

Biology of Invasive Termites: A Worldwide Review

Theodore A. Evans,^{1,*} Brian T. Forschler,²
and J. Kenneth Grace³

¹Department of Biological Sciences, National University of Singapore, 117543, Singapore; email: theo.evans@nus.edu.sg

²Department of Entomology, University of Georgia, Athens, Georgia 30602; email: bfor@uga.edu

³College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa, Honolulu, Hawaii 96822-2271; email: kennethg@hawaii.edu

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*Corresponding author

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Abstract

The number of recognized invasive termite species has increased from 17 in 1969 to 28 today. Fourteen species have been added to the list in the past 44 years; 10 have larger distributions and 4 have no reported change in distribution, and 3 species are no longer considered invasive. Although most research has focused on invasive termites in urban areas, molecular identification methods have answered questions about certain species and found that at least six species have invaded natural forest habitats. All invasive species share three characteristics that together increase the probability of creating viable propagules: they eat wood, nest in food, and easily generate secondary reproductives. These characteristics are most common in two families, the Kalotermitidae and Rhinotermitidae (which make up 21 species on the invasive termite list), particularly in three genera, *Cryptotermes*, *Heterotermes*, and *Coptotermes* (which together make up 16 species). Although it is the largest termite family, the Termitidae (comprising 70% of all termite species) have only two invasive species, because relatively few species have these characteristics. Islands have double the number of invasive species that continents do, with islands in the South Pacific the most invaded geographical region. Most invasive species originate from Southeast Asia. The standard control methods normally used against native pest termites are also employed against invasive termites; only two eradication attempts, in South Africa and New Zealand, appear to have been successful, both against *Coptotermes* species.

Introduced: describes a species outside its native range due to human transport

Native or natural habitat: the original community of species of an area with no or little human modification

Invasion: the expansion of an established nonnative population outside its native range

WHAT IS AN INVASIVE TERMITE?

Termites have only recently been labeled invasive (34, 105, 116) despite knowledge of spread beyond their native ranges. The first worldwide review in 1969 found “17 species for which there is unequivocal evidence of their establishment in new habitats” (39). Yet these introduced species were not considered invasive: “Introduced species frequently become of considerable economic importance, although they are rarely able to invade native habitats and are almost always restricted to the human-modified environments of houses, buildings, and cultivated crops” (39). These 17 species gained attention precisely because they were important pests in human constructions (2, 10, 25, 63, 116). One consequence of this attitude was use of the presence of a species in a native tree or natural habitat as a criterion to identify the native range, e.g., most recently Peru and Chile for the West Indian drywood termite, *Cryptotermes brevis*, the most widespread species (105). This strict distinction between natural and modified habitats is now known to be false.

Molecular diagnostic tools developed for species identification have demonstrated that introduced termites have invaded native habitats. *Reticulitermes santonensis* was considered native to western France, in part because it is found in forests there. However, mitochondrial DNA sequence data have shown that *R. santonensis* is an invasive population of *Reticulitermes flavipes* (6, 7), a native of the southeastern United States introduced into France before 1840 (9, 128). Similar genetic detective work has found that *R. flavipes* is invasive in Uruguay, Italy, and Chile as well (7, 41, 113). *Nasutitermes polygynus* was considered native to New Guinea because it was found abundantly in forests there (96). Yet *N. polygynus* from New Guinea and *Nasutitermes costalis* from the Caribbean Islands have been synonymized with *Nasutitermes corniger*, a species native to Central and South America (106, 107). The absence of inquiline staphylinid beetles was used to demonstrate that the native range of *Coptotermes formosanus* is China and Taiwan (67). The presence of *Co. formosanus* in Japanese forests indicated 300 years of introduced residence rather than native status (116), a phenomenon exhibited by that same species in US forests (114) 60 years after introduction (63, 116).

Time is the crucial factor in the invasion of native habitats by termites, as demonstrated by these examples of misidentified termites. The long time period is partly a function of the longer life cycles of wood-eating insects compared with other insects (27); e.g., *Reticulitermes* and *Coptotermes* spp. colonies require 5 to 10 years to mature (i.e., produce imagos) (47, 64). These time periods suggest that *N. corniger* was introduced into New Guinea at least 100 years ago, during the Dutch colonial period. The Dutch had colonies in the native range of *N. corniger*: Paramaribo, Suriname; Mauritsstad (now Recife), Brazil; Sint Marten, Saba, and Sint Eustatius in the Lesser Antilles; and Aruba, Curaçao, and Bonaire in the Leeward Antilles. Population-level molecular comparisons may illuminate this possibility for *N. corniger* and for other species such as *Cryptotermes havilandi*, which is invasive in the coastal cities and forests of East Africa (98) and likely originated from West Africa (129, 133).

CHARACTERISTICS OF INVASIVE SPECIES

Wood-eating is one of the three characteristics common to all 28 invasive termite species (34). The ca. 2,750 described termite species eat a wide variety of plant matter and have been classified into four feeding types (29). Types I and II eat nondecomposed plant matter, recognized easily as wood, grass, or leaf litter; they differ only in their symbiotic gut flora. Types III and IV eat decomposed plant matter; Type III feeds at the plant matter–soil interface, whereas Type IV feeds on particulate or dissolved plant matter within mineral soil (true soil-feeders), and these two types comprise approximately 50% of all termite species. All invasive species are Type I or Type II

Table 1 Feeding group, food, nest types, and secondary reproductives of invasive termites compared with their evolutionary clades (family/subfamily/group/number of species)^a

Clade (no. of species)	Feeding group ^b : food ^c		Nesting ^d		Secondary reproductives ^e	
	Clade	Invasive	Clade	Invasive	Clade	Invasive
Lower termites						
Mastotermitidae (1)	Type I: W	Type I: W	I	I	E	E
Hodotermitidae (20)	Type I: G	–	X	–	NA	–
Termopsidae (20)	Type I: W	Type I: W	S	S	NS	NS
Kalotermitidae (430)	Type I: W	Type I: W	S	S	NA	N
Serritermitidae (2)	Type I: W		X		EN	
Rhinotermitidae (330)	Type I: W	Type I: W	SIX	SI	EN	EN
Higher termites						
Termitidae						
Macrotermitinae ^f (330)	Type II: WGL	–	X	–	A	–
<i>Foraminitermes</i> group (10)	Type II: D	–	M	–	?	–
Apicotermitinae (195)	Type III, Type IV: DS	–	M	–	A	–
Termitinae ^g (595)	Type II, Type III, Type IV: WGLDS	–	IXM	I	ENA	?
<i>Cubitermes</i> group (165)	Type IV: S	–	C	–	NA	–
Nasutitermitinae (650)	Type II, Type III, Type IV: WGLDS	Type II: W	IXM	I	ENA	EN

^aSee References 29 and 32.

^bFeeding groups: Type I, solid plant food and gut flagellates; Type II, solid plant food and no gut flagellates; Type III, decomposed plant matter–soil interface; Type IV, mineral soil.

^cFood: W, wood; G, grass; L, litter; D, decomposed material; S, mineral soil.

^dNesting: S, single piece; I, intermediate; X, separate piece; M, continuously mobile.

^eSecondary reproductive: E, ergatoid; N, nymphoid; A, adultoid; S, soldier; ?, uncertain.

^fNote the Macrotermitinae culture fungus does not eat wood directly.

^gThe Termitinae are paraphyletic.

and eat or infest sound wood (including the Termopsidae; 72); indeed, there has been not one documented introduction or unintended transport of termites that eat litter, grass, or any type of soil (34, 39).

Nesting in wood is the second characteristic. Termites have a range of nesting behaviors, and three broad categories are recognized (1). (a) Single-piece nesters live, nest, and eat in one single piece of wood (or multiple pieces bound tightly together; 44). (b) Intermediate-piece nesters start as single-piece nesters, but they search for and eat other pieces of wood, one of which becomes the new nest once the original is eaten completely. (c) Separate-piece nesters build a nest separate from their food and forage away from their nest to find food. A fourth category, continuously mobile (no permanent nest), can be found among those Type III and IV soil-feeders that eat their way through the soil (29, 32). Invasive species are either single-piece nesters (the 12 species in Termopsidae and Kalotermitidae), or intermediate-piece nesters (all other species) (Table 1).

The third characteristic is the capacity to produce secondary (also known as supplementary) reproductives. Termites have two types of reproductives. All species have primary reproductives formed from alates, which are the standard imago adult of all hemimetabolous insects. They also have the ability to produce secondary reproductives, usually through neoteny of nymphs (known as nymphoid reproductives) and through neoteny of workers or pseudergates (both known as

Primary reproductives: imagos that found new nests and colonies independently after a mating flight

Secondary reproductives: usually neotenic reproductives derived from nymphs, workers, pseudergates, or soldiers that replace primary reproductives; only found new colonies dependently, i.e., with workers

Propagules: packages of reproductively capable individuals transported to regions where they are not native

ergatoid reproductives), or through the retention of alates (known as adultoid reproductives) (86, 95, 119). Invasive species have a greater capacity to produce secondary reproductives; in particular, they can produce ergatoid and nymphoid secondary reproductives (**Table 1**) (34, 86).

TRANSPORTED PROPAGULES

Wood-feeding, nesting in wood, and frequency of production of secondary reproductives combine to create propagules for transport (75, 76). Wood is the traded and transported commodity, but it must contain termites capable of reproducing to become a propagule. All wood containing either Termopsidae or Kalotermitidae termites should become a propagule, because all individuals in these families can become reproductive, with the exception of kalotermitid soldiers (34, 86, 95, 119). If wood containing the nest is cut such that no reproductives are present in the transported section, these individuals can develop into secondary reproductives (35, 86). Wood size is a factor as well; drywood termites can be transported in objects as small as a book (48). Invasive *Cryptotermes* species prefer, or at least accept, pieces of wood smaller (8 cm^3) than pieces accepted by native and noninvasive species (35).

Workers (or pseudergates) form the most numerous caste in termite colonies, and these castes are often facultatively fertile in most lower termite species and obligatorily sterile in most higher termite species (**Table 1**) (86, 95, 119). Therefore, propagules are most likely to be created by species able to form ergatoid reproductives, because any food resource with foraging workers can become a viable propagule at any time of year; species include *Mastotermes darwiniensis*, *Reticulitermes* spp., *Heterotermes* spp., and *N. corniger* (86, 120). Propagules are less likely to be created by species with only nymphoid reproductives, but more likely if the nymphs forage away from the nest, including *Coptotermes* spp. (34, 36, 52, 63, 93).

Population genetic data provide confirmation for inbreeding through multiple related secondary reproductives in invasive populations for *M. darwiniensis* (42), *R. flavipes* (17, 18, 30), *R. grassei* (28), *Co. formosanus* (3, 56, 125), and *Co. gestroi* (24, 25). The pattern has also been found in *N. corniger* (4). There is variation in latitude for *R. flavipes* and *Co. formosanus* in the United States (see table 2 in 123), yet further studies are needed to determine a definitive pattern across all invasive species.

SOURCES AND SINKS OF INVASIVE TERMITES

South and Southeast Asia (Indo-Malaya) are the source of the greatest number of invasive species (seven), followed by South America (six), Australia (five), Africa (two), North America (two), the Caribbean Islands (one), East Asia (one), and Europe (one) (**Figure 1**). All source areas are continental, except for the Philippines (*Heterotermes philippinensis*) and perhaps for the Caribbean Islands (*Heterotermes* n. sp.; 115). This pattern appears to relate to trade, which is the most important variable for probability of invasion (132), although little formal analysis has been done. The two most important areas for raw materials during the European colonial era, which used wooden ships, were Central and South America, and South and Southeast Asia. Spanish trading during this time likely spread *Cr. brevis* from Peru to the Caribbean Islands, Central America, and beyond (105). Australia has become one of the most important trading partners of South Pacific nations over the past century; raw logs and cut timber (especially recycled railway ties/sleepers) have been implicated as the source of several Australian species in New Zealand (10, 92), Fiji (37), and New Guinea (118).

Islands are the most invaded habitat (**Figure 1**). The islands of the Pacific Ocean are the most invaded region, with 13 species, followed by islands of the Caribbean Sea (nine), North

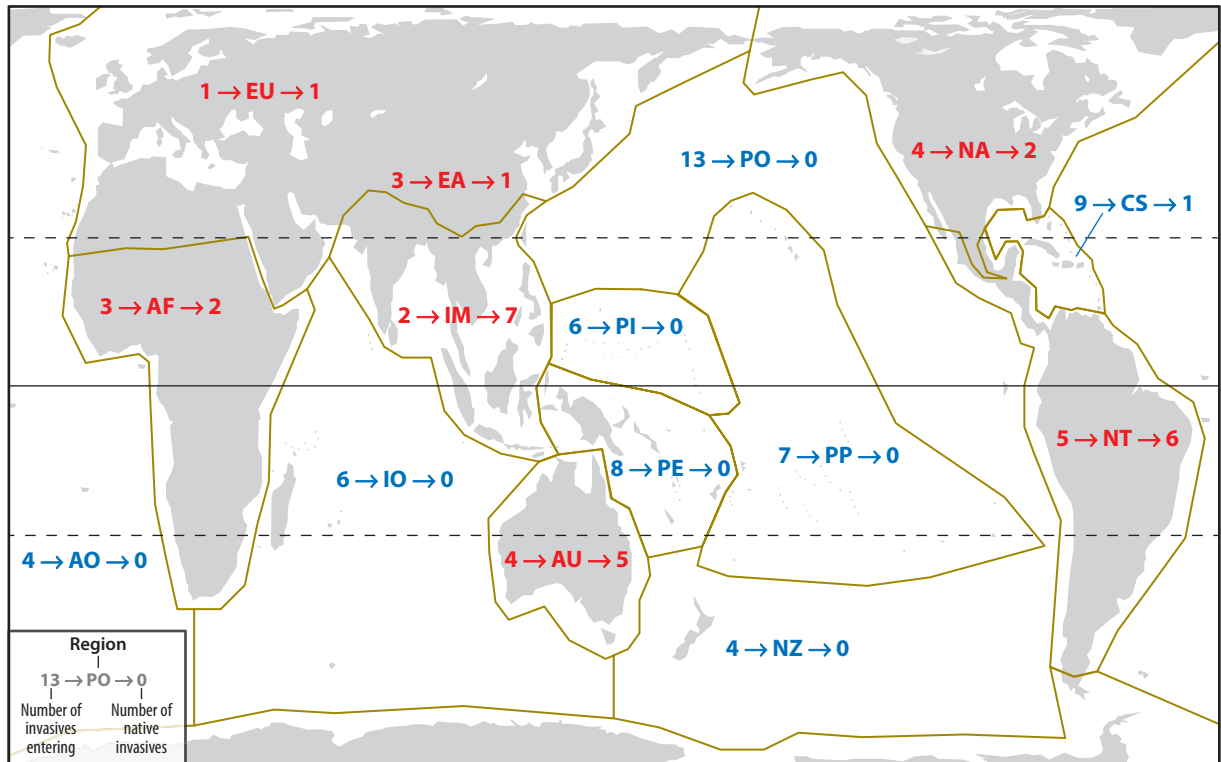


Figure 1

Number of invasive termite species and biogeographic regions (modified after Reference 122; *dark yellow lines*). Continental regions (*red*) are EU, Europe in Palearctic; EA, East Asia in Palearctic; AF, Afrotropics; IM, Indo-Malaya (~South and Southeast Asia); AU, Australia; NA, Nearctic (~North America); NT, Neotropics (~South and Central America). Islands in oceanic regions (*blue*) are AO, Atlantic Ocean; CS, Caribbean Sea; IO, Indian Ocean; and PO, Pacific Ocean, which has been subdivided into NZ, New Zealand; PI, Micronesia; PE, Melanesia; and PP, Polynesia. Number to left of region is the number of invasive species entering the region; number to the right is the number originating from the region. The equator is depicted by the solid line; the tropics are represented by dashed lines.

America (eight), islands of the Indian Ocean (six), South America (five), Australia (four), islands of the Atlantic Ocean (four), East Asia (three), Africa (three), South and Southeast Asia (two), and Europe (one). North America appears to be an anomaly in this list. However, most invasive species in North America are found only in southern Florida, which could be considered more part of the Caribbean than continental North America. Excluding Florida lowers the number of invasive termites in North America to four.

The pattern of continental species invading islands was observed forty years ago; invasive populations on continents were noted as limited to the coasts (39). The present-day pattern is similar; however, several species have penetrated inland into continents (**Figures 2–5**). This is seen most clearly for *Cr. brevis* in Brazil (23) and *Co. formosanus* in the United States, which have spread from the initial coastal sites of Louisiana, South Carolina, and Texas across ten states, to locations several hundred kilometers inland (8, 60, 80, 114, 135). As discussed above, improved molecular identification tools have shown invasive species well inland, e.g., *R. flavipes* in France and *N. corniger* in New Guinea.

Eradication: the complete removal of all individuals of an invasive species from an invaded country

Relative ease of detection may partly explain this pattern. Detection of novel termites is easier on islands (especially those distant from continents), as islands have few or no termite species (31). The appearance of a wood-destroying species is likely to be noticed in houses where none was previously known. Detection is harder on continents because termite diversity is higher, unless the introduced species is very different. Detection of *R. flavipes* in Uruguay and Chile and *Co. formosanus* in South Africa and the United States was rapid because there were no native congeneric species. In contrast, *R. flavipes* in France and *N. corniger* in New Guinea was not detected quickly because of the native congeners. The number of local expert termite taxonomists is likely also important; Florida, the most invaded state in the United States, also has a very active termite taxonomy program. If so, then invasions in much of Africa, Asia, and South America will be difficult to detect.

Preventing the establishment of invasive species is a part of the ecosystem resilience concept (33, 91). If resilience is conferred by related species or feeding types, then the regions with the greatest diversity should prove to be the most resilient. There is mixed evidence for this concept. For example, the kalotermitid *Cr. brevis* is absent from Asia (39, 105), which has a moderately high kalotermitid fauna (31, 32). Yet *Cr. brevis*, *Cr. dudleyi*, and *Cr. havilandi* have invaded most of the Caribbean Islands and South America and Madagascar, even though these areas have the highest diversity of kalotermitids on the planet (31, 32). No rhinotermitids are known to have invaded South and Southeast Asia, which has highest diversity of rhinotermitids and Type I and Type II intermediate nesters, yet *R. flavipes* is invasive in France, and *Co. formosanus* is invasive in Japan and the United States, both of which have native rhinotermitid species. These patterns depend on accurate identification, which may be an issue, as indicated above, or the invaders may outcompete the native species because of the sheer number of colony members (89, 112) or because they can better resist predators (131).

LIST OF INVASIVE SPECIES

There are now 28 invasive termite species. Of these, 14 species have been discovered since 1969 (39) (indicated below as “new”), 10 have increased distributions, and 4 have no change in distribution. Three species listed in 1969 are no longer considered invasive. Two were misdiagnosed and are now considered to have been introduced without establishment: *Neotermes insularis* (Kalotermitidae) from eastern Australia was found in New Zealand (39) but is now absent (10, 92), and the same is true for *Co. heimi* (Rhinotermitidae) from the Indian subcontinent in Java and Singapore (34). The third species, *Co. frenchi* (Rhinotermitidae), has been successfully eliminated by human control efforts (see below). The date of discovery of a new introduction is given in parentheses; “pre” is added to the date when the discovered infestation was extensive, suggesting long-term presence before discovery; and “unknown” is used when the invasive species was distinguished from well-established (and thus likely long-term) infestations.

Mastotermitidae

Mastotermes darwiniensis spread from tropical northern Australia to Lae in Papua New Guinea (pre 1959), probably transported during or soon after World War II (46). An eradication program (1962–1973) used organochlorine insecticides in soil and arsenic dust in buildings, some of which were eventually burned to the ground, and was believed to be successful. However, termites reappeared in buildings attacked previously (early 1990s; 118), and new infestations were discovered in previously unattacked buildings in 2002. The termites have since moved to trees, infesting 42 species of native and exotic trees, and the current infested area is now seven times larger than

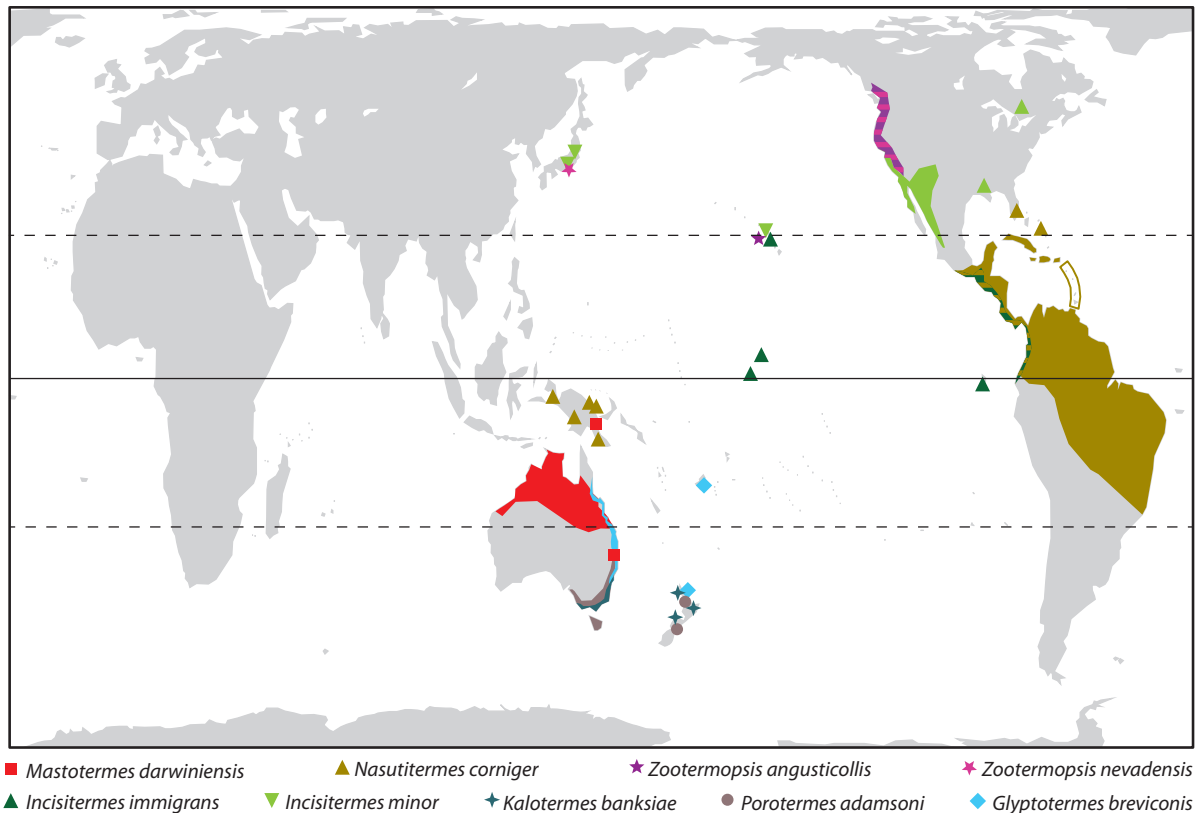


Figure 2

Native (colored areas) and invasive (symbols) distributions of nine species of invasive termites, from the Mastotermitidae (*Mastotermes darwiniensis*), Termopsidae (*Porotermes adamsoni*, *Zootermopsis angusticollis*, *Zootermopsis nevadensis*), Kalotermitidae (*Glyptotermes brevicornis*, *Incisitermes immigrans*, *Incisitermes minor*, *Kalotermitidae banksiae*), and the Nasutitermitinae subgroup of Termitidae (*Nasutitermes corniger*). Stripes represent areas where native distributions overlap. The equator is depicted by the solid line; the tropics are represented by dashed lines.

the area known from 1973 (118). *M. darwiniensis* has also spread within Australia, to the Gold Coast (pre 2008), approximately 800 km south of the native range (34) (Figure 2).

Termopsidae

Porotermes adamsoni from southeast Australia was introduced into New Zealand by imported railway wooden sleepers/ties in 1941; it is now found in five locations in the North Island and one in the South Island, in imported sawn timber and trees (10, 92) (Figure 2). *Zootermopsis angusticollis* (new) from western North America is considered established in Hawaii (1999) (45, 54) (Figure 2). *Zootermopsis nevadensis* (new), also from western North America, was first discovered in 2000 in forested parkland in Kawanishi, Japan (65) (Figure 2).

Kalotermitidae

Glyptotermes brevicornis (new) originates from the southeast coast of Australia and is invasive in New Zealand (pre 1983) (10) and Fiji (pre 1942) (37, 39) in localized areas in native trees (Figure 2). *Incisitermes immigrans* is native to the Pacific coast of Panama to Peru and was introduced into

Established:

describes a species that has accomplished a self-sustaining population outside its native range; imagos are produced

various Pacific Islands, including the Galápagos (unknown), Fanning and Jarvis Islands of Kiribati (unknown), Polynesia, Hawaii (unknown), and Japan (1995) (22, 39, 45, 65) (**Figure 2**). *Incisitermes minor* (new) originates from the southwestern United States and northern Mexico. It is invasive in the eastern United States (1995) (110); Toronto, Canada (1989) (43); Ninghai, Zhejiang Province, China (1937) (136); and islands of the Pacific Ocean, including Hawaii (~1999) (45) and Japan (1975) (84) (**Figure 2**). *Kaloterme banksiae* (new) from the southeast coast of Australia established in three locations in New Zealand (1942) (10) but has received little attention since it was first reported (**Figure 2**).

Cryptotermes brevis originates from coastal deserts of Peru and Chile (105) but was widespread throughout Central and South America by the time it was named (1853 in Jamaica) (22, 23). Thus, arrival dates of this most widespread invasive species are unknown for most locations but are likely to be post-Spanish conquest of Peru (in 1532). Invaded localities outside the Americas include Africa [Port Said, Egypt (105); Boma, Democratic Republic of the Congo; Njala, Sierra Leone; Cape Town and Durban, South Africa], Australia (~1941) (90), Pacific Islands of Polynesia (Easter Island, Marquesas, Hawaii, Midway Island) and Melanesia (Fiji, New Caledonia, Tonga) (all unknown), Atlantic Ocean islands [Saint Helena Island, Madeira Island (pre 1953), the Azores (2002), Canary Island] (12), and Lisbon, Portugal (87). A mature colony was recently discovered (and now fumigated) in New Zealand, introduced via a wooden figurine from Peru ten years prior to its discovery (11). The wide invasive distribution of this species is due likely to its ability to create viable propagules, as demonstrated by as many as eight separate colonies of *Cr. brevis* found in wooden pallets (44) (**Figure 3**).

Cryptotermes cynocephalus from the Philippines is found throughout Southeast Asia and may be native there; it is invasive in Sri Lanka (unknown), several locations around Cape York Peninsula, Australia (pre 1942); Rabaul, Papua New Guinea (pre 1942); and Hawaii (2000) (40, 111) (**Figure 3**). *Cryptotermes domesticus* from Southeast Asia has now spread throughout China (Hainan and Guangzhou Provinces), Taiwan, and Japan (all unknown), to Australia (pre 1942) (40) and across the Pacific Ocean (all unknown) to islands of Melanesia [Port Moresby and New Britain, Papua New Guinea (46); Solomon Island; Fiji; Samoa (59, 68)], of Micronesia [Guam (~1949), Fanning and Flint Islands of Kiribati], and of Polynesia (Marquesas, Oeno Island of the Pitcairns, and Austral and Society Islands of Tahiti), and to Panama in Central America (34, 39) (**Figure 3**).

Cryptotermes dudleyi also originates from Southeast Asia and has spread to India (Orissain Lower Bengal) and Bangladesh (Khulna, both unknown) across islands of the Indian Ocean (Cocos and Keeling Islands, Madagascar, Mauritius, pre 1950) to East Africa (Kenya, Tanzania, Somalia, and Uganda, all dates unknown) (98, 133). It has been found in few Pacific locations, such as northern Australia (pre 1942) (40) and Micronesia (Guam and Marshall Islands), but more so in the Caribbean Islands (Jamaica and Trinidad) (103) and South America (Panama, Costa Rica, Colombia, and Brazil, all dates unknown) (22, 23) (**Figure 3**).

Cryptotermes havilandi comes from tropical West Africa and spread (all dates unknown) to Fernando Pó Island and westward to the Caribbean Islands (Antigua, Barbados, Guadeloupe, Saint Kitts, Nevis, Saint Lucia, Saint Vincent, Little Tobago, Saint Croix, and Saint Thomas) (102, 103), Guiana (Kartabo), Suriname (Paramaribo), and Brazil (Santos and Guaratuba) (23). It also spread eastward to Tanzania, to islands in the Indian Ocean (Madagascar, Comoro, and Europa), and to India and Bangladesh (13, 77) (**Figure 3**).

Rhinotermitidae

Heterotermes convexinotatus (new) has a wide range in South America, from Mexico to Argentina, and is invasive in (all dates unknown) the Greater (Hispaniola and Puerto Rico) and Lesser

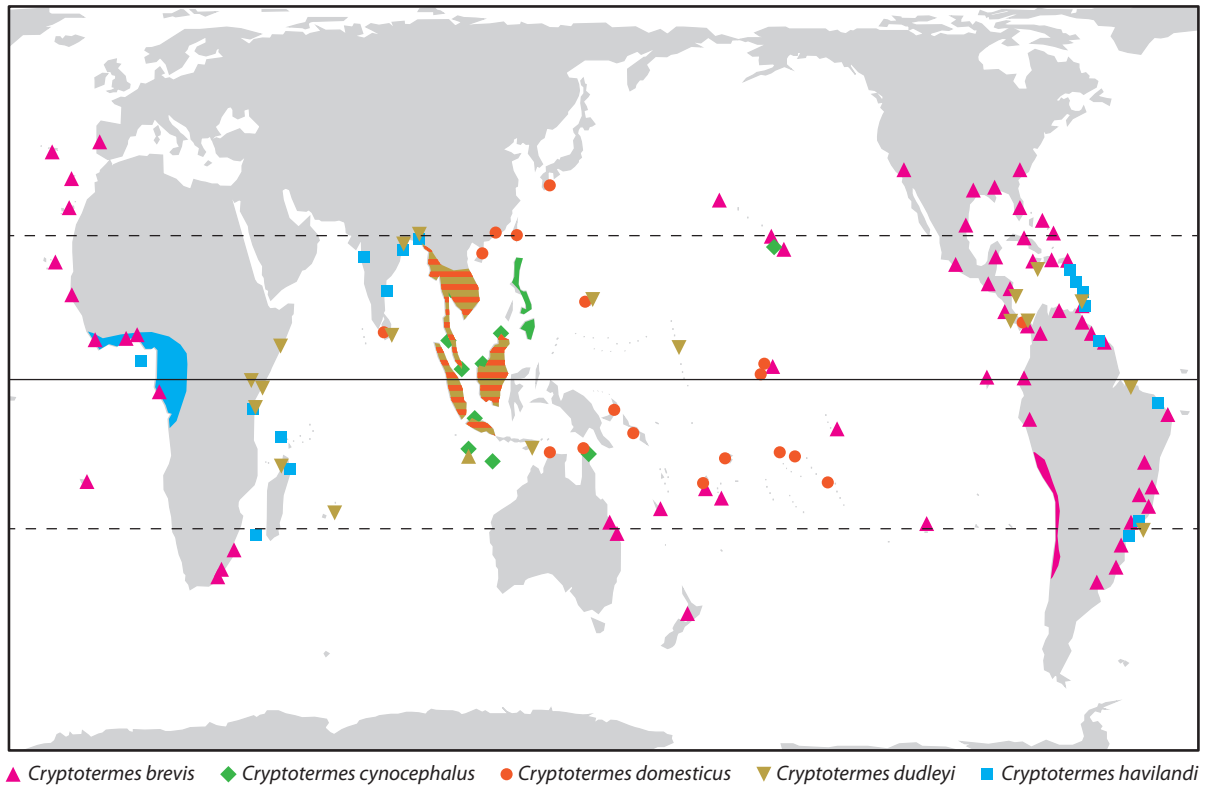


Figure 3

Native (colored areas) and invaded (symbols) distributions of five species of invasive *Cryptotermes* from the Kalotermitidae. Stripes represent areas where native distributions overlap. The equator is depicted by the solid line; the tropics are represented by dashed lines. The symbols indicate published records only. *Cryptotermes brevis* is very common in tropical South America and somewhat common in North America; *Cryptotermes cynocephalus* is very common in Southeast Asia.

Antilles (Antigua, Barbados, Curacao, Martinique, Saint Kitts, and Saint Maarten) (115) and in the Galápagos (88) (**Figure 4**).

Heterotermes perfidus has unknown origins and may not be a valid species. It is known only from Saint Helena Island in the south Atlantic Ocean (~1840), where it was introduced from a slave ship that traveled between West Africa, South America, and the Caribbean Islands (39). All these locations have native *Heterotermes* species; two from South America (*H. convexinotatus* and *H. tenuis*) are invasive elsewhere, and perhaps *H. perfidus* originates from there as well. An alternative source is suggested by the four (invasive) ant species on Saint Helena Island, which are either pantropical or African (34, 117) (**Figure 4**). *Heterotermes philippinensis* from the Philippines is invasive in Madagascar and Mauritius (unknown) and is found in the forests of regions Diana and Sofia, Madagascar (19) (**Figure 4**). *Heterotermes* n. sp. (new) was found in Miami, Florida (1994), but it may be the Caribbean Island species *H. cardini*, *H. convexinotatus*, or *H. tenuis* (see 34); if not, its origin is unknown (115) (**Figure 4**). *Heterotermes tenuis* (new) is native from Central America to the Guianas, and is invasive in the Lesser Antilles (Grenada Guadeloupe, Saint Lucia, and Saint Vincent) and Trinidad and Tobago (all dates unknown) (115) (**Figure 4**).

Reticulitermes flavipes originates from the eastern United States and has spread to Canada (Toronto, 1938; Winnipeg, 1987) (43), the Bahamas (1998) (100), Europe [Vienna, Austria (1837);

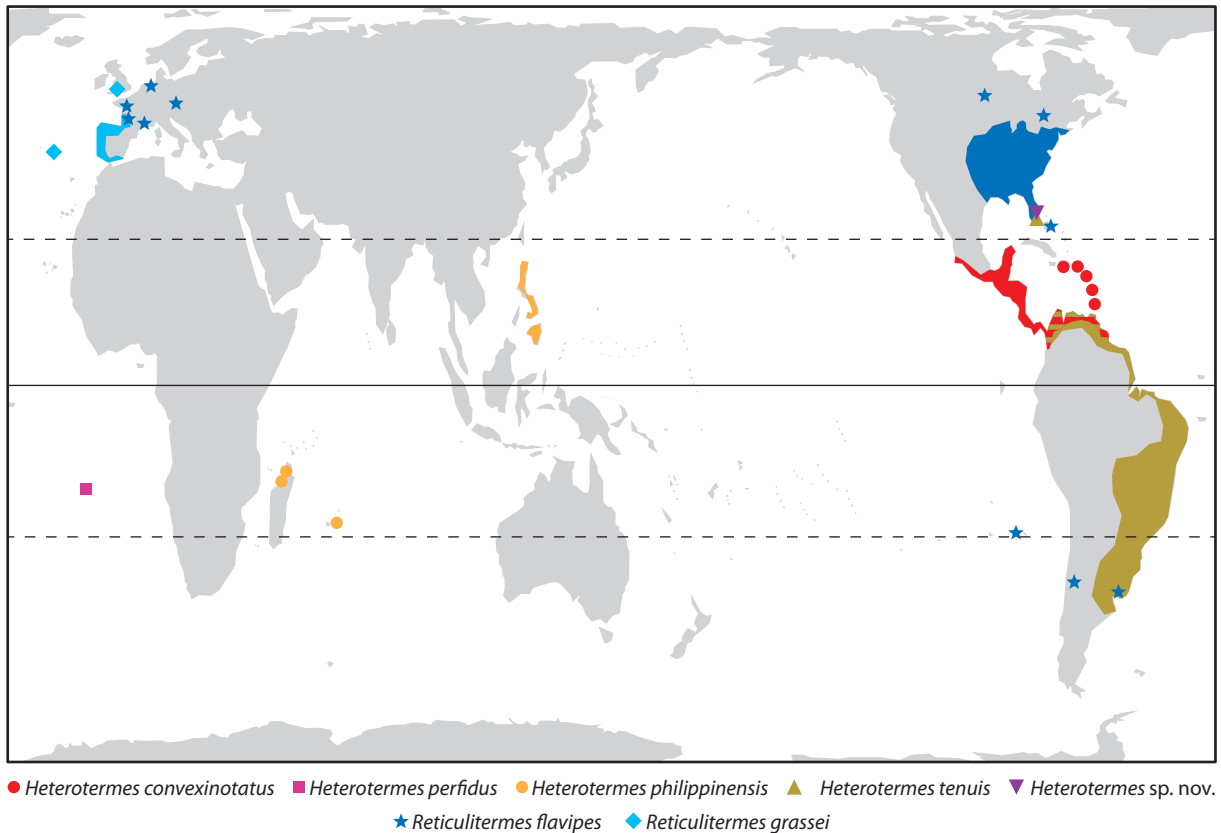


Figure 4

Native (colored areas) and invaded (symbols) distributions of seven species of invasive *Heterotermes* and *Reticulitermes* from the Rhinotermitidae. Stripes represent areas where native distributions overlap. The equator is depicted by the solid line; the tropics are represented by dashed lines.

Hamburg, Germany (pre 1937); and southwestern France (pre 1840)] (30), and South America [Montevideo, Uruguay (~1960) (2), and Santiago, Chile (1986)] (113), from where it likely was carried to Easter Island (unknown) (7). The probability of propagules forming may be higher in this species because of its placement of nymphs in food resources (73). Baiting has been used against *R. flavipes* in Santiago and was found to perform better than alternative treatments using area-wide management population suppression criteria (94) (**Figure 4**).

Reticulitermes grassei (new) comes from southwestern Europe (France and Spain) and has established in Britain (Saunton, 1994) (61, 126) and in Faial Island of the Azores (~2000) (87). An eradication program under way in the United Kingdom began in 1994 with a synthetic pyrethroid insecticide. Termites were rediscovered four years later. Baiting was used and termite activity ceased by 2000 (126); however, termites were found again in 2009 (14) (**Figure 4**).

Coptotermes acinaciformis is native to Australia and was introduced into Auckland and New Plymouth, New Zealand (~1930), via railway sleepers/ties and telephone poles (82). Continuous management has eliminated populations locally, yet new locations likely associated with more recent introductions into the North Island and one into the South Island have been reported, including in native trees (10, 92). It was also found in Suva, Fiji (1939), but did not establish there

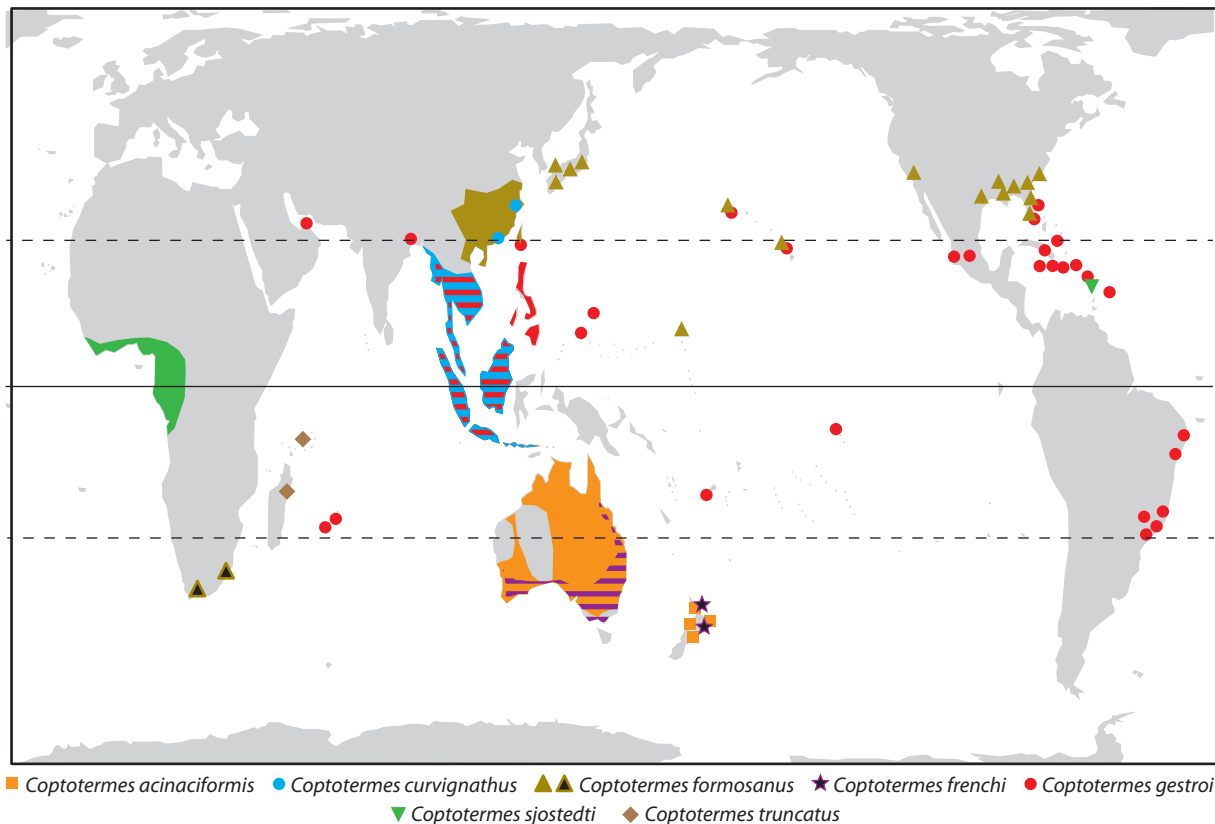


Figure 5

Native (colored areas) and invasive (symbols) distributions of seven species of invasive *Coptotermes* from the Rhinotermitidae. Stripes represent areas where native distributions overlap. The equator is depicted by the solid line; the tropics are represented by dashed lines. Symbols with black center indicate a population that has likely been eradicated.

(39, 68) (**Figure 5**). *Coptotermes curvignathus* (new) is from Southeast Asia and has been reported as a serious pest in two locations in southern China (unknown) (136) (**Figure 5**).

Coptotermes formosanus originates from southern China and Taiwan (67, 74); it is invasive in Japan (~1700) and crossed to Marshall Island (unknown), Midway Island (unknown), and Hawaii (1907), and later appeared in the continental United States (~1950s) (116). The spread of this species in the United States is the best-documented termite invasion. It was recorded first in Charleston, South Carolina, from alates only (1957) (20), and then in Lake Charles and New Orleans, Louisiana, and Houston, Texas (1965–1967), from two independent introductions (8, 53, 57, 130) but was likely introduced a decade or more earlier (63). In 40 years it has spread to 42 cities in 25 parishes in Louisiana (16, 80), in 35 years to 14 counties in Texas (55), in 22 years to 25 counties in Mississippi (1984) (114), and in 25 years to 40 cities in 20 counties in Florida (1980) (109). It is now found in these states as well as Alabama, California, Georgia, North Carolina, and Tennessee, having spread primarily through movement of infested wood, especially recycled railway ties/sleepers (80, 60), and potted plants and furniture (5). Natural forests have been invaded as well, possibly with higher populations (as inferred from higher alate numbers) (114). Baiting has been used in area-wide management of *Co. formosanus* in New Orleans since 1998

(69). Colonies have disappeared within one to two years, although termites from new colonies have reinfested quickly, from railways (58) and parks (79, 85). It was recorded in South Africa (1974) at two locations (Simonstown in Cape Province and Komatipoort in Natal Province). An eradication program drenched the buildings and surrounding soil with organochlorine insecticides, and then the buildings were burned down (21). *Co. formosanus* has not been sighted for 36 years (83) (**Figure 5**).

Coptotermes frenchi is native to southern Australia and has been introduced into four locations in New Zealand (1938) (82). This species is considered eradicated from New Zealand after the use of arsenic dust in buildings and power poles and organochlorine insecticides in soil; there have been no reports of it for 29 years (10, 92) (**Figure 5**).

Coptotermes gestroi comes from Southeast Asia and has spread west to Mauritius (1936) and Réunion Island (1957) and north to Taiwan (2001) (121, 74). It has been transported across the Pacific Ocean to Polynesia [Midway Island (unknown), Hawaii (1963, 1999) (134), Marquesas Island (pre 1932)], Micronesia (Yap, Guam, Marshall Island, all unknown), and Fiji (pre 2009). It is found in Mexico (2000) (38), Florida (1996) (109), and throughout the Caribbean Islands, including the Turks and Caicos Islands (unknown) (Grand Turk, Providenciales), Greater Antilles (unknown) (Cuba, Jamaica, Grand Cayman, Little Cayman, and Puerto Rico), and Lesser Antilles (1937) (Antigua, Barbados, Barbuda, Saint Kitts, Nevis, Virgin Gorda, Monserrat) (26, 62, 101, 102, 108, 134), and is spreading along the south Atlantic coast of Brazil (pre 1923) (Rio de Janeiro, Santos, and São Paulo) (22, 23, 25) (**Figure 5**).

Coptotermes sjostedti (new) originates from tropical West Africa and has established in one location in the Lesser Antilles (Guadeloupe Island, pre 1999) (104) (**Figure 5**). *Coptotermes truncatus* (new) has unknown origins and may not be a valid species. It was identified from Tamatave, Madagascar, and the Republic of Seychelles in 1897 and has spread into the forests of northeast Madagascar (19, 127). It may be *Co. formosanus* from China, *Co. gestroi* from Southeast Asia, or *Co. intermedius* from West Africa (51). *Co. gestroi* seems more likely because it is found in the nearby Mauritius and Reunion Island, along with two other Southeast Asian termite species also found in Madagascar, *Cr. dudleyi* and *H. philippinensis* (34, 39) (**Figure 5**).

Termitidae

Nasutitermes corniger (new) is widespread from Central to South America and the Caribbean Islands (22, 23, 106). It is invasive in three locations, Abaco Island of the Bahamas (unknown) (34), Florida (pre 2001) (99), and New Guinea (unknown) (107), where it was long considered another species (see below), and is found in native forests (**Figure 2**). It was considered eradicated from Florida in 2004 but was rediscovered in the same locations in 2012 (15).

Termes hispaniolae (new) is from the coast of Central and South America. It has a disjunct distribution in the Caribbean Islands: Hispaniola and Puerto Rico; Guadeloupe, Saint Croix, and Saint Thomas (102); and now New Providence and South Andros Island (~2002). This distribution may suggest human transport, which has been observed in shipments of firewood entering Barbados from British Guyana (39).

FUTURE PATTERNS

The known 28 invasive species are likely to increase their ranges, as 10 of the 17 known invasive species did between 1969 and 2011. The four species without a range increase had no new information reported, so an increase may have occurred for them also. Eight species appear on the

cus of invading natural habitats; almost all were discovered in nonnative locations within the past 50 years. They have been found outside buildings, infesting native trees in urban streets and parks, and in patches of remnant forest within or adjacent to urban areas. These eight species include *M. darwiniensis* in Papua New Guinea (118), *Porotermes adamsoni* in New Zealand (92), *Zootermopsis nevadensis* in Japan (65), *Glyptotermes brevicornis* in New Zealand (10), *Cr. brevis* in Hawaii (45, 111), *Cr. domesticus* and *Cr. dudleyi* in parts of Australia and New Guinea as well as Samoa (40, 46, 59), and *Co. gestroi* in Cuba (26). These habitats may be simply geographic routes from urban centers to the surrounding countryside, or they may suggest a stepping-stone adaptation process from urban to natural habitats.

New molecular tools are likely to continue to produce exciting results, such as resolving the true identities of *Heterotermes perfidus* and *Coptotermes truncatus*. *H. perfidus* was introduced into and described from Saint Helena Island before 1850, and *Co. truncatus* was identified in Madagascar and the Seychelles in 1897 (see List of Invasive Species, above). Others may be synonymized, as is the case with *Co. gestroi*. This species was originally described from Thailand, Myanmar, and Assam (India) but now includes the junior synonyms *Co. havilandi* from Peninsular Malaysia and Indonesia and *Co. vastator* from the Philippines, and may also include other species from India and Sri Lanka (66, 137, 138). A similar situation exists for *N. corniger* and three likely junior synonyms from Central America and the Caribbean Islands (23). The large increases in range caused by synonymies pose questions about native distribution of these species; trade has existed for centuries or millennia in Southeast Asia and South America. Identifying the original native habitat will require detailed population-level genetics, as is being undertaken for *Co. formosanus* (8, 57, 74, 123, 124, 125). These tools are not trouble free, especially when only one sequence or shorter mitochondrial sequences are used (115); therefore, caution still needs to be employed (81, 97).

Any new invasive species is likely to resemble the existing 27: wood-eating, Type I or Type II single-piece or intermediate-piece nester, with secondary reproductives, from an area with a high volume of trade; solid-wood packing material is likely to be increasingly important (e.g., 49). Most likely there will be more kalotermitids (especially *Cryptotermes* species) and rhinotermitids (especially *Reticulitermes*, *Heterotermes*, and *Coptotermes* species), but termitids (*Nasutitermes* and, perhaps, *Microcerotermes* and *Amitermes*) may join the list. Only a small minority of termites are invasive, even among the most invasive families, Kalotermitidae and Rhinotermitidae. The three characteristics common to all invasive species are also common to other termites that are not known to be invasive; thus, they are insufficient by themselves to explain invasiveness. Other factors may also be important, such as higher and faster production of neotenic secondary reproductives and food choices of invasives compared with those of noninvasive congeners (35, 70, 71). More work is needed to elucidate these differences.

Eradication attempts are likely to remain difficult to assess. Termites are cryptic organisms, hidden inside wooden objects, buildings, trees, and soil; thus, the success of eradication is measured by the period of time since the invasive species was last seen. Two eradications are considered successful, that of *Co. formosanus* from South Africa after 36 years without detection (83) and that of *Co. frenchi* from New Zealand after 29 years without detection (10, 92). Of the many other eradication attempts, two are notable owing to the reappearance of the invasive species after a long period without detection: *M. darwiniensis* from Papua New Guinea after approximately 20 years without detection (118), and *R. grassei* from the United Kingdom after 10 years without detection (14). These eradication attempts may yet be successful, or eradication may transform into ongoing management, as for the locally rare *Cr. brevis* in Australia (90), the locally abundant *I. minor* in Japan (84), *R. flavipes* in Chile (94), and the now widespread and abundant *Co. formosanus* in the United States (55, 80, 109, 114).

CONCLUSIONS

Invasive termites are increasing in number and geographic area; better preventive measures are required to slow or stop the spread of these species. Comparisons with other invasive social insects are likely to be biologically informative, especially ants, of which 147 species are invasive (78). Yet there is one difference between termites and ants that is likely to be important for preventive measures: Termite introductions always appear to be due to wood. Therefore preventive measures against termites are likely to be the same as those used for other wood-eating insects. Perhaps lessons for preventing new introductions might best be learned from *Anoplophora glabripennis*, the Asian longhorned beetle, for which standards for heat treatment and chemical fumigation in international trade have been set (50). More careful consideration of treating wood in domestic trade, such as recycled railway ties implicated in the spread of *Coptotermes formosanus* in the United States (60, 80), is also required.

SUMMARY POINTS

1. The number of invasive termite species has grown from 17 in 1967 to 28 today.
2. The distribution of invasive species (especially from urban to natural habitats) is growing, as measured by the number of invaded locations, the size of invaded area at each location, and the habitat types.
3. All invasive termites eat wood, nest in their food, and easily produce secondary reproductives. These characteristics combine to make propagules for transport.
4. Islands have the most invasive species, especially those in the Pacific Ocean (13 species) and the Caribbean Sea (9 species).
5. The most invasive species come from the tropical regions of South and Southeast Asia (Indo-Malaya; 7 species) and South America (6 species), probably because these regions were major sources of commodities for trade.
6. Standard pest control methods have been used in eradication attempts, and success is difficult to determine due to the cryptic habits of termites. Only two species have been successfully eradicated: *Coptotermes formosanus* from South Africa and *Co. frenchi* from New Zealand.

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