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Not just urban: The Formosan subterranean termite, *Coptotermes formosanus*, is invading forests in the Southeastern USA

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Abstract *Coptotermes formosanus*, known in its native China as the 'House White Ant', was introduced to the southeast USA likely in the 1950s, where it is known as the Formosan subterranean termite. In the USA it is best known as a pest of buildings in urban areas, however *C. formosanus* also attacks live trees along streets and in urban parks, suggesting it may be able to invade forests in the USA. A survey of 113 forest patches around Charleston South Carolina and New Orleans Louisiana, where *C. formosanus* was first recorded, found that 37% and 52%, respectively, were infested. Resistograph measurement of internal hollows in tree trunks in forest patches infested with *C. formosanus* found infested sites contained more and larger hollows compared with non-infested sites. Compared with forest patches free of *C. formosanus,* infested patches had 32% more trees with hollows in Charleston, and 115% more in New Orleans. Similarly, compared with patches free of *C. formosanus*, hollows were 2–3 times larger in infested patches in Charleston, and 2–6 times larger in New Orleans. *Quercus* (oak) and *Acer* (maple) were the most damaged trees in Charleston, whereas *Carya* (bitternut hickory), *Taxodium* (bald cypress), *Nyssa* (blackgum) and *Liquidamber* (sweetgum) were the most damaged in New Orleans. As termite damaged trees are more likely to die, these differing damage levels between tree species suggests that *C. formosanus* may alter community structure in US forests.

Keywords Forest pest · Formosan subterranean termite · Isoptera

Introduction

Coptotermes formosanus is the most common termite in urban areas in its native China and Taiwan; it dominates urban areas so completely it is known as Jiā báiyǐ or the 'house white ant' (Wang et al. 2002; Zhung and Liu 2003). It is an invasive species, established in Japan, Marshall and Midway Islands, Hawaii and the continental USA (Evans et al. 2013). The termite likely arrived in several ports of the southeastern USA post World War 2, certainly by the 1950s (Beal 1987; Chambers et al. 1988). In the following 60 years, *C. formosanus*, known in the USA as the 'Formosan

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subterranean termite' or FST, has spread to over 120 urban areas in 10 southeastern states, having spread primarily through movement of infested wood, especially recycled railway ties/sleepers, but also potted plants and furniture (Atkinson et al. 1993; Messenger et al. 2002; Jenkins et al. 2002; Lee et al. 2009; for review see Evans et al. 2013).

Almost all field research on *C. formosanus* in China, Japan and the USA has occurred in urban areas, and focussed on pest control, especially in buildings and other human constructions (e.g. Wang et al. 2002; Zhung and Liu 2003; Lax and Osbrink 2003; Guillot et al. 2010). There were early observations in the USA that this species can infest and consume the heart wood of live trees in urban areas (Lai et al. 1983; Beal 1987; La Fage 1987; Henderson and Forschler 1996), however the focus on buildings meant the threat to urban trees planted along streets or parks did not receive attention until later (Osbrink et al. 1999; Mankin et al. 2002; Osbrink and Lax 2002, 2003; Messenger et al. 2005).

The infestation and consumption of living trees suggests that *C. formosanus* may be able to spread from urban areas and invade forests. In Japan, *C. formosanus* are found in forests in the southern islands (Mori 1987; Abe and Watanabe 1981; Yasuda et al. 2000; Iwata and Kodama 2007) and are used for field testing of wood preservatives (e.g. Tascioglu et al. 2013). The congeneric Southeast Asian species *C. gestroi* was observed attacking and hollowing living rubber trees (*Hevea brasiliensis*, native to South America) in Malaysia over one century ago (Bailey 1901; Ridley 1909), prompting the belief that native trees in natural forests were immune to termite attack. This belief changed with better survey methods (e.g. Harris 1966a, b; Roy-Noël 1966; Tho 1982). It is now understood that *Coptotermes* species native to Africa, South America, Asia and Australia have evolved to feed on and nest inside living trees, in both plantations and natural forests (for a review see Cowie et al. 1989; also Bandeira 1993; Apolinárioa and Martius 2004; Werner and Prior 2007; Jasmi and Ahmad 2011; Lee et al. 2015, 2017). Indeed, the common name for *Coptotermes* in Australia is 'tree-piping termite' (Andersen and Jacklyn 1993).

There is evidence that *C. formosanus* appears to be spreading naturally from urban areas into surrounding forested lands in the USA. Two other studies from Mississippi found alates (the winged reproductive termites) in non-urban habitats, including forests, sometimes in higher numbers than in rural areas (Sun et al. 2007; Lax and Wiltz 2010). Although suggestive, there are two potential sources for bias in those methods. First was the use of light traps. Light traps attract flying adult termites, and a light trap in dark forest may attract more alates from further away than a light trap in an urban setting (Bowden 1982; Muirhead-Thompson 1991; Yela and Holyoak 1997). Second was the proximity of human activity. The light traps in 'forested locations' were sometimes close to human constructions, highways, or railways (Sun et al. 2007; Lax and Wiltz 2010), therefore human transport also may account for collecting *C. formosanus*. In addition to alates, Little et al. (2014) also surveyed for foraging worker and soldier termites in more than 7000 stumps in 11 clear-cut pine plantations. They only found native *Reticulitermes* species in 5% of the stumps, perhaps indicating the difficulty of finding *C. formosanus* in locales with low densities.

If *C. formosanus* is spreading into forests, it may affect tree species composition. In laboratory testing of commercial lumber samples, *C. formosanus* preferred to eat birch, pine, maple, and oak over sassafras, cypress and cedar (Morales-Ramos and Rojas 2001). Surveys of trees along streets and parks suggest similar patterns (La Fage 1987; Osbrink et al. 1999). Attack by various *Coptotermes* species reduced growth, fecundity and survival of trees in many countries (Gray and Buchter 1969; Speight and Wylie 2001; Werner and Prior 2007; Werner et al. 2008; Zorzenon and Campos 2015). If these results from laboratory tests are indicative, and if US trees respond similarly, then *C. formosanus* may change forest communities in the USA.

We aimed to determine: whether *C. formosanus* had invaded natural forest communities in the southeastern USA. If so, then we aimed to measure the level of damage to standing trees in forests, and to determine whether *C. formosanus* had a feeding preference based on damage level. We surveyed forested areas in and on the periphery of Charleston South Carolina and New Orleans Louisiana because these are among the oldest known urban infestations in the continental USA, and populations of *C. formosanus* and tree infestations appear to be particularly high in New Orleans (King and Spink 1969; Chambers et al. 1988; Osbrink and Lax 2002; Messenger et al. 2005). We chose forested areas, patches, 10 km or less from urban areas as potentially infested and > 50 km as potentially clear patches, because the natural rate of spread of termites is slow, limited by weak alate dispersal (around 0.2–1 km; Messenger and Mullins 2005; Shelton et al. 2006; Hu et al. 2007; Connétable et al. 2012; Mullins et al. 2015), and perhaps 4–8 years until incipient colonies mature and produce alates (Thorne et al. 2002; Grube and Forschler 2004); values used in models of termite spread (Cameron et al. 2008; Tonini et al. 2013; Hochmair et al. 2013; Suppo et al. 2018).

Methods

Resistograph

The Resistograph is an instrument used to determine rot and hollows in wood, such as wooden poles and trees. The physical resistance to drilling is measured, using a 150 mm long × 2 mm diameter bit rotating at 1000 rpm, which correlates to the density of the wood, and is accurate enough to detect tree rings (Rinn et al. 1996; Mattheck et al. 1997). Detection of hollows and wood rot was indicated by zero resistance for hollows or lower density, and less resistance, for rotted wood, respectively. Researchers, managers of utility poles and foresters use Resistographs routinely to determine the status of wood (Moore 1999; Isik and Li 2003; for reviews see Johnstone et al. 2013; Gao et al. 2017). The Resistograph was used to find hollows in three species of urban trees infested by *C. formosansus* in New Orleans, demonstrating the utility of the instrument for investigating termite infestations (Osbrink and Lax 2002).

Study locations

We identified forested sites termed locales (9 in Charlestown and 8 in New Orleans) within 100 km from each city centre, using local maps and Google Earth, and surveyed 71 and 113 forest patches within locales for each city, respectively (Table 1). We choose forest patches greater than five hectares with a lower level of human disturbance, as determined by: no internal roads, presence of large native trees, and local knowledge of managing authorities (Table 1). We conducted a standardised search in two stages at each forest patch. In the first search stage we walked a 200 m × 2 m transect located approximately in the centre of the patch and examined all standing and fallen dead timber (usually stumps and logs) for *C. formosanus*, including visual search and a microwave detection device, Termatrac® (Evans 2002a). We cut into stumps and logs with axes to search for live termites or hollows caused by their feeding. We rolled logs so that the soil and the underside of the log was exposed, to search for live termites or their tunnels. The second search stage occurred when we found *C. formosanus*. We searched a circular area, 30 m radius, from any *C. formosanus* infested stump or log for additional infestations (King and Spink 1969; Evans 2002b). We categorised forest patches with no *C. formosanus* as ‘clear’, and those with at least four infestations as ‘infested’; forest patches with one to three infestations were not used. We searched a total of 184 forest patches around Charleston SC and New Orleans LA, of which 113 were retained for the study (Table 1).

Tree trunk data

We collected data on possible *C. formosanus* infestation of live trees in the forest patches designated clear and infested. We placed new transects (100 m × 2 m) at least 5 m apart so they did not overlap and identified all trees along those transects, then measured each for hollows using a Resistograph (F-series, IML-Instrumenta Mechanic Labor GmbH, 1275 Shiloh Road, Ste. 2780–30144 Kennesaw, GA, USA). We drilled tree trunks two to four times, between 30 and 120 cm above ground level. The instrument recorded a graphical trace of wood resistance against linear depth, from which we extracted four metrics. (1) number of hollows (number of separate instances of resistance at zero), (2) length of ‘sound’ wood (length of trace at maximum resistance), (3) length of ‘hollows’ (length of trace at zero), and (4) length of ‘weak’ wood (length of trace between maximum resistance and zero). We recorded measurements on 370 trees (Table 2). We converted the lengths of hollows and weak wood to proportions of total trace to control for variable drilling length (min = 79 mm, max = 150 mm, average = 139 mm).

Table 1 The number of forest patches searched for *Coptotermes formosanus* in locales in the two main regions of Charleston and New Orleans

Region locales	Clear	Infested	Total	% FST
Charleston				
Cordesville/Frances Marion NP	5	0	5	0
Berkeley/Power Station	5	0	5	0
Mt Pleasant	7	0	7	0
Daniel Island	6	6	12	50
North Charleston	14	1	15	7
Charleston downtown	0	2	2	100
West Ashley/Charles Towne Landing	0	10	10	100
Bess Ferry Rd	2	0	2	0
James Island	6	7	13	54
Total	45	26	71	37
New Orleans				
McNeil	1	3	4	75
Picayune	5	0	5	0
North New Orleans	0	5	5	100
Chalmette	0	4	4	100
Gretna	7	2	9	22
Lower Algiers	2	4	6	67
Jean Lafitte Park	3	4	7	57
Bayou Cygnette State Park	2	0	2	0
Total	20	22	42	52
Grand total	65	48	113	42

Analysis

Clear and infested forest patches thus become two treatments in a ‘natural experiment’. We compared the number and size of hollows between forest patches infested with *C. formosanus* to those that were clear of the termite. We were not able to attribute all hollows or soft wood found in tree trunks to *C. formosanus*, however any increase in hollows was interpreted as due their presence. We compared the frequency of infestation of forest patches between Charleston and New Orleans in two ways, first with a *t* test using forest patches as replicates within locales, considering that *C. formosanus* distribution may be clumped due to human factors, and second with a Fisher’s exact test ignoring locales. We analysed tree species data for each city separately, because species composition differed between cities (Table 2). We analysed resistograph metrics (number of hollows, proportion of weak wood and proportion of hollows) with generalised linear models (GLM) with three factors: (1) presence of *C. formosanus*, (2) city, (3) tree species, but only trees found in both cities using post hoc pairwise comparisons tested by LSD. We square-root/arcsin-transformed length proportions to improve homogeneity of variance assumptions.

Results

We searched 71 patches in nine locales around Charleston; of these, 26 patches (37%) were found to be infested. Within locales, the percentage of patches with *C. formosanus* ranged from 0 to 100%; five of the nine locales had less than 50% infestation of patches. We searched 113 patches in eight locales around the New Orleans region; of these 48 patches (42%) were found to be infested. Within locales, the percentage of patches with *C. formosanus* ranged from 0 to 100% with only three of nine locales in New Orleans having less than 50% infestation while infested locales in Charlestown provided 5 of 9 with less than 50% infestation (Table 1). The average infestation rate of forest patches within locales in Charleston (34.5 ± 14.5%) was not was significantly different from those in New Orleans (52.6 ± 14.4%;

Table 2 Tree species identified in forest patches in Charleston and New Orleans

Species	Common name	Count	
		Charleston	New Orleans
Quercus falcata	Southern Red Oak	10	
Quercus laurifolia	Laurel Oak	7	
Quercus nigra	Water Oak	26	17
Quercus virginiana	Live oak	6	2
Quercus sp.	Unknown		17
Acer negundo	Boxelder		3
Acer rubrum	Red Maple	16	16
Liquidambar styraciflua	American Sweetgum	22	6
Carya cordiformis	Bitternut Hickory	10	
Carya illinoinensis	Pecan		5
Nyssa sylvatica	Blackgum	13	4
Celtis laevigata	Sugar Hackberry	2	43
Ulmus americana	American Elm	3	26
Pinus taeda	Loblolly Pine	42	2
Magnolia grandiflora	Magnolia	8	1
Ostrya virginiana	Ironwood	6	
Morus rubra	Red Mulberry	2	
Ilex opaca	American Holly	1	
Liriodendron tulipifera	Yellow poplar	1	
Taxodium distichum	Cypress		10
Salex nigra	Willow		23
Melia azedarach	Chinaberry		1
Platanus occidentalis	Sycamore		3
Sapium sebifera	Chinese tallow		11
Unknown	–		4

$t_{15} = 0.889$, $p = 0.388$). Also, the infestation of patches considered without locales did not differ between the two regions (Fisher's exact $p = 0.118$).

We drilled 176 trees with the Resistograph in Charleston. In clear forest patches, 67% of the trees had hollows (44 hollow trees of 66 total trees), compared with infested forest patches, where 80% of the trees had hollows (88 of 110 total trees), which was a significant difference ($\chi^2 = 5.021$, $df = 1$, $p = 0.025$). We drilled 194 trees with the Resistograph in New Orleans. In clear forest patches, 27% of the trees had hollows (23 of 86 total trees), compared with infested patches where 55% had hollows (60 of 108 total trees), which was a significant difference ($\chi^2 = 16.235$, $df = 1$, $p < 0.001$). Trees in Charleston had more hollows than those in New Orleans, in clear patches ($\chi^2 = 23.185$, $df = 1$, $p < 0.001$) and infested patches ($\chi^2 = 16.858$, $df = 1$, $p < 0.001$) (Fig. 1). The hollows in Charleston were frequently small (1–2 mm), near the surface, and may not represent termite attack.

The number of internal hollows in drilled trees, among tree genera found in both cities, differed significantly with termite presence, with more hollows per tree in *C. formosanus* infested forest patches compared with clear patches ($F_{1,822} = 16.192$, $p < 0.001$). There was no difference between regions ($F_{1,282} = 1.998$, $p = 0.159$), but there were significant differences between tree genera ($F_{7,282} = 3.263$, $p = 0.002$), there was an interaction between region and tree genera ($F_{7,282} = 2.777$, $p = 0.008$). This was because there were more hollows per tree in *Celtis* in Charleston compared with New Orleans, and more hollows per tree in *Pinus* in New Orleans than Charleston (Fig. 2).

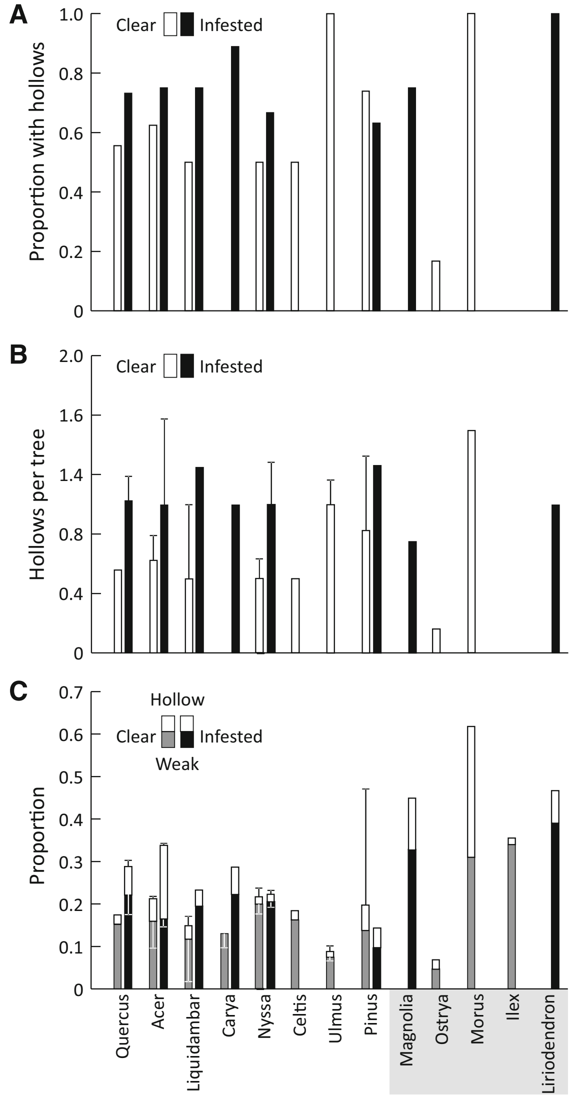

Fig. 1 Hollows in trees in Charleston. **a** Proportion of trees in a patch with hollows. **b** Average number of hollows per tree. **c** Average proportion of resistograph trace either hollow or weak wood. Tree names in grey found only in Charleston

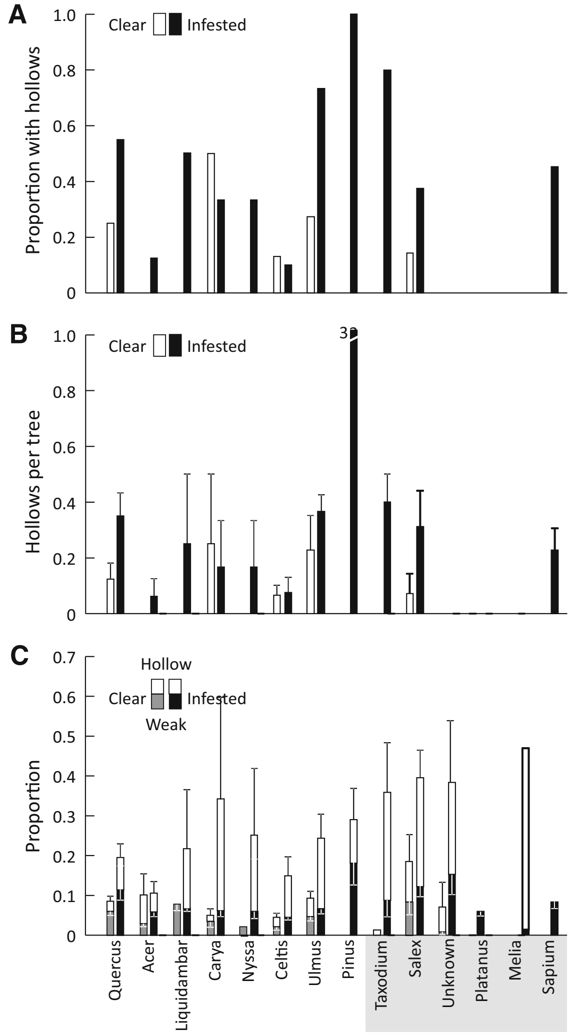

Fig. 2 Hollows in trees in New Orleans. **a** Proportion of trees in a patch with hollows. **b** Average number of hollows per tree. **c** Average proportion of resistograph trace either hollow or weak wood. Tree names in grey found only in New Orleans

The proportion of Resistograph traces that were not solid wood by tree genera found in both cities differed significantly with termite presence, with more hollows in *C. formosanus* infested forest patches ($F_{1,288} = 16.283$, $p < 0.001$), and more weak wood as well ($F_{1,288} = 5.340$, $p = 0.022$). The proportion of traces did not differ significantly between cities for hollows ($F_{1,288} = 0.322$, $p = 0.571$), but did for weak wood, with more in Charleston than New Orleans ($F_{1,288} = 73.516$, $p < 0.001$). There were no significant differences between tree genera for hollows ($F_{7,288} = 1.027$, $p < 0.412$), but there were for weak wood ($F_{7,288} = 3.631$, $p = 0.001$), with *Celtis* and *Ulmus* lower than other genera.

If the difference in proportion hollow in trees from clear and infested forest patches was due to *C. formosanus*, then relative differences between tree genera may indicate food preference. The change in proportion of the Resistograph trace that was hollow between clear and infested forest patches (i.e. clear – infested) varied among tree genera and city (Fig. 3). Two tree genera showed a decrease in both cities: *Quercus*

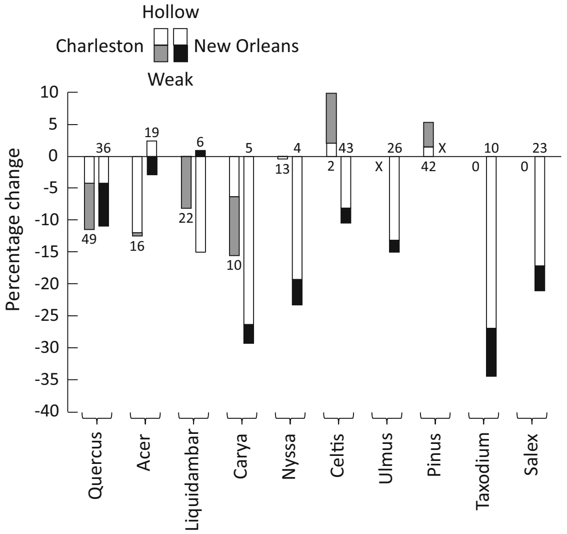

Fig. 3 Average proportional difference in hollow sizes in trees (clear – infested/clear) from Charleston and New Orleans. Numbers are sample sizes, below column for Charleston and above column for New Orleans; X indicates an absence of trees from either clear or infested patches, meaning proportional change could not be calculated

(oak) and *Carya* (bitternut and pecan), the latter with a large decrease in New Orleans. *Acer* (maple) was the only genus that showed a decrease in the proportion of hollows between infested and clear patches in Charleston. There were six tree genera with decreases in New Orleans: *Liquidambar* (sweetgum), *Nyssa* (blackgum), *Celtis* (sugar hackberry), *Ulmus* (elm), *Taxodium* (Bald Cypress) and *Salex* (willow); note that the latter two genera were found only in New Orleans. *Pinus* (pine) did not show a marked change. The overall average difference in hollow size in infested forest patches in Charleston was 3.4 ± 2.1%, whereas for New Orleans it was 14.6 ± 3.0%.

Discussion

Coptotermes formosanus had a greater impact on forest patches around New Orleans than Charleston. This broad pattern was evident from four observations. First, about half of the forest patches in New Orleans were infested with *C. formosanus*, compared with about one-third in Charleston. Second, although more trees in Charleston had at least one hollow, the relative difference between clear and infested forest patches was greater in New Orleans. Third, although the number of hollows in trees was greater in Charleston, the relative difference between clear and infested forest patches was greater in New Orleans. Consideration of the second and third observations together suggests that many of the (mostly small, around 1 mm) hollows found in trees in Charleston were not due to *C. formosanus*. Fourth, the difference in the size of the hollows was greater in New Orleans than in Charleston.

The higher infestation rate and damage to trees in New Orleans compared with Charleston may be due to the warmer temperature and wetter climate of New Orleans relative to Charleston (New Orleans is about 3°S of Charleston, with average monthly maxima 1.2 °C warmer and minima 3.1 °C warmer, and 289 mm more annual rainfall) (climate data from NOAA). Alternatively, it may be due to a greater original influx of termites, believed to have come on naval vessels returning from action in East Asia (Beal 1987; Chambers et al. 1988).

The difference in size of hollows measured by the Resistograph trace between clear and infested forests suggested that *C. formosanus* was attacking trees differentially. Maples were relatively heavily eaten in Charleston, but were untouched in New Orleans, whereas *Liquidamber*, *Nyssa*, *Celtis* and *Ulmus* were more heavily attacked in New Orleans than Charleston. This may be due to the alternative food sources. There were many more *Pinus* in Charleston, which may be a less desirable food source than *Liquidambar*, which was also common in Charleston. Also, *Celtis* and *Ulmus* were rarer in Charleston. Oaks were attacked, but the relatively small hollows found in the trees in the forested patches was a surprise. The data from oaks planted in urban areas, including streets and parks of New Orleans, suggested that oak may be particularly vulnerable (La Fage 1987; Osbrink et al. 1999). This may be due to the urban setting where tree density and diversity is much lower than in forests, therefore *C. formosanus* may have little choice but to eat what is available.

The data collected in the current study broadly match those from previous work. King and Spink (1969) and Beal (1987) reported *C. formosanus* attacked *Taxodium* (bald cypress) *Pinus taeda* (pine); *Sapium sebiferum* (Chinese tallow), and *Myrica cerifera* (wax myrtle bushes), in Lake Charles, ca. 300 km from New Orleans, although the infested area was reclaimed swamp, and thus does not represent natural habitat. Surveys of park and street trees have found extensive damage to oak and maple trees in Charleston, New Orleans and elsewhere in Louisiana (Chambers et al. 1988; Osbrink et al. 1999; Brown et al. 2007). Baldcypress was reported to be extensively damaged in parks in New Orleans (Osbrink and Lax 2002). There was one difference between the current field study from the laboratory study of Morales-Ramos and Rojas (2001): *Taxodium* (bald cypress) and *Salex* (willows) trees had the largest hollows in the field, but were not favoured in the laboratory. This may be due to the growing conditions because both genera live in flood-prone areas, and termites may become isolated in single trees during wetter times of the year (Henderson and Forschler 1996). The colony would be limited to a single food source, that tree, and therefore foraging effort would be focussed in that single tree, resulting in greater wood consumption.

Although range expansion from naturally dispersing winged termites is likely to be slow, human assisted range expansion has been rapid. In Louisiana and Texas *C. formosanus* spread to 30 counties over 40 years (Messenger et al. 2002; Howell et al. 2001; Brown et al. 2007), and in Florida and Mississippi to 40 counties over 20 years (Scheffrahn and Su 2005; Sun et al. 2007). This was due to humans moving infested wood, especially railway sleepers/crossties (Jenkins et al. 2002; Messenger et al. 2002). In comparison, the spread of *C. formosanus* in South Carolina appears to have been slower, taking 40 years to spread to three counties (Chambers et al. 1988; Benson et al. 2000). This may be due to differences in human transportation of infested timber, or differences in the genetic makeup of the *C. formosanus* population in Charleston, which is distinct from those elsewhere in the USA (Husseneder et al. 2012). Or it may be due to lower temperature, as mentioned above. In any case, it seems plausible that *C. formosanus* may spread into forested habitat from any infested urban location.

A few termite species are now known to have invaded natural forest habitats. For example, *Reticulitermes flavipes* (once named *R. santonensis*) from the USA has invaded forests in France, and *Nasutitermes corniger* from South America/Caribbean islands has invaded forests in New Guinea (See Evans et al. 2013 for review). Two invasive species of *Coptotermes* have spread into forests, however with different levels of success. *C. formosanus* has invaded forests in Japan (Abe and Watanabe 1981; Yasuda et al. 2000; Tascioglu et al. 2013), whereas *C. gestroi* has spread into forest margins in Taiwan (Chiu et al. 2016). The difference appears to be the presence of the fungus growing species, *Odontotermes formosanus* (Macrotermitidae) in Taiwan. In general, fungus growing termites form larger colonies (see Evans et al. 1998), and appear to be competitively dominant, and so exclude *C. gestroi* (Chiu et al. 2016). Japan lacks fungus growing species, and the most abundant wood eating species is *Reticulitermes speratus*. The situation is similar in the USA, with no fungus growing termites and several *Reticulitermes* species. Therefore, it appears likely that the spread of *C. formosanus* into US forests will more closely resemble the process in Japan than Taiwan.

There have been many other invasive insects that damage forested lands in the USA. There are over 450 species of exotic insects recorded in the USA since European settlement, 63 of these are considered serious pests estimated to cause around $3.8B damage (Aukema et al. 2010, 2011). Although *C. formosanus* was identified as one of the 450 species, it was not considered to have high impact in forests (Lovett et al. 2006; Aukema et al. 2010; Gandhi and Herm 2010) although costs in urban areas have been noted (Pimentel et al. 2005). Instead, the most important forest ‘poster pests’ include four species; *Lymantria dispar* (European Gypsy moth), which attacks numerous deciduous tree species yet favour oak (Tobin et al. 2012), *Agrilus planipennis* (Emerald ash borer) from east Asia, which prefers *Fraxinus* (Herms and McCullough 2014), *Adelges tsugae* (Hemlock woolly adelgid) from East Asia, which attacks hemlock and spruce trees (Orwig et al. 2002), and *Anoplophora glabripennis* (Asian longhorned beetle) from China which feeds mostly on maple (Hu et al. 2009). In addition to these transcontinental invaders, there are additional invaders from lower latitudes of North America moving northwards, including *Dendroctonus frontalis* (Southern pine beetle), and *D. ponderosae* (Mountain pine beetle), which attack pines (Evangelista et al. 2011; Birt and Coulson 2015).

There are several differences between the invasion of *C. formosanus* and the aforementioned forest insect pests. The first is diversity of food species. Most major forest insect pests target one or few closely related tree species, whereas *C. formosanus* can attack a wide diversity of trees from most families. Another difference is speed and ease of detection. The other insect pests attack leaves, bark or phloem producing obvious effects on tree health in the span of a single growing season, making for easier detection and monitoring compared to wood attacking, cryptic, underground-moving termites. In general, the other insects breed annually or faster, and fly further distances. Therefore, the effects of most forest insect pest are fast to appear, easy to observe and document. In contrast, the spread of *C. formosanus* into forests will be difficult to monitor and their impact on forest health difficult to predict.

Interpreting the results of this study need some caution because of the clumped distribution of termite colony impacts on the local landscape. First, there was large variation in infestation rates between forest patches within and between the two cities, so averages within and across cities may not prove meaningful for infested locales. Second, there was variation in forest patch community structure, with different types and quantities of tree genera between cities, and even between forest patches within cities. Nevertheless, these are the first data that show unequivocally that *C. formosanus* has infested forest patches, outside of urban areas, and that this East Asian termite may have preference for different trees in different regions of the USA. The current study extended the list of potentially vulnerable tree species, to hackberry, bitternut hickory, pecan and elm. The long-term effects of *C. formosanus* on tree communities in USA forests is yet to be definitively determined.

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