Wylie and Peters 1987).

Knowledge gaps and research needs

Despite years of ongoing study into *C. brevis* biology, many factors related to the termite are not fully understood. Several challenges to research can be credited for this, including their cryptic nature, which hampers observations (Grace et al. 2009); slow reproductive rates and small colony sizes, which limit laboratory trials (Korb and Thorne 2017); and issues in initial identification, which reduce opportunities for study (Bobadilla et al. 2020). Such gaps in knowledge provide opportunities for future research that emphasises management strategies.

Knowledge of the timber species susceptible to C. brevis attack is incomplete in Australia; a key area of research into mitigating the impact of the species, therefore, should be its host preferences and the susceptibility of Australian timbers. This information is vital for determining long-term preventative strategies. The study could be approached in two ways: investigating the ability of primary colonisers to establish in various wood species, and testing whether colonies can maintain themselves effectively in those species. The first of these strategies requires alates as the dispersive stage responsible for host selection, while the second, involving free-choice and no-choice tests to determine feeding preference, can be performed using pseudergates that will actively consume the host and attempt to propagate the colony. For both strategies, colonies must be maintained in the test material for a minimum of six weeks to enable assessment of colony viability. Other factors that influence infestation success, such as wood moisture content, temperature, the position of infestations in structures, and the factors that trigger alate dispersal, also need to be studied.

Further investigation into timber susceptibility could be aided by understanding the chemical changes in wood during digestion. Work is ongoing into the specifics of lignocellulose digestive processes in termites in general (Ni and Tokuda 2013), but this should be explicitly investigated in C. brevis to observe differences that may contribute to timber host selection or the potential to manipulate timber to render it indigestible to this species. Such a study would need to chemically identify, using mass spectrometry techniques, the changes in wood composition that occur at various digestion points that can be achieved by sampling the selected wood species before, after and at multiple points during digestion by the termites. This knowledge can be combined and compared with host preference information to assess whether the chemistry of wood digestion can explain differences in colony success and viability or whether other factors influence the interaction.

The ability of *C. brevis* to attack a given timber species is likely related to its gut microbiome because these organisms

are crucial for degrading the lignocellulose matrix and coping with extractives. Termite-microbiome interactions have been investigated in other species (Abdul Rahman et al. 2015; Maurice and Erdei 2018), but the microbiota of the C. brevis gut has not been investigated thoroughly. The capacity to release the energy stored in wooden material is not fully understood and may lead to novel techniques in the manufacture of biofuels for energy generation (Okolie et al. 2021). Identifying microorganisms found in the C. brevis gut would enable comparisons with other termite species to highlight differences that could be exploited in specific termite prevention. Moreover, investigations could be undertaken to better understand the adaptations that the C. brevis gut microbial community is able (and often forced) to make when various environmental stressors such as temperature, diet and moisture levels are applied. Discoveries in this area could enhance understanding of termite feeding and provide new targets for management strategies. The availability of comprehensive analytical methods, including next-generation genetic sequencing and metabarcoding, means it is possible to identify the entire microbiome within an organism (Levy and Myers 2016). These methods should be applied to C. brevis to better understand symbiotic systems in the gut. However, investigating unknown populations of microorganisms in this way can be difficult because effective primers for amplifying DNA fragments during polymerase chain reaction are not always available (Marchesi et al. 1998; Lang and Orgogozo 2012).

The chemical ecology associated with social recognition within and between colonies, and the invasion history of *C. brevis* in Australia, are also not well studied. Much is known about the social structure of the species and the recognition of colony members. However, identification of the cuticular chemicals involved in recognition has only been investigated in other species (e.g. Bagnères et al. 1998; Dronnet et al. 2006). A better understanding of the biochemistry involved in *C. brevis* cuticular expression and chemical ecology could provide targets for novel treatments. For example, attract-and-kill options currently deployed against other pest species (Campos and Phillips 2014) use attractant pheromones to draw in the insects before lethal treatment is applied.

The first noted instances of *C. brevis* establishment in Australia were in Maryborough in the 1960s. However, it is unclear if these were the result of a single invasion and the termite spread from there, or whether populations originated in multiple introduction events, as suggested by Peters (1990a). The invasions of termites in Hawaii (Gentz et al. 2008) and the Azores (da Rocha Bravo 2011) comprised multiple invasion events. This information can inform biosecurity strategies by prioritising relevant prevention methods: that is, border control and inspection if there are numerous events, and the treatment of infestations if they are shown to have spread from a single invasion. The monitoring of *C. brevis* in Queensland using alate trapping is also warranted to determine differences in its behaviour there compared with other areas of the world where it has been introduced.

Improved methods for detecting and monitoring *C. brevis* in infested timbers are required for ongoing management. As outlined above, it is challenging to locate *C. brevis* in structural timbers. Although the locally made low-energy microwave-technology-based Termatrac T3i can detect drywood termites *in situ* non-destructively (McDonald et al. 2022b) and can assist in initial detections of termite colonies and ongoing

monitoring following treatment, it is not always simple. False positive signals may be caused by user body movements and moving objects, such as vehicles, water running through pipes, heavy machinery, plants swaying in the wind, airborne debris, and children or animals on the opposite side of the inspection surface (e.g. a wall). Therefore, other detection methods need to be tested in Australia, such as the use of canines. Around the world, several termite-control firms have incorporated sniffer dogs in their termite-detection efforts because of the difficulty involved in visual inspections and the need for detecting early infestations. A well-trained termite-sniffer dog can detect live termites and damage that might not be picked up by sophisticated detection tools or skilled inspectors (Browne et al. 2006). Dogs are already being used for the detection of fire ants in Australia (Wylie et al. 2020). A dog trained explicitly on the scents of live C. brevis and fresh frass could help detect C. brevis, even young and small colonies.

To further improve termite monitoring, the analysis of *C. brevis* frass may lead to the development of a system for estimating the age of frass of unknown origin if results show reliable differences. The ability to estimate the age of termite frass as a proxy for colony status may aid in assessing the success of treatment and the need for further intervention. Anecdotal reports that the frass of *C. brevis* becomes darker with age (DAF 2019) or changes significantly in volatile profile could be further investigated with the potential to optimise treatment of ongoing infestations.

The pest-control industry in Queensland has little to no experience in dealing with *C. brevis*. It has limited understanding of the biology and behaviour of the pest because few technicians receive formal practical training in drywood-termite identification as part of the national competency framework. Therefore, the industry needs to be trained in the detection, treatment and monitoring of *C. brevis*. Incorporating drywood termites into relevant Australian Standards may assist in this regard (Horwood et al. 2022).

Conclusion

Cryptotermes brevis is an important pest species in Australia and globally. A better understanding of its biology and behaviour offers the potential to develop improved management strategies, which would benefit the global economy by reducing the impact of this timber-feeding species in many countries worldwide.

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Appendix

Appendix Table 1. Primary data of wood types and resulting Cryptotermes brevis colony success after a six-week no-choice feeding trial

Wood types	Density (kg m ⁻³) Mean ± SE	Termite survival (%) Mean ± SE	Proportional change in termite mass Mean \pm SE	Frass produced (mg) Mean ± SE	Wood consumption (mg) Mean \pm SE
Hoop pine	481.7 ± 30.7	57 ± 5	+0.103 ± 0.111	31.0 ± 4.1	24.2 ± 23.4
Radiata pine	474.0 ± 14.4	65 ± 8	+0.247 ± 0.031	32.4 ± 1.5	32.8 ± 14.7
Southern pine hybrid	466.1 ± 24.0	77 ± 4	+0.192 ± 0.021	30.3 ± 4.3	68.7 ± 36.4
Shining gum	577.0 ± 23.8	82 ± 6	+0.306 ± 0.021	36.6 ± 3.5	93.0 ± 14.8
Silky oak	521.4 ± 14.7	65 ± 6	+0.064 ± 0.057	12.2 ± 4.6	28.0 ± 11.5
Spotted gum	991.7 ± 14.4	50 ± 8	$+0.002 \pm 0.053$	11.1 ± 3.4	15.9 ± 9.8
Hoop pine laminate	649.4 ± 0.2	79 ± 7	+0.141 ± 0.139	38.6 ± 6.5	75.2 ± 11.4
Filter paper	N/A	71 ± 7	+0.242 ± 0.050	3.1 ± 0.4	N/A

N/A = not applicable; SE = standard error.